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**WING VENATION AND THE PHYLOGENY
OF THE FORMICIDAE¹**
(HYMENOPTERA)

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(Plates VIII and IX)

INTRODUCTION

The wing venation of ants is a valuable taxonomic tool, but its full potentialities are far from realized. Former myrmecologists have utilized the cells of the wing as a systematic aid, while the veins which bound and form the cells have received little attention. As should be made clear by the discussion below, the lack of attention to the veins themselves has warped and hindered the entire approach to the subject. The reason for the old approach probably can be found in the inconsistencies among former attempts at homologizing the wing veins of the entire order Hymenoptera. Without a guiding homology, myrmecologists have fallen back on an arbitrary system or systems of wing vein nomenclature which often differed in details from author to author and from genus to genus. Rohwer and Gahan (1916) have illustrated the confusion which has reigned in the past among various hymenopterous groups.

Attempts at founding a secure homology of the primitive hymenopterous wing have more recently met with what seems to be a high degree of success. The work of Ross (1936) is accepted here as the logical starting point for analysis of the formicid venational elements. Those wishing to follow this paper back to its logical origin should by all means see Ross' lucid explanation and

¹ We are greatly indebted to Dr. F. M. Carpenter, who originally inspired this investigation and who has aided greatly in ways too numerous to mention. We also wish to thank Dr. J. C. Bequaert and Dr. P. J. Darlington, who read the manuscript and suggested certain changes.

helpful figures. At least three other workers have recently accepted Ross' paper as a basis for homologizing venation in other groups within the Hymenoptera, and there seems to be no reason why the wings of all or most of the families of the order will not eventually be brought into proper relationship on the same basis.

Another factor hindering the development of an adequate venational nomenclature in the ants has been the much-lamented variability of the pattern in many of the common forms. Some species of *Lasius* and *Aphaenogaster*, for instance, show great variation in presence or absence of major vein-elements and in the positions of important veins. It is our observation, however, that the degree of instability shown by such well-known forms does not extend to all the species of the Formicidae. Some whole genera show a highly constant pattern which is followed by all species examined; other genera show venational variation which is constant for the species, but varying from one species to another. A large number of species are variable within strict limits, and in many, a constant difference is shown between male and female.

The great emphasis on instability is misleading since the very genera which often show a high degree of venational variability are usually those which are most variable in other characters as well. Inasmuch as many of these are predominantly holarctic-dominant groups, they have been the first to come to the attention of European and North American specialists, and these specialists have naturally formed a bias against the taxonomic employment of the venation. Even in the holarctic-dominant genera and subgenera, with their unstable and apparently rapidly evolving populations, we need not abandon the use of venation as a legitimate taxonomic instrument. These very species often furnish fine examples of venational evolution in progress, as Emery has intimated on several occasions. The fact that we often cannot use venation as a hard and fast key character does not alter the promise of the wings in phylogenetic studies.

Emery has (1913) already made a promising start in the use of wing venation in defining large groups such as tribes; his classification, as set forth in his monumental contribution to the *Genera Insectorum* (1910-1925), relies heavily on the wings. Emery and his contemporaries were, as mentioned above, seriously hampered

by lack of attention to the veins themselves and by the absence of a proper homology of the hymenopterous wing elements.

We cannot here profitably discuss the differences between our system of nomenclature and that formerly employed in treating ant wing venation; the interested reader may gain the best comparisons by putting figures like those given by Emery (1913), Wheeler (1908) or Donisthorpe (1927) next to our plates and comparing vein for vein.

HOMOLOGY OF FORMICID FOREWING VENATION

In applying the nomenclature of Ross to the ant wing, we must consult Ross' figures (1936, pl. 1, figs. 5, 9) and then wings of some ants considered primitive on other morphological (and ethological) grounds. We should naturally turn first to the Myrmeciini, since these have been stated by many authors to possess qualifications on many counts as the most primitive or generalized of living ants. *Promyrmecia* (our fig. 3), a common myrmeciine ant from Australia, does show a relatively liberally veined wing compared to some other ant genera. The weak vein labelled *1r* is present in many *Promyrmecia* and *Myrmecia* species; it is present and constant in position in such a large percentage of the myrmeciine specimens in the Museum of Comparative Zoology collections that we cannot consider it a mere adventitious anomaly. Furthermore, *1r* is indicated in part or entirely in other tribes of the Ponerinae, the sub-family among ants which has received the most consideration as the parent group from which the other sub-families have arisen.

We have selected another primitive ponerine, *Platythyrea*, as a convenient type to display the chief venational features occurring in the ant wing (figs. 1 and 23). *Platythyrea* shows practically the same venation as do the myrmeciines, and the parts appear to be strictly homologous in both groups. In fig. 1, an interesting feature is the presence of the stub labelled *Rsx*, a fairly common and probably atavistic anomaly found in lower ponerine genera like *Myrmecia*, *Promyrmecia*, *Amblyopone*, etc., as well as *Platythyrea*.

