

HOMOLOGIES OF THE WING VEINS OF THE APHIDIDÆ, PSYLLIDÆ, ALEURODIDÆ, AND COCCIDÆ.*

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INTRODUCTION AND GENERAL CONSIDERATIONS.

This study of wing venation was undertaken in the hope that it might, for the one small group of Homopterous insects it concerns, supplement in some slight measure other work in wing-vein homologies which has been so vital a problem for insect phylogeny.

The incentive to this study is to be found in "The Wings of Insects" by Comstock and Needham. The choice of the particular group here considered was due to a personal interest in aphids and to the fact that the homologies of the wing-veins of this family were at that time practically untouched.

From the first the work has been under the direction of the Department of Entomology, Cornell University and it is a pleasure to acknowledge the kindness of Professor Comstock during my association with this department as a student, and the patient aid and constant interest and sympathy in my task of Doctor MacGillivray.

To Professor Oestlund at the University of Minnesota is due thanks for the determination of certain species of aphids which are included in this study and for the personal interest with which he has anticipated the results.

Although the work has been entirely under the supervision of the Department of Entomology, Cornell University, the great bulk of the data has been accumulated at Orono, Maine, instead of Ithaca, New York. Several months of each winter during the progress of the problem, however, have been spent at Cornell in revising data and in such consultation as has insured against certain misinterpretations and other errors due to inexperience in this type of work. At such times the essential points have been in so far as is possible with the greenhouse aphids available, verified while *in residence* in Ithaca, and the work with the Coccidæ and Aleurodidæ has been done in the Entomological laboratory at Cornell University.

Since 1903 each season's collection of aphids in Maine with detailed notes has given me a very fair idea of where to secure

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given species and upon what plants at any time during the entire season. This has given me a range of from 95 to 105 available species belonging to at least 16 different genera and representing all the types of venation in the entire family.

At the Maine Station two insectaries (one an unheated building of use only during the summer, and one a hot house), have both been available for the segregation of colonies of aphids taken previous to the development of wing pads in order that they could be used at exactly the right time. This made possible a large amount of material safe from the depredations of predaceous insects and parasites, a condition which could never be relied upon with chance collections in the open.

In view of the fact that for the work in hand, no specimen could be used for the study of wing tracheation except during the first few minutes after emergence from the last molt, and that the nymphs could be studied only during a very limited time before the developing wings became much folded in the sac, and that some species gave conspicuously better results than others by virtue of such reasons as the slightly different angle at which the wing pad of certain species are held, or to differences in color, etc.:—it will be evident that the conditions outlined have been most propitious for the study of this particular problem with aphids.

The reasons for approaching the homologies of the wing veins of insects by a study of the tracheæ that precede the veins were so fully set forth and their validity so thoroughly demonstrated by Comstock-Needham* ten years ago that this phase of the question has long been too familiar to call for general discussion here.

However, with each new group of insects studied in this way conditions exist which may have a special bearing on the subject. For instance, an ontogenetic study of the wings of certain insects is not of any value in determining the homologies of the veins‡ in which case entire dependence must be placed on a careful comparison of the veins of the mature wing.

On the other hand with wings so highly specialized by reduction of veins as those of the Homopterous group with which this paper is concerned, the subject is a hopeless one to approach from

* The Wings of Insects. *Amer. Nat.* XXXII and XXXIII, 1898 and 1899.

‡ MacGillivray, A. D., *Wings of the Tenthredinoidea* 1906. *Proceedings of the Nat. Museum.* Vol. XXIX, page 574.

the comparison of the veins themselves. What chance is there on the basis of the mature wings alone to homologize except by the merest guess the veins of the Aleurodidæ with those of the Psyllidæ?

Yet fortunately and, in many instances, to my utmost surprise, it was found that practically the whole story of the venation of the group of four families here concerned lies revealed in the preceding tracheation and no one who follows that story closely can fail to recognize in the two surviving veins of Aleurodes for instance the radial sector and cubitus. (See page 122).

One of the simplest but prettiest and most clearly cut of the demonstrations of the value of the tracheation in this connection is to be found by comparing the venation and tracheation of *Chermes* which shows at once that it is the wavering and unstable R_1 which is lacking and not M as has heretofore been considered. (See page 111). And the vagaries of R_1 in the whole group form a fascinating study by themselves.

But exciting and interesting as is the story the tracheæ trace, the quest for the homologies of the wing veins of aphids has lain along a path tedious in many respects and beset with many difficulties.

The tracheæ of aphid wings are very delicate, and when filled with the medium in which the wing is mounted they become invisible, so that many of the examinations and sketches made had to be finished with rapidity, and often many mounts prepared to verify a single point.