Working directly, we may identify all the veins in the ant wing without difficulty until we reach the apical stretches of the radial sector and median veins (so-called). Ross admits the difficulty of

properly homologizing the veins of this area, and we can add nothing to the certainty of such homologization. We have named the two veins *Rs* and *M* in an arbitrary manner. Because of the sporadic occurrence of the stub we call *Rsx* in the lower ponerines, it appears possible that our *Rsf5* represents the same vein that Ross, in his figure of the hypothetical generalized hymenopter, calls *Rs1*. Ross' *Rs2* would then correspond very nicely to our *Rsx*, which is connected to *M* by the crossvein we label *r-m* as a direct correspondence with the similarly positioned vein in Ross' fig. 5.

The treatment of this vein (*r-m*) involves some uncertainties, especially since we have found disagreement between such other clistogastran families as the Tiphidae, Mutillidae, and Plumariidae in the venation of the area in question. The first- and last-named families are represented here by their respective genera *Anthobosca* (fig. 2) and *Plumarius* (fig. 7). Both of these forewings are very ant-like in venation, and there seems to be a close relationship on other anatomical grounds between at least the first of these and the primitive ants. The first radial crossvein (*1r*) is present in a weakened condition in many Tiphidae (subfamilies *Anthoboscinae*, *Myzininae*, *Thynninae*), and the common primitive characters of antennal segment numbers (13 in male, 12 in female), development of first antennal segment into a lengthened scape, tendency toward separation of the first postpropodeal segment from the remainder of the gaster by a constriction and toward loss or weakening of the wings in the female sex, etc., etc., are evidences of a close relationship between the tiphids and the ants. We may also mention ethological features possessed in common by both Formicidae and Tiphidae, and it is this sort of thing that Wheeler stressed (1928) when he indicated the tiphids as his choice for the logical ant ancestors.

In choosing an ant ancestor on largely ethological grounds, however, one may easily miss the point that habits and habitat, while often affirming morphological similarities between two groups, can just as easily be the basis upon which convergent anatomical details are formed. While we do not suggest that the striking points of morphological similarity between the tiphids and the ants are necessarily all convergent ones, we do point to the venational pattern of the apical section of the ant wing, especially to *Rsx*, to show that

the ants cannot easily be derived from any member of the true Tiphiiidae recent or fossil. An examination of a specimen each of Cockerell's Florissant (Miocene) genera *Geotiphia* and *Lithotiphia* shows that Turner (1912) was probably correct in assigning the former to *Anthobosca*; certainly there is nothing about the fossils to suggest that they are very different from recent types of tiphiiids occurring in other parts of the world, or that they are protoformicids. Pate (1947) reviews the subfamilies of the Tiphiiidae and suggests that the Anthoboscinae are closest to the ancestral type of that family. Bradley (in Wheeler, 1933, pp. 104-105) suggests that the Anthoboscinae are to be regarded as the most likely ant precursors. Reid's (1941, pp. 417-418) discussion and diagram, based largely on a study of thoraces of wingless hymenopters, also suggests a tiphiiid-like ant ancestor.

In the face of the large body of opinion holding like views, we will agree only to the statement of Reid: "Tiphiiid-like." We do not believe that the common ancestor from which probably arose the tiphiiids and the ants would today necessarily be recognized as belonging to the family Tiphiiidae.

The correspondence of $R_{s,r}$, the apical stub considered above, may or may not be with the so-called *accessory* vein of the Mutillidae. If this correspondence is valid, then the ants must be considered as having lost $2r-m$ and retained $3r-m$, which is the site of attachment of the accessory vein in the mutillids. The accessory vein is possibly the tip of a branch of R_s . If this is so, then the anterior half of " $3r-m$ " would be a part of this same branch, while the posterior half would represent the true $3r-m$. Similar difficulties show themselves in the same region of the wing of *Plumarius* (fig. 7), a wing which otherwise agrees nicely with those we have been considering.

A study of the concave wing folds, thought to be rudimentary veins in the apical section of the wing, will probably some day lead to a solution of the homologies of this section of the aculeate forewing. For practical purposes, such a solution does not presently greatly concern us. Whether the vein we have labelled $r-m$ represents the primitive $2r-m$ or $3r-m$, or a combination of one of these and part of R_s , there is one fact we are reasonably sure of: this is the only one of the veins remaining to the ant wing which has any

possible claim to be considered part or all of any *radio-median* crossvein. Among ants, therefore, it seems best to designate this vein simply as *r-m*, a practice we have followed. In ants, with the possible exception of some anomalous stubs projecting posteriorly from *M* in *Dorylus* species (fig. 11) and in occasional specimens of *Amblyopone* (camera lucida sketches by J. Clark *in litt.*), there remains no trace of *2m-cu*, a vein characteristic of tiphiiids. The latter vein is lacking in *Plumarius* and many Mutillidae we have examined, but other morphological considerations would seem to rule out the latter family as being ancestral or even very closely related to the ants. The male of *Plumarius* is certainly not a very promising candidate for ant ancestry, since the species we have seen lack a number of the requisite protoformicid features. We do not know the female of *Plumarius*; as a matter of fact, very little is known about either morphology or ethology of the small group to which *Plumarius* belongs. (See Bischoff 1913, Brues 1924, Bradley 1921.) A study by some future worker may prove us wrong, but on the basis of our present study, we would place *Plumarius* at some distance from the ants in a phylogenetic sense. We have also examined two species of *Rhopalosoma*, which has an ant-like wing venation and certain suggestive body features, but this genus likewise is not considered by us to be very close to the ants. Other families examined have all proven merely suggestive of formicid affinities; in fact, it is surprising how many families of Hymenoptera have the first postpropodeal segment set off partially or wholly from the remainder of the gaster by a constriction, a character which is often considered diagnostic of the Formicidae. Many of these families are further possessed of quite ant-like wings in at least some genera, making the task of proving relationships quite difficult. Our conclusion as to ant ancestry postulates an early split in a line from which both the formicids and anthoboscines arose, the latter either giving rise to, or arising very close to, the stocks of the Thynninae and other tiphiiids. We do not support the view of Wheeler (1928) and Haskins (1939) that the ants arose from a "bethyloid" stock. Although we will admit that it seems likely that the ethological background of the protoformicids and bethylids expresses some relationship between the two families, these are by no means the only families which can be placed in a large group of

wasps sharing basic similarities in habits; the bethylids form a relatively small and specialized part of this group.

Other than the losses already noted which have combined to produce the ant venation, the only major change noted from Ross' fig. 5 involves the loss of all the veins in the anal region but *1A*. It would seem practical to call this vein *A* when dealing with strictly intraformicid taxonomy. Most of the families which could conceivably be closely related to the ants show similar reduction in the anal area of the forewing.

We have not investigated the hindwings very extensively. Figs. 22 and 23 illustrate the hindwings of *Anthobosca* and *Platythyrea* respectively. In the ant, *r-m* and *cu-a* are drawn back to the basal half of the wing; otherwise, the ant and *Anthobosca* are quite similar. We have not shown the hamuli, which are present in an irregular subbasal set and a more regular and compact preapical set. A detailed investigation of modification of both venation and the hamuli of the hindwing will possibly be of value in elucidating phylogeny within the Formicidae, but we cannot undertake such a study here.

In using the forewings as they betray relationships among the hymenopterous families and genera, the assumption is that progression from the generalized to the specialized is a matter of essentially irreversible reduction, fusion, or outright loss of venational elements. This seems to hold true among ants. Once a vein or section thereof is lost, it never reappears in succeeding generations except as an "atavism" marked by great instability of form and position, and one which often is absent from most specimens of the species in which it occurs. "Reappears" may, in fact, be the wrong word, since it is probable that the genetic factors responsible for the "atavisms" are carried in some form even in populations where the overt expression of the character is infrequently or never observed.

DEVELOPMENT OF VENATION AMONG THE SUBFAMILIES OF THE FORMICIDAE

Having established in a reasonably satisfactory manner the primitive wing venation, let us see what happens to the wings among the more specialized ants. In searching through a large collection,

such as the one resting in the Museum of Comparative Zoology, we concentrated first upon the task of locating forms which had relatively primitive, i.e., unreduced wing venation. We succeeded in finding species in the subfamilies Dorylinae, Pseudomyrminae, Myrmicinae and Dolichoderinae which possessed all the abscissae found in *Myrmecia* and *Platythyrea* except *1r* and *R.s.x.* In the Dorylinae, furthermore, *Cheliomyrmex* (fig. 8) showed occasional specimens in which *1r* had been retained as a well-marked vein. Many ponerine genera were found also to conform to this generalized plan, as would be expected. In most, if not all cases, the genera containing species with liberally veined wings were those considered primitive in their respective subfamilies by other authors, on grounds other than wing venation.

From the primitive types in each subfamily, reaches a graded series of ever more poorly veined wings, the loss of elements in certain species being very nearly complete. A closer study of the series at hand shows that reduction takes place in a usually similar and quite orderly way in different subfamilies and tribes. The same stages in reduction of selected members of different subfamilies may offer startlingly similar patterns, as witness figs. 4, 9, 12 and 18, then 13 and 19, then 17 and 20. Although the process of reduction shows many irregularities in detail among the subfamilies, it will perhaps prove valuable to review the usual kind of progressive change as a more or less general phenomenon. The interesting exceptions will be discussed later.

The first elements to be lost are the crossvein *1r* and the stub *R.s.x.* *Messor* (fig. 13) shows an angularity of the radial sector and sometimes the suggestion of a spur which probably is to be accounted for by the former presence of *1r*. A very early change of a less noticeable character is the slow fusion of the base of *Mf1* along *CuA* until it is found to diverge from *CuA* distad of crossvein *cu-a*. This movement is highly significant to our discussion, since the origin of *Mf1* distad of *cu-a* is almost certainly a situation derived from one in which *Mf1* arose proximad of *cu-a*. This set of circumstances is amply demonstrated by reference to Ross' figs. 3, 5 and 9 and our figs. 2, 3, and 6 to 11.

The species of the Myrmeciini (fig. 3), certain primitive members of the Amblyoponini, and Carpenter's fossil *Eoponera* (fig. 6) show

the intermediate situation where *Mf1* is lined up or nearly lined up at its base with *cu-a*. This condition is very constant in, and highly characteristic of, the myrmeciines as shown by a large number of specimens of many species. The species of the Dorylinae (figs. 8-11) without exception show *Mf1* as a very oblique vein arising well proximad of *cu-a*. All of the members of the higher subfamilies which we have seen (with the exception of a few degenerate types like *Basiceros* and its relative *Rhopalothrix* in the Myrmicinae) plus by far the great majority of the Ponerinae and all cerapachyines, show *Mf1* branching from the cubital vein distad of *cu-a*. The facts of venation to this point seem to show that the Dorylinae split off from the main formicid stock at a very early date, and that they cannot easily be derived from the ponerines. The dorylines may even represent a separate line derived independently from that which gave rise to the ponerines and higher subfamilies. An interesting corollary to this theory, and one we shall enlarge upon further below, is the strong probability that the relationship assumed to exist between the cerapachyines and the dorylines is mistaken.