The wings studied in connection with this problem were prepared in two ways. Part of them were mounted in glycerine jelly after the method described by Comstock-Needham* and part of them were mounted in xylene damar. With wings so small and delicate as the aphids wings the latter was found in the main more satisfactory. It took the balsam less time to penetrate and render the tracheæ invisible which would have been an objec-

*"In making mounts of this kind our usual procedure was to spread a drop of melted glycerine jelly on a slide and allow it to cool; then to dissect off the wings (generally under water), taking with them just enough of the thorax to include the basal attachments of the tracheæ; then to place these wings upon the solidified glycerine jelly on the slide; then to lower upon the wings a heated cover glass, causing the jelly to melt enough to envelope the wings; and then to cool the mount speedily on a cake of ice, a marble slab, or in a draught of cold air. Rapid cooling is imperative, for in melted glycerine jelly the tracheæ soon become filled and the smaller ones are then invisible." The Amer. Nat. Vol. XXXII, page 45.

tion except that even the balsam mounts remained usable for a sufficient time to secure camera lucida drawings of the points in question. In preparations for photomicrographs the glycerine jelly mounts were better.

After comparing the two methods the balsam mounts were used almost altogether as they were quicker and simpler to prepare and a much larger proportion of usable mounts were made in this way.

The wings of freshly emerged aphids were severed from the body together with a portion of the thorax, to preserve the basal part of the tracheæ and to block to some extent the penetration of the balsam.

In some species, where the shape of the body and the angle at which the wings are set permitted it, the aphid itself with wings attached was mounted after beheading the insect and puncturing the tip of the abdomen. The legs had also to be removed. The pressure of the cover glass in these mounts generally forced the body fluids from the openings at the two extremities and often excellent tracheal preparations were secured in this way. It could be applied only to a limited number of species, however.

Only wings of freshly emerged aphids are available for the study of the wing tracheæ, as before the wings are hardened enough for the first flight, the tracheæ have become either entirely invisible or so nearly so that they are useless for the questions in hand. It thus becomes necessary to select the individuals in the first few minutes after molting. This can readily be done by taking the palest insects while the wings are yet white, that is, before they begin to become transparent. An abundance of material was kept on hand by the collection of large colonies of aphids whenever any were found, the wing pads of which indicated that the final molt was approaching.

It was more difficult to secure the wing pads at the critical moment. The wing pad of the aphid nymph is not only small but it is relatively thicker and softer and narrower than those of many insects and the developing wing is for the most part so crumpled that the courses of the tracheæ are impossible to follow. So soft is the tissue of the nymphal pad and so loose do the tracheæ lie within it, that the slightest pressure is likely to misplace them or rupture them, and render the preparation useless. By selecting the nymphs of such species as had the flatter wing pads,

the best results were obtained. However, none of the aphids are so easy to manipulate for the tracheation of the wing pads as are the flat padded psyllids.

* * * * *

Although the possibilities of interesting features of wing tracheation of the aphids were by no means exhausted with any species; for the problem at issue,—the homologies of the wing veins,—no point was left in question. Wings of more than two thousand of newly emerged aphids were examined. Where possible a single point was verified for all the variations of wing types from *Lachnus* to *Chermes*. Where a point arose that certain species showed better than others it was exhaustively studied by making numerous mounts of those species which had any bearing upon it.

As for the range of material used, approximately 100 species belonging to 16 genera were drawn upon. Many of these were discarded after a few mounts,—as for instance after the condition for the genus *Aphis* was clearly ascertained other species of this genus did not give additional data. Many species were found unsatisfactory to work with by reason of size, density of color or other conditions and were discarded after a few trials.

The genera from which most of the data were accumulated and in all of which the tracheation was demonstrated repeatedly and conclusively, are *Lachnus*, *Melanoxanthus*, *Callipterus*, *Chaitophorus*, *Myzus*, *Macrosiphum*, *Rhopalosiphum*, *Aphis*, *Schizoneura*, *Mindarus*, *Pemphigus*, *Tetraneura*, *Hamamelistes*, *Chermes* and two new genera still in manuscript. These genera present practically the whole variation of the types of aphid venation from the more generalized to the more specialized.

The more logical presentation of the four families considered in this paper would be in the following order,—Psyllidæ, Aphididæ, Aleurodidæ and Coccidæ, but as the problem was undertaken primarily for the Aphididæ and as the investigation was devoted for the most part to them, the part dealing with the aphids is presented first. The work with the other families, though sufficient to indicate the homologies of the veins, has been so much slighter in amount that it seems more fitting to give secondary place to the Psyllidæ even though this necessitates a break in the systematic sequence.