If we ignore the dorylines for the moment and turn again to the general trends of venational reduction seeming to run parallel in the different subfamilies, we observe that the next step is the contraction of *Mf2*. To see how this happens, consult the following pairs of figures: 12 and 13, 18 and 19, 4 and 5. The latter pair of figures also illustrates part of the next step: the base of the vein representing the second and third free abscissae of *Rs* has begun to fuse along the basal part of *Mf3*, fig. 5. The relative scarcity of species showing the stage represented in figures 5, 13 and 19 seems to indicate that the situation following complete contraction and loss of *Mf2* is a highly unstable one calling for further readjustment of adjacent vein-elements. This readjustment may take a number of forms, but in essence, it involves reduction of the two veins stretching from the distal end of *Rs+M* to *r-m* to a single vein. This seems usually to be accomplished by the fusion of *Rsf2·3* with *Mf3* from the base outward (fig. 5) or by the disappearance of *Rsf2·3* by "withering" either piecemeal (fig. 14) or all at once, as is suggested by the weak appearance of this vein in forms like *Stigmatomma rothneyi* (Forel). Another possibility,

suggested by certain forms related to *Aphaenogaster*, is that *Mf3* may drop out. This is probably rarer than loss of the part of *Rs*, but *Veromessor* (fig. 15) and *Novomessor* often show stubs which suggest that it may occasionally happen.

During or just before the loss of this longitudinal element, whichever part it may be that is lost, there is an important change in which the crossveins *2r* and *r-m* become approximated and continuous, or "lined up." This lining-up usually involves the contraction of the fourth free abscissa of *Rs*, but in some cases (*Amblyopone*), *Rsf4* may become aligned with, and persist as a part of, the *2r·r-m* complex abscissa.

The next step involves *r-m*, which usually does one of two things. It can either contract directly to produce the pattern characteristic of the Formicinae and many Dolichoderinae and Myrmicinae, figs. 17, 20, 21, or it can swing² so as to become aligned with *Mf3*, as in many small myrmicines, etc., figs. 16. Beyond this, reduction may proceed in several directions, though *m-cu* (or *Mf1*, as illustrated in figs. 20 and 21) and *cu-a* are among the earliest losses. The stages illustrated in figs. 17, 20 and 21 seem to be rather stable, as evidenced by the large number of ants which have gone to, but not beyond, this form of reduction.

Radical reduction in body size seems to upset the stability of even this pattern and to be correlated with still further reduction. The adoption of strongly hypogaecic habits also seems to foster reduction in all subfamilies, and parasitic forms often show radical reduction probably correlated with weakened powers of flight.

Extreme reduction is seen in *Leptanilla* among the genera allied to the dorylines, among certain small degenerate ponerine genera like *Probolomyrmex* and *Ponera*, and among several groups in the higher families such as the higher dacetine genera. We have observed, as have other workers, that single tribes or genera may run nearly the whole gamut of the reduction series, while other tribes and genera display uniform venation through all their species. This

² There is evidence that some myrmicines (*Aphaenogaster mariae*, etc.) may lose *r-m* completely, while keeping the central part of the radial sector. This produces a pattern like that in our *Octostruma*, and it may be that in all or most myrmicines which have arrived at this stage the vein we have labelled *r-m* in fig. 6 is really *Rs2·3*.

has raised a great deal of mistrust of wing venation as a taxonomic character, an attitude on the part of myrmecologists which is probably healthy as long as it does not reach the extreme where venational characters are utterly rejected. The veins, it must be remembered, are subject to change just as are mandibles, antennae, petioles and other structures which may show a wide range of variability within a single genus. The emergence of other structural characteristics which are sufficiently distinct to place a species in a new genus or tribe should not always be expected to show correlation with a striking venational change; rather, the opposite seems often true in ants. It should not be forgotten that specialization is differential; three or four clear-cut and taxonomically useful characters usually do not spring into being simultaneously to produce a new genus.

A SHORT SURVEY OF VENATION DETAILS IN VARIOUS FORMICID GROUPS

Dorylinae and Leptanillinae

As we have stated above, the Dorylinae seem to represent a line arising from a pre-ponerine stock. This is supported by the evidence of the thorax as treated by Tulloch (1935, pp. 101–103, 108, 109–111, pls. 9, 10), although Tulloch concludes differently. Reid (1941, p. 422) states, "The thorax of the Cerapachyinae is of a uniform type and seems to have affinities with the thorax of certain of the tribes of the Ponerinae. The condition of the worker thorax does not support the view that this subfamily is intermediate between the Ponerinae and the Dorylinae, for the thorax of *Dorylus* is less specialized than that of the Cerapachyinae." Reid's view corresponds very well with the evidence from the wings we have examined.

Our figures 8–11 probably correspond very well to the actual types of the reduction series leading to a wing like that of *Dorylus* (fig. 11). *Cheliomyrmex* (fig. 8) certainly looks like the most primitively veined doryline. It retains *1r* as a fairly common atavism, and *Mf1* arises far in toward the base of the wing. In *Eciton* (fig. 9) *1r* no longer occurs, and *Mf1* is beginning to fuse along *CuA* so that its posterior end is farther from the base of the

wing. *Aenictus* (fig. 10) shows the loss of $Rsf2\cdot3$ and the approximation of the veins $2r$ and $r-m$, a state of affairs very similar to that found in higher subfamilies (figs. 17 and 20), but with these differences: $Mf2$ has not previously contracted, and $r-m$ shows little inclination to change either its shape or position. The posterior end of $Mf1$ is getting still closer to $cu-a$, and $Rsf1$ has contracted strongly. *Dorylus* (fig. 11) has carried the contraction of $Rsf1$ to completion, so that $Rs+M\cdot Mf2$ seems to take its origin directly from $R+Sc$. $Mf1$ is rather close to $cu-a$, being little more than the length of the latter vein distant from it. *Dorylus fimbriatus* and some other large *Dorylus* males commonly show very inconstant adventitious veins springing from the posterior side of $Mf3$. These are possibly present due to a need for further strengthening of the wing correlated with the increased weight of the body; they may represent distorted atavisms of branches of M and possibly remnants of $m-cu$. One could almost derive these genera from one another in a straight line of descent such as illustrated by our sequence in figs. 8–11, but there are indications from other body characters that the internal doryline phylogeny is not quite so simple as our display of wings appears to hint.

The position of the leptanillines is debatable. They are usually treated as a subfamily by modern authors, and the venation is so highly reduced in the forms we have seen that little may be deduced from them concerning relationships to the other subfamilies.

Ponerinae, Including Cerapachyinae

Some of the paragraphs above have already treated the primitive features, as well as degenerate types, among the ponerines. We can treat the subfamily only briefly here.

The *Myrmeciini* have already been discussed in some detail. Outstanding features are the frequent presence of $1r$ and traces of $Rs.r$, also the position of the base of $Mf1$ (fig. 3).

Amblyoponini.—These ants seem to be rather closely allied to *Myrmecia*, though not necessarily derived from the myrmeciines, as many authors have assumed. *Amblyopone (Stigmatomma)*, including *Fulakora*, shows progressive venational reduction in its species, starting with a form very much like *Myrmecia*, except that $1r$ is rarely if ever present, and proceeding to the stage where

Rsf2·3 drops out completely. *Amblyopone* (*Amblyopone*) has already been discussed in part above. The "normal" condition in this subgenus includes the complete absence of *Rsf2·3*, but several freak specimens of various species, of which Mr. John Clark has very kindly sent me camera lucida sketches, show various distorted remnants of *Rs* free abscissae 2 and 3, and *1r*. Some of these specimens show that, with the contraction of *Mf2*, the part of *Rs* in question becomes detached basally from its former connection to the apex of *Rs+M*. The free basal end of *Rsf2* may then be attracted toward the stigma and eventually attached there. All this may happen without the loss of *1r*, resulting in a small, arcuate "bow-and-arrow" vein attached to the posterior-proximal side of the stigma. Mr. Clark's very complete series of drawings indicate very clearly how this unstable system arises and disappears, and it is to be hoped that he will publish these figures in the near future. *Mystrium* and *Myopopone* show venation much like that of *Amblyopone* (*Stigmatomma*), often with the base of *Mf1* arising distad of *cu-a*.

Other ponerines are very diverse, but many of the tribes show primitive genera or all genera to possess venation much like that of *Platythyrea* (fig. 1). As has been mentioned above, all these "higher" ponerines show a first free abscissa of *M* arising well distad of *cu-a*, except in degenerate forms where *cu-a* has been lost. In most genera, *1r* does not appear.

We consider the cerapachyines as no more deserving of subfamily rank separate from the ponerines than are other aberrant groups such as the Odontomachini. The wing venation (fig. 4) supports the implied view of Reid, cited above, that the cerapachyines are merely specialized Ponerinae. We hold this opinion even after reviewing the evidence of the male genitalia, larval structure, and ethology put forward by Wheeler and other authors.

Reid (op. cit., p. 421-422) relates the cerapachyines to the Amblyoponini and the Proceratiini on the basis of thoracic structure in the worker, and this placement is probably not too far off in our opinion. The proceratiines, represented by relict forms in many parts of the world, are highly specialized in "degenerate" direction, and due to their tendency to lead a highly hypogaecic or otherwise cryptobiotic existence show marked reduction in wing venation.

The Ectatommini show a wide range of venational patterns, with some of the more primitive forms like *Rhytidoponera* occasionally displaying *1r* as an atavism. Reduction in other genera is more marked, *Gnamptogenys* (fig. 5) being intermediate in the reduction series. Some species of *Stictoponera* show still further reduction, and some small species in which the wings are not yet known may show extreme reduction. The Proceratiini and the Ectatommini seem to be very closely related, and it is possible that they should be united into one tribe. In this group is best sought the ancestor of the Myrmicinae.