THE COURSE OF A VEIN.

In the following pages the "course" and the "free part" of veins are frequently mentioned. By the free part of a vein is meant all that portion that is not coalesced with any other vein. As for instance in Fig. 36, the free part of Cu_2 is all that portion of Cu_2 between the point where it separates from Cu_1 and the margin of the wing.

As to the course of the vein it has been convenient to consider each of the branches of any vein as extending from the base to the margin of the wing, as is made plain by the following quotation:*

"If radius and its five branches be taken as an example, the stem part, always designated as R , would be considered as being a combination of all the branches of radius, or as $R_1 + 2 + 3 + 4 + 5$, which divides into R_1 and R_5 . In like manner the stem of the radial sector would be considered as being a combination of all the branches of the radial sector, or as $R_2 + 3 + 4 + 5$, which divided into $R_2 + 3$ and $R_4 + 5$, and these in turn into R_2 and R_3 , and R_4 and R_5 , respectively. So that in tracing out the course of any of the branches of radius by drawing a pencil along them, as R_4 , beginning at the base of the wing, we would pass first over the stem of R , then over the stem of the radial sector, then over $R_4 + 5$, and finally over the free part of R_4 ."

COALESCENCE OF TRACHEÆ.

A comparison of the tracheation of the wing pad of an aphid nymph with that of the wing of the recently emerged aphid of the same species reveals the fact that there are fewer basal tracheæ in the later than in the earlier stage, although the terminal branches are the same in number. For instance, there are four tracheæ which branch from the body trachea in the nymphal wing pad of *Schizoneura rileyi* (fig. 21) and only two tracheal stems at the base of the newly emerged wing of the same species (fig. 22). Similarly as there are four tracheæ at the base of the nymphal wing pad of the species of *Aphis* which I have studied and of *Callipterus ulmifolii* while there are but two basal tracheæ in the newly emerged wings of these same species, this is shown to be the normal condition for the family in the more generalized genera. In the nymphal wing pad of *Mindarus* (fig. 18) three

* MacGillivray, A. D., Wings of Tenthredinoidea. Proc. U. S. Nat. Museum Vol. XXIX, page 576. 1906.

of these tracheæ unite before they reach the body tracheæ, approaching the condition of the mature wing.

This change in the condition of the corresponding tracheæ at different stages has been designated in this paper as the "coalescence" of tracheæ, as this term seems to express the relation of the tracheæ of the mature wing to those of the nymphal wing pad. This sort of coalescence of tracheæ is a constant factor in the aphids, not alone as to the main tracheal stems but a similar tendency is shown in the branches of the tracheæ. For instance notice that the medial trachea in figure 21 branches decidedly nearer the base of the wing than the medial trachea in figure 22, these branches being coalesced to much nearer the margin of the wing than in the earlier stage.

How or when this coalescence takes place the writer has as yet made no attempt to ascertain. No pains has been spared, however, in accumulating evidence that it does occur, or in making sure that it is an actual union of tracheæ and not an approximation. A 1-6 objective was usually sufficient for the examination of the cases in question. Where it was not, an oil emersion was used. The manner and time of the coalescence is a mystery well worth solving but it is only the *fact* of this coalescence and not its method which has any bearing on the present problem—the homologies of the veins. However, it is a problem which the writer hopes to undertake in the near future.

Besides the normal coalescence of the basal portions of medial, cubital, and the first anal tracheæ just described, very rare instances of abnormal coalescence occur. Figure 2 shows a wing of *Melanoxanthus* in which the radial, medial and cubital tracheæ are anastomosed for a considerable distance.

Attention is also called to Plate XIX, which shows three unusual examples of tracheation. Normally the forewing of *Chermes* has two basal tracheæ as in the more generalized genera, and as is shown in figures 24 and 28. But in this highly specialized genus the tracheation seems to be unstable. Figure 26 shows an instance of anastomosis similar to that in figure 2, while figure 27 represents a single tracheal stem at the base of the wing, a condition which approaches the normal condition of the hind wing of *Chermes* (fig. 30.) On the other hand figure 25 records an instance where the first anal trachea is separate from the common stem of the medial and cubital tracheæ to the base of the wing, giving in this case three basal tracheæ.

In the study of the tracheation in the Psyllidæ the writer has been confined to a single species, and we have here even a more striking degree of normal coalescence of tracheæ than in the Aphididae. For instance, as is shown in figure 33, the seven tracheæ are distinct to the body trachea in the nymphal wing pad, while figure 34 records the normal tracheation of the freshly emerged wing, the three most important tracheæ, the radial, medial, and cubital tracheæ, are coalesced into a common stem at the base, and for a considerable distance the medial and cubital tracheæ are stalked after the radial trachea has separated from them.

We have, then, a very striking difference in the relation of the tracheæ of the nymphal wing pad and those of the freshly emerged wing, in both of these families of insects.

COSTA AND SUBCOSTA OF APHIDIDÆ.

The costal vein extends along the cephalic margin of the wing. No trachea precedes this vein in the freshly emerged wing.* Neither is a costal trachea present in any nymphal wing pad of the species examined by the writer. Further, no evidence of a vestigial costal spur from the body trachea is to be found in the several species examined for this point. Perhaps the most striking evidence of a costal vein aside from the stiffening of the costal margin is the fact that in severing the wing from a freshly killed aphid, the yellow body fluids frequently flow into this vein and extend along to about the region of the stigma (fig. 4).

In like manner no trachea precedes the vein subcosta in any species examined of the sixteen genera (see page 105) of aphids from *Lachnus* to *Chermes* which I have studied for this point. No item in this work has been more carefully investigated than the possibility of a subcostal trachea.

Indications of such a trachea have by no means been lacking. For instance, the fold of the vein subcosta appears very early in the freshly emerged wing (long before the other veins) and is therefore frequently the only vein indicated at the time the tracheæ are visible. For many mounts of many species this forming vein resembles a tracheal line closely enough to be mistaken for one unless exceedingly great care is taken to secure

* Comstock and Needham. Wings of Insects. Page 858. " * * * there are often channels present which do not contain tracheæ. This is oftenest true of two large channels at the lateral margins of the wing. Of these the costal remains abundantly lined with cells, which ultimately form the strong costal vein. Its trachea is often atrophied, probably owing to the disadvantageous position of its base in relation to air supply, as we have hitherto indicated."

wings immediately after emergence. Handlirsch* thus mistook this forming vein for a trachea in his preparation of *Schizoneura lanigera*.

Wherever there has been the slightest chance that a subcostal trachea might be present, exhaustive investigation has been made until no possible doubt of its absence remained.

Again, for some species, one of the secondary branches of the radial trachea near its base might easily be mistaken for a subcostal trachea so far as its position goes. *Chermes pinifoliae* (fig. 26) serves as an illustration of this. But these secondary branches are very variable even for the same species and after examining large series of mounts little difficulty is experienced in distinguishing the tracheæ of the main veins from secondary branches.

The only trachea found during the whole time possible to interpret as the subcosta was a single mount out of hundreds of *Mindarus (abietinus* Koch?) where an exceedingly short branch from the radial trunk near the base occurred, larger than the ordinary secondary tracheæ. This may be an abortive subcostal not entirely atrophied. Or it may be merely an abnormality.

This species of *Mindarus*, collected in great abundance from Balsam fir in the vicinity of Orono is apparently the same as *abietinus* Koch. But as it has not yet been compared with specimens from Europe it is given in this paper accompanied with a question mark.

Another opportunity for confusing a branch of the radial trachea for a subcostal trachea is found in wings where the path of the tracheal branch of radius chances to coincide with that of the newly forming subcostal vein. Such a case is shown in the tracheation of *Pemphigus acerifolii* (fig. 12) where the trachea follows the stigmal margin that the subcostal vein is later to bound. But the branches of the radial trachea are quite as likely to cut directly across the path of the forming subcostal vein as to coincide. *Chermes abietis* (fig. 24) will illustrate this.

The point, however, which gave me most trouble was the fact that very frequently the fold in the wing caused by the forming subcostal vein bent the branches of the radial trachea to such an extent that their connection with the radial trachea was obscured and a series of tracheal branches resulted which had every appearance of rising directly from the region of the subcosta.

* Handlirsch, A. Fossilen Insekten. Plate VIII. Fig. 9.

The absence of a costal trachea is by no means unusual.* The aphid wing is characterized by the reduction of tracheæ and the loss of the subcostal trachea is only one more step in the general trend of reduction. What the aphid lacks in main tracheal trunks, however, it makes up in secondary ramifications, and a glance at the tracheation of *Chermes abietis* (fig. 24) will show that the absence of costal and subcostal tracheæ does not indicate that this portion of the wing is untracheated. Perhaps the abundance of secondary tracheæ explains the absence of unnecessary costal and subcostal tracheæ. At any rate they might in some cases be mistaken for one of these main tracheæ. Refer again to *Chermes abietis* (fig. 24) where the ends of the radial branches are so interwoven as to have the appearance of a continuous subcostal trachea. And where the channel of the subcostal vein hides the radial connection, we have frequently the occurrence of what appears to be a strong subcostal trachea with branches extending toward the radius. Further, in case the radial connection of all these tracheæ, except a single one near the base of the wing, is obscured, as sometimes happens, there is, to all superficial appearances, a clear indication of a strong subcostal trachea.