The species *Eoponera berryi* Carpenter (fig. 6), represented by a fossil wing from the Eocene of Tennessee, is peculiar in having most veins reduced in length and crowded into the center of the wing. In spite of this crowding, the elements seem to be the same and to rest in the same relative positions they hold to one another in the lower ponerines. The wing is very large in size, and Dr. Carpenter has expressed doubts to us about his placement of it in the original description (1929). Since we know of no hymenopterous group where it fits better than in the lower Ponerinae, we see no reason to dissociate it from that group. The large size of the wing is not a drawback to this placement, since it is probable that the early ant fauna was composed mostly of very large ants. We have published the figure here in the hope that some worker having a wide acquaintance with various hymenopterous wings may be able to suggest a better placement for it.

Myrmicinae and Pseudomyrminae

These two subfamilies are possibly related. In wing venation, the pseudomyrmines have remained generalized relative to the larger subfamily. Some species of *Pseudomyrma* (fig. 12), while having lost *1r*, still retain *Mj2*. In most *Pseudomyrma*, however, *Mj2* has been lost through contraction, and this is the state of affairs in the Old World forms we have examined. Most of the forms we have seen showed no further reduction, however, and probably most *Tetraoponera* and *Pseudomyrma* show patterns like those of figs. 12 and 13. *Viticicola* is reduced to a pattern like that of fig. 16.

In the Myrmicinae proper, we could find no specimen with a clear-cut first radial crossvein or stub thereof, even among the genera considered primitive on other grounds than wing venation. The only genus we found at all consistently displaying an uncontracted *Mf2* was *Ephedomymex*, which is often considered a subgenus of *Pogonomyrmex*. In *Messor* (fig. 13) *Rsf2·3* is weakening, as is also seen in many *Aphaenogaster* species. In *Pogonomyrmex* and *Myrmica* (fig. 14) we can find the gradual stages by which *Rsf2·3* disappears, while *Veromessor* (fig. 15) and *Novomessor* often show a recurrent stub which probably corresponds to the distal end of a missing *Mf3*. A great many myrmicines have reached one of the next two alternative stages, both of which involve changes in *r-m*. These changes have been discussed earlier in this paper, and we need merely to refer the reader to figs. 16 and 17 for an understanding of the two common types. (See footnote 2 on a previous page.)

In certain genera, especially in the very small alate forms of the higher Dacetini, the veins are often reduced to the point where it is proper to say that the venation is completely blanked out. Quite often the stigma remains, however, with sometimes a small inverted T-shaped appendage projecting from it posteriorly; this appendage represents *2r* and the adjacent parts of *r-m* or *Mf3* proximally and *Rsf5* distally. *R+Sc*, *Rsf1*, *Mf1*, *CuA* and *M+CuA* are also quite persistent veins, often simply weakening in a gradual way until nothing but feeble furrows or disturbed lines of microtrichia mark their former presence.

Dolichoderinae and Formicinae

The Formicinae have been considered by a few authors as probably descended from a dolichoderine stem. The wing venation is clearly in agreement with this idea, so we proceed as though the formicine wing pattern were a reduction of the primitive dolichoderine type.

Fig. 18 shows a primitive living dolichoderine, *Dolichoderus attelaboides* (Fabricius), the wings of which possess all veins found in the Myrmeciini except *1r* and *Rsx*. *Dolichoderus* probably arose either from the now almost extinct Aneuretini, or from a ponerine which also gave rise to the aneuretines. We have not

seen any aneuretine wings, since the only existing genus, *Aneuretus* Emery, is known with certainty only from the worker. The Aneuretini were once numerous and diverse, as is attested by the two genera Wheeler described from the Baltic Amber. Of the two genera, both with well-developed stings, *Protaneuretus*, as figured by Wheeler (1914, pp. 71-74, fig. 31), is not un-myrmicine in habitus, despite its single petiolar node. As a matter of fact, the petiole is of such a form that it could just possibly represent two petiolar nodes fused together. Someone having access to recent or fossil aneuretines could easily investigate this interesting possibility, and it is also possible that a comparative count of the postpropodeal segments in the various subfamilies would shed some light on the subject. It is perhaps better, however, to follow the conventional view that the aneuretines are directly descended from the Ponerinae. The fact that the *Protaneuretus succineus* female is scarcely larger than the worker tends to support this view.

Paraneuretus, of which Wheeler (op. cit., pp. 73-77, fig. 31) described two species, has a worker with a habitus like that of many formicines. The males of both species are known, but Wheeler unfortunately did not figure either. Wheeler says of the wings, ". . . with a discal, two complete cubital cells and a closed marginal cell, the venation closely resembling that of *Iridomyrmex*." Since the *Iridomyrmex* wing venation differs from species to species, we cannot very well say whether or not *Paraneuretus* possesses important features like *Mf2*. One needs only to consult figs. 1, 10, 13, 18, 19, 20 and 21 to appreciate the fact that a mere statement that the "first discoidal" cell is present and closed is apt to conceal the very interesting and taxonomically valuable condition of the venation which bounds and thus forms the cell.

It seems possible that *Iridomyrmex* and the other dolichoderines with thin collapsible integument, plus also the formicines, arose from something pretty much like *Paraneuretus*. While the genera *Dolichoderus* and *Hypoclinea* (figs. 18, 19) are rather conservative in venation, with usually the partial or total contraction of *Mf2* and sometimes the alignment of *2r* with *r-m* as the only signs of advancement, some other dolichoderines of higher groups display considerable reduction.