Altogether the absence of the subcostal trachea was one of the most troublesome points to establish. Each clue was followed, however, until the evidence was absolutely conclusive.

Although no subcostal trachea is present, there seems to be no other conclusion except to consider that the vein subcosta is present in the large main vein channel of the wing, and extends from the base of the wing to the stigma where it approaches the margin of the wing. Indeed it seems not at all unlikely that this stiff vein fold at the base of the aphid wing is responsible for the atrophy of the subcostal trachea. The radial trachea from its position can elude the pressure and run alongside, but this obstruction alone would seem sufficient to explain the loss of the subcostal trachea in the Aphididæ.

RADIUS OF APHIDIDÆ.

The tracheation of *Myzus cerasi* (fig. 3) gives a fairly typical two-branched radial trachea. This type persists for the family of Aphididæ except in the Chermesinæ where this trachea is not branched. This trachea is one of the two main tracheæ which enter the wing, and from the phylogenetic standpoint the chief

* See Footnote, page 108 (Costa and Subcosta).

interest concerning it is centered in the cephalic branch, or the trachea preceding vein R_1 .

In the case of two widely separated Hemiptera, a Cicada and a Coreid, this trachea was found to be but weakly developed in the nymphal wing pads,* being apparently crowded out by the strong subcostal trachea, and it was not succeeded by a vein,—the vein R_1 being completely absent in these two insects.

With the aphids no such crowding of the radial trachea occurs, for, as has been shown, the costal and subcostal are both absent.

It is, however, of great phylogenetic interest to find that in the tracheation of the aphids, the weak character of this same trachea (that is the one preceding vein R_1) is evident. In *Lachnus*, probably the most generalized genus in the family, this branch is scarcely to be distinguished from the secondary branches of the radial trachea and is emphasized chiefly from the fact that it is succeeded by a vein R_1 (fig. 1). And in all of the generalized genera it is characterized by a wavering and uncertain course. It is consistent with this general tendency to find that this is the tracheal branch which if it appears at all in the specialized Chermesinae is so weakly indicated as to become indistinguishable from the secondary branches and loses its significance as it is not succeeded by a vein, vein R_1 being absent in the Chermesinae.

The wings of the Chermesinae are at a glance conspicuously of a different type from those of the more generalized aphids, and this difference in venation has heretofore been interpreted as due to the absence of media (the "third discoidal"). Especial attention is called, therefore, to figures 28 and 29. These are two drawings made of the same identical wing of *Chermes pinifoliae*,—figure 28 drawn immediately after mounting when most of the tracheae showed, and figure 29 drawn from the same mount 24 hours later when the tracheae had cleared and become invisible and the veins are apparent instead. These drawings indicate the character of the difference between the *Chermes* venation and that of the more generalized genera. R_1 has disappeared and R_s , losing its characteristic curve, lies along the caudal margin of the stigma. Media, apparently to replace the position and function thus deserted by the radial sector, migrates forward to approximately the position which the "stigmal vein" or radial sector occupies in the generalized genera. This is an interpretation which could in no wise be settled except by appeal to the trachea-

* Comstock and Needham. Wings of Insects. pp. 245—251.

tion, and it is perhaps as pretty an illustration as can be found of the conclusive evidence which tracheation can sometimes bear in a doubtful case of venation.

The same condition is shown in *Chermes abietis* (figs. 24 and 25).

Although the radial trachea has no main branches except R_1 and the sector, this trachea very frequently as is the case of the other tracheæ, bears a great number of secondary ramifications. These secondary branches are omitted in many of the drawings accompanying this study as they are the first to clear and become invisible,* and were frequently neglected when first attention was concentrated on other points. However, a glance at *Chermes abietis* (fig. 24) and *Lachnus strobi* (fig. 1) representing the genera at the extreme ends of the Aphididæ show the general condition of these radial ramifications which are further treated under the discussion of the subcosta (see page 108).

With an understanding of the tracheation, little explanation is required for the vein radius. Except for the *Chermesinæ*, the free part of R_1 forms the caudal boundary of the stigma and extends to the margin of the wing. The radial sector originates in the vicinity of the stigma and curves strongly to near the tip of the wing. The main stem of radius extends from the junction of these branches to the base of the wing in a line about parallel to the subcosta,—forming indeed a part of that strong main composite vein channel of the wing.

In *Chermesinæ*, radius is unbranched, as has been explained, and takes a straight course from the base of the wing to the extremity of the stigma. A double adjustment takes place here. Correlated with the loss of R_1 , which in the more generalized genera bounds the stigma along its distal edge, is a straightening of the caudal margin of the stigma and a straightening of the course of the radial sector so that the radial sector runs along the edge of the broadened stigma in this type of wing (figs. 31 and 32).

MEDIA OF APHIDIDÆ.

For a correct interpretation of media an understanding of the tracheation is necessary. The freshly emerged wing of *Myzus cerasi* (fig. 3) gives a fairly typical tracheation for the more generalized wings. The medial trachea will here be seen, as is true for all the genera of Aphididæ, to be the second of the two main tracheæ to enter the wing from the body cavity. This trachea

* See discussion of preparation, page 103.

lies uniformly parallel to the radial trachea, usually separated from it by an appreciable distance, though often touching it, but not, except in rare instances,* really coalesced with the radial trachea. As we approach the wings most specialized by reduction of tracheæ, we come first to *Schizoneura* (fig. 22) and *Mindarus* (fig. 19) as examples of the medial trachea with but two branches, and then to such wings as those of *Pemphigus*, *Tetraneura*, *Hamamelistes* and *Chermes*, where media is unbranched. The migration of the medial trachea to approximately the position occupied by the radial sector which in turn migrates to meet the margin of the stigma, is characteristic of the Chermesinæ, and has just been discussed under the treatment of radius.

The tracheation of the adult wing, however, does not suffice to make perfectly evident the relation of media to cubitus. For instance, so far as has yet been demonstrated, what is here interpreted as $M_3 + 4$ (fig. 22) might perhaps be understood as cubitus coalesced with media as Vickery† has explained it, or what is here interpreted as cubitus might be homologized as a branch of media as Handlirsch‡ has done. Fortunately the tracheation of the wing pad of the nymphs of certain species make this point entirely clear. Reference to the nymphal pad of *Schizoneura rileyi* (fig. 21) gives an unmistakable demonstration concerning the point at issue. Four main tracheæ are seen to be separate to the place of connection with the body trachea. These are the fore-runners of radius, media, cubitus and the first anal vein. The two-branched media and the unbranched cubitus of *Schizoneura* are thus clearly seen to be preceded by distinct tracheæ separate to the base of the wing pad, and the relation of media to cubitus in the mature wing becomes at once apparent and the degree of basal coalescence evident.

After the foregoing discussion of the tracheation little remains which needs to be said concerning the vein media. For approximately one-half the length of radius media is coalesced with $R + Sc.||$ and nearer the base of the wing similarly with the proxi-

* For discussion of coalescence and anastomosis of the tracheæ, see page 106.

† Vickery, '08, page 9. Figure 2.

‡ Handlirsch. Die Fossilen Insekten und die Phylogenie der Rezenten Formen. 1906-08. Taf. VIII, figures 9 and 10.

|| "The figures show that in some cases what appears as a single vein is formed about two closely parallel tracheæ. This is shown in the case of the bases of the second and third principal tracheæ, counting from the costal margin of the wing, the radial and medial tracheæ. This illustrates a fact of frequent occurrence, that what appears to be a single vein may be formed by the coalescence of two primitive veins." Comstock-Needham, Wings of Insects, p. 48.

mal portions of cubitus and the first anal vein. The free part of media occupies about the center of the distal half of the wing. Its maximum number of branches is three, — M_1 and M_2 and $M_3 +_4$ (fig. 8). The first step at reduction is in such wings as *Schizoneura* and *Mindarus* where M_1 and M_2 are coalesced, giving a two-branched media $M_1 +_2$ and $M_3 +_4$ (figs. 20 and 23). These two branches in turn are coalesced, resulting in the unbranched media $(M_1 +_2 + M_3 +_4)^*$ in the wings having the most reduced venation.

The connection between the free parts of media, cubitus and the anal vein and the composite main vein is frequently broken, on account, probably, of the strong ridge in the wing caused by this vein. This part of media being in the central portion of the wing is not, apparently, so necessary to the strength of the wing as the veins on either side, and starting from the broken basal connection media is found in various degrees of atrophy, in some species one-third to one-half of the base of the free part of media being lacking (fig. 17).

CUBITUS OF APHIDIDÆ.

Cubitus is present in all the genera of Aphididæ and in all of them unbranched.

The tracheation of the freshly emerged wing and of the wing pad explains cubitus and its relation to the other veins.