The most primitive of the formicines known both from the amber and as existing species show a well-advanced reduction of venation. In such genera as *Myrmoteras*, the wing has reached a stage of reduction similar to that of *Daceton* (fig. 17) and $Rs+M$ is contracting markedly. In *Opisthopsis* (fig. 20) the contraction of $Rs+M$ is completed, setting the stage for a reduction which seems to be restricted to the Formicinae: instead of $m-cu$ disappearing to open the "discoidal" cell, it appears that $Mf1$ drops out. We assume this to be true because of certain recurrent spurs or nodes often seen in formicine genera like *Phasmomyrmex* (fig. 21) *Pseudolasius*, etc. Also, the distance to the small crossvein $cu-a$ is increased in such a way as to suggest that the "basal vein" of older authors now has a different composition than it did primitively. Posteriorly the new vein is made up of $m-cu$, which now meets $Rsf1$ as though to fuse with it into an " $Rs+m-cu$," but since $Rs+M$ and free abscissae 2, 3 and 4 of Rs have earlier disappeared in various ways, the two veins of the false "basalis" now join to meet the proximal end of $Mf3$. In the great majority of the formicines which have lost the "discoidal" cell, there is no recurrent stub to show that $Mf1$ has been lost, but nevertheless, we believe that this is the way such genera as *Camponotus* arrived at their present venation. The formicine type of venation, as was remarked upon earlier, seems to be quite stable with or without the "discoidal" cell, so that there is little further reduction of much taxonomic value in most groups.

In the foregoing paragraphs we have tried to give an idea of some major tendencies in the development of the venation of the ant forewing. Much remains to be done in the way of verification and amplification of our ideas on the subject. A study of the hindwing is badly needed in conjunction with a more detailed study of the forewing, and the findings should be applied to correct the systems within the subfamilies which Emery and others have founded upon the cells. We cannot here enter upon such protracted study as is called for. The study appears excellently suited as the subject for a postgraduate thesis, provided, of course, that sufficient representative material is available to the student.

A survey of the venation of the subfamilies of the Tiphiiidae *sensu* Pate (1947) convinces us that the nomenclature suggested by

us for *Anthobosca* in figure 2 will prove easily traceable through most if not all the genera of that family, and workers in various other groups of aculeates may also find the particular patterns which concern them easily reducible from the anthoboscan type.

EXPLANATION OF SYMBOLS USED IN TEXT AND PLATES

Longitudinal veins

R+Sc	Radius + Subcosta
Rsf1, Rsf2, etc.	Radial sector; first, second, etc., free abscissae
Rs+M	Radial sector fusion with median
M+CuA	Median fusion with anterior cubital
Mf1, Mf2, etc.	Median; first, second, etc., free abscissae
CuA	Anterior cubital
CuP	Posterior cubital (present as a fold)
A	Anal (first anal)
St	Stigma
x	Irregular ("adventitious") veins

Crossveins

1r, 2r	First, second radials
r-m	Radio-medial
m-cu	Medio-cubital (first)
cu-a	Cubito-anal

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EXPLANATION OF FIGURES

PLATE VIII

Forcings

- Fig. 1.—*Platythyrea punctata* (Fred. Smith), female. Ponerinae: Platythyreini.
- Fig. 2.—*Anthobosca chilensis* Guérin, female. Tiphidae: Anthoboscinae.
- Fig. 3.—*Myrmecia* sp., male. Ponerinae: Myrmeciini.
- Fig. 4.—*Cerapachys manni* Crawley, male. Ponerinae: Cerapachyini.
- Fig. 5.—*Gnamptogenys mordax* Fred. Smith, female. Ponerinae: Ectatommini.
- Fig. 6.—*Eoponera berryi* Carpenter (Eocene fossil), sex and tribe uncertain. (Adapted from Carpenter 1929.)
- Fig. 7.—*Plumarius hirticornis* (Ern. André), male. Plumariidae.
- Fig. 8.—*Cheliomyrmex nortoni* Mayr, male. Dorylinae: Ecitini.
- Fig. 9.—*Eciton (Labidus) coecum* (Latr.), male. Dorylinae: Ecitini. (After M. R. Smith 1944.)
- Fig. 10.—*Aenictus pachycerus* Fred. Smith, male. Dorylinae: Ecitini.
- Fig. 11.—*Dorylus (Rhogmus) fimbriatus* Schuckard, male. Dorylinae: Dorylini.