Attention is called to figure 22, *Schizoneura rileyi*, which gives a fair illustration of the cubital trachea. Its basal portion is coalesced with those of the medial and anal tracheæ. In most wings the free portion of the cubital trachea originates about midway between the medial and first anal tracheæ. In some instances however, the cubital trachea runs along parallel with the medial trachea for some little distance. Figure 9, a mount of a newly emerged hind wing of *Macrosiphum pisi*, is an unusual instance even for the species in question, where the cubital trachea runs parallel with the medial to almost the base of the wing before it becomes coalesced. On the other hand, in the wing of *Hamamelistes spinosus* (fig. 15) a greater degree of coalescence has taken place and the cubital and first anal tracheæ branch from the medial on a common stem, and proceed some little distance before separating.

* See page 106 for a discussion of the course of a vein.

The tracheation of the wing itself, however, is not sufficient to define cubitus beyond question, and numerous mounts of nymphal wing-pads were examined with this end in view. Perhaps the most satisfactory is that of *Schizoneura rileyi* (fig. 21) in which a portion of the body trachea is seen with four main wing tracheæ, the fore-runners of radius, media, cubitus and the first anal vein.

Cubitus is here clearly shown in its relation to media and the first anal and the peculiar complications of the venation of the adult wing are thus explainable as coalescences with media on the one hand or the first anal on the other. *Schizoneura rileyi* was the only species in which the writer has succeeded in getting the connection of these four nymphal wing tracheæ with the body trachea, but mounts of *Callipterus ulmifolii* showed four main tracheæ distinct to the base of the pad, as did also mounts of *Aphis* sp. In the last nymphal stage there is a tendency, in some species at least, for the basal portions of the medial, cubital and first anal tracheæ to become coalesced, giving the two main tracheal stems of the mature wing. This is shown in a wing pad of the last nymphal stage of *Mindarus* (fig. 18) where the four main tracheæ are distinct nearly to the base of the pad where three of them become coalesced before reaching the body trachea.

The vein cubitus so closely follows the cubital trachea that a further discussion concerning it is not necessary.

THE ANALS OF APHIDIDÆ.

The same mounts which explain cubitus show just as clearly the first anal and its relation to the other veins. We have then the unmistakable homologies of four of the wing veins of Aphididæ traced in the courses of the tracheæ of the freshly emerged wings and the wing pads of the nymphs: the "first discoidal" being the first anal, the "second discoidal" being the cubitus, the "third discoidal" or "cubital vein" being the media and the "fourth discoidal" or "stigmal vein" being the radial sector.

This seems enough to ask of the tracheæ of a highly specialized wing, but they do tell even more. They give constantly the second anal which appears in the freshly emerged wings for all the genera studied by the writer, as a delicately marked and fairly regularly placed trachea. No vein is formed about this trachea so that it has no other significance for the venation than to help determine that the anal vein here homologized as the first anal

has not been so homologized without tracheal evidence that it is not the second or third anal,—a statement further elucidated by the appearance of a third anal trachea in many freshly emerged wings. Figures 1 and 3 and others give the second anal trachea in its characteristic position, and figures 2, 4, 6 and others give a few of many mounts showing the third anal trachea also. These last anal tracheæ are among the first of the tracheæ to become invisible, so that in drawings made with other points in view, they are frequently not indicated, as they had cleared before the other points at issue had been finished.

The presence of the second and third anal tracheæ in the nymphal wing pad has not been established in those species of aphids in which the nymphs were studied. What the history of these tracheæ is, then, previous to their appearance in the recently emerged wing is not yet ascertained.

THE HIND WING OF APHIDIDÆ.

The hind wing of *Chaitophorus populicola* (fig. 7) will serve as an illustration of the tracheation of the hind wings of the more generalized genera. In figure 9 of the *Macrosiphum pisi* the four tracheæ are distinct to very near the base of the wing. Usually a greater degree of coalescence has taken place even for this species.

By referring this wing to the front wing of *Chermes* (Plate XIX) we can readily homologize the unbranched radial trachea, the simple medial trachea, the cubital trachea and the first anal. Like the second anal of the fore wing, the first anal of the hind wing appears only as a trachea and is not followed by a vein.

The same tracheæ occur in the other more generalized genera, and also in *Pemphigus* (fig. 13) where the front wing is specialized by the reduction of veins in media. When we reach *Chermes* (fig. 30), however, we find, in spite of the wealth of secondary tracheæ, only the radial and medial tracheæ marking the courses of succeeding veins and these are coalesced at the base.