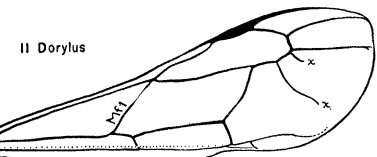
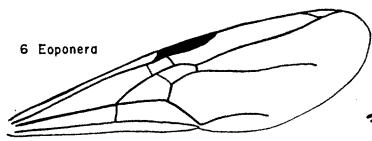
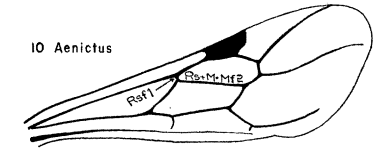
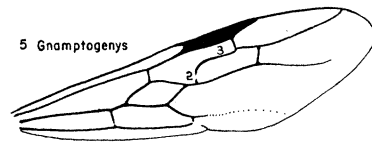
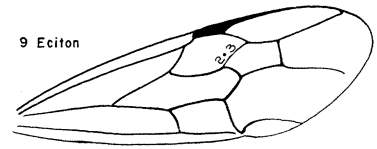
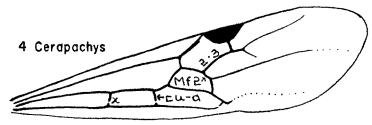
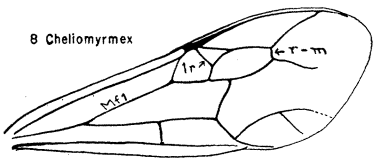
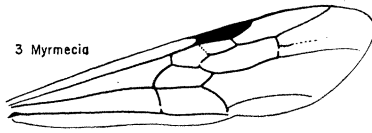
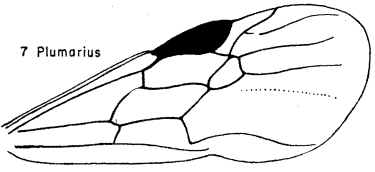
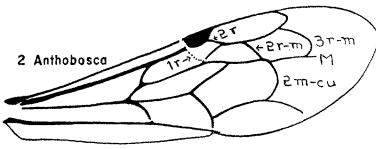
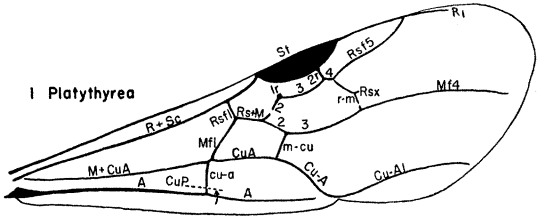
PLATE IX

Forewings

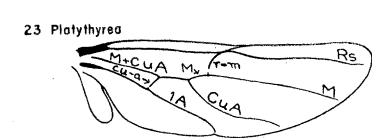
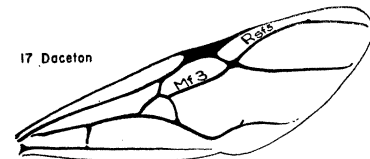
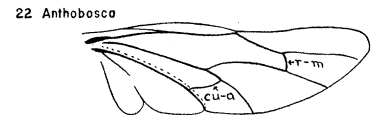
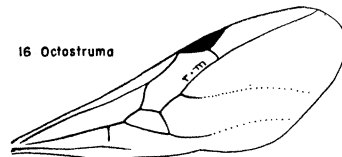
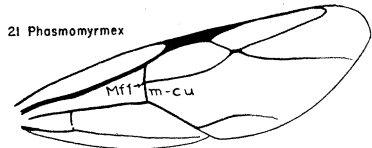
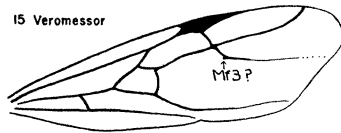
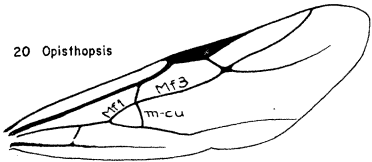
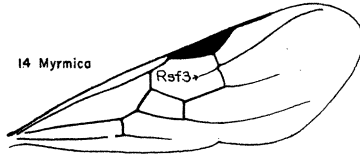
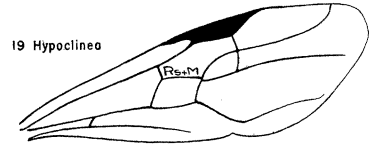
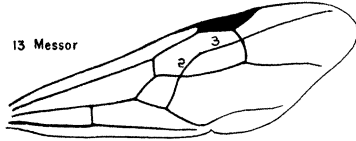
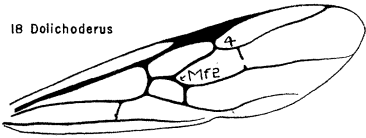
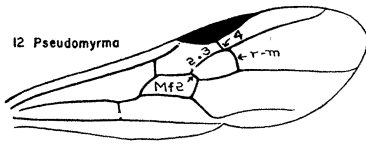
- Fig. 12.—*Pseudomyrma lyncea* (Spinola), female. Pseudomyrminae.
Fig. 13.—*Messor barbarus* Linnaeus, female. Myrmicinae: Pheidolini.
Fig. 14.—*Myrmica punctiventris* Roger, male. Myrmicinae: Myrmicini.
Fig. 15.—*Veromessor pergandei* Ern. André, male. Myrmicinae: Pheidolini.
Fig. 16.—*Octostruma* sp., female. Myrmicinae: Basicerotini.
Fig. 17.—*Daceton armigerum* (Latr.), female. Myrmicinae: Dacetini.
Fig. 18.—*Dolichoderus attelaboides* (Fabr.), female. Dolichoderinae: Dolichoderini.
Fig. 19.—*Hypoclinea mariae* (Forel), female. Dolichoderinae: Dolichoderini.
Fig. 20.—*Opisthopsis haddoni* Emery, female. Formicinae: Camponotini.
Fig. 21.—*Phasmomyrmex (Myrmorhachis) polyrhachoides* Emery, female.
Formicinae: Camponotini.

Hindwings

- Fig. 22.—*Anthobosca chilensis* Guérin, female.
Fig. 23.—*Platythyrea punctata* (Fred. Smith), female.



BROWN AND NUTTING—WING VENATION



BROWN AND NUTTING—WING VENATION