The venation of the hind wing is, then, homologized, as follows: the marginal costa and the very faint subcosta, both of which, due to the lack of mechanical necessity found in the front wing, are not well developed; the radius represented by the radial sector only; the media always simple; and in the more generalized genera, cubitus. The venation of *Tetraneura* (fig. 17) is of interest. The front wing has the venation of *Pemphigus* and

the hind wing lacks the cubitus and is, therefore, a step in the direction of *Chermes*.

Although we find the same veins in the hind wings of *Macrosiphum solanifolii* (fig. 8) and *Pemphigus acerifoliae* (fig. 13) for instance, these two wings appear different on account of the difference of position of the veins. The radial sector takes the same course in both wings, but the free part of cubitus originates much nearer the base of the wing in *Macrosiphum* while usually in *Pemphigus* cubitus is coalesced with media to the point where media branches off from the course of radius. This peculiarity is correlated with a similar manifestation in the front wing of *Pemphigus* and is doubtless due to the long narrow wings of this genus.

In *Chermes* (figs. 30 and 31) as was stated in the discussion of the tracheation, only veins radial sector and media are represented, and the hind wing of *Phylloxera* (fig. 32) has retained only the radial sector.

PSYLLIDÆ.

The tracheation of the psyllid wing is instructive both because it throws light upon the interpretation of the venation of the psyllid wing and because it bears strong additional evidence in support of the conclusions arrived at for the aphid wings.

Fig. 33 gives the tracheation of the fore-wing pad of the nymph of *Psylla floccosa* Patch. It will be seen by reference to this that there is no coalescence for these tracheæ at this stage. They all branch separately from the body trachea. There are seven tracheæ: the costal; a short trachea lying at the very margin of the wing pad; the unbranched subcostal extending in a line about parallel to the costal margin of the pad and lying very close to the costal trachea at the base; the radial, terminating in two long branches, the forerunners of R_1 and R_s ; the two-branched medial; the typical two-branched cubital; and two anal tracheæ.

This comes surprisingly close, for a wing so highly specialized, to the hypothetical type of Comstock-Needham.

The newly emerged wing shows a decided change in the appearance of the tracheæ, but the change is due to basal coalescence instead of any radical change in the number or branching of the tracheæ.

The tracheation of the freshly emerged wing of *Psylla floccosa* (Fig. 34) shows the degree of this change. The costal trachea has

disappeared as is frequently the case.* The subcostal and second anal tracheæ have migrated to very near their respective margins of the wing, but are both distinct. The first anal, a slender but distinct trachea, follows the course of the claval suture. The proximal portions of the radial, medial and cubital tracheæ are coalesced into a common stem at the basal fourth of the wing. This main stem divides into two tracheæ, the radial and the common stem of the medial and cubital. The latter soon separates again into the free portions of the medial and cubital tracheæ.

There is a greater degree of coalescence in the tracheation of this psyllid wing than occurs in that of the aphid wing as the radial trachea is always (except in very unusual variations as cited, page 107) separate to the base of the freshly emerged aphid wing.

The venation of *Psylla floccosa* (fig. 36) coincides with the tracheation of the freshly emerged wing very closely. Subcosta strengthens with the costa the cephalic margin of the wing. The second anal in a similar way reinforces the anal margin at the base. The first anal is so delicately traced along the claval suture that it cannot function as a strengthening rod in the wing as do the other veins. Indeed it has frequently been considered not a true vein.

Radius, media, and cubitus share about equally the burden of strengthening the wing. They are coalesced as a common main stem at the base. The relation of media and cubitus is similar to that of the same veins in the wing of the aphids and this typical two branched cubitus bears further evidence of the correctness of the interpretation of cubitus in the aphid wing.

R₁ responds to the mechanical necessity for strengthening the front of the wing. It is the only vein present in this region and upon it falls the burden as well as the approximate position usually assumed by the subcosta in many insect wings. R_s is a strong vein and reaches the margin near the apex of the wing.

The tracheation of the freshly emerged hind wing of *Psylla floccosa* resembles that of the front wing closely. (Fig. 35). The subcostal and second anal tracheæ lie near their respective wing margins, as in the front wing. The first anal trachea occu-

* "Its trachea is often atrophied, probably owing to the disadvantageous position of its base in relation to air supply, as we have hitherto indicated." Comstock-Needham: Wings of Insects, page 858.

pies the same position as in the front wing. Similarly there is a common stem of the radial, medial and cubital tracheæ. The medial trachea, however, is unbranched, and the tracheal branch preceding R_1 is wanting.

The loss of R_1 is significant. This vein is one of the least stable of the Hemipterous wing veins. Its complete absence has been established for the Cicada and a Coreid.* In the front wing of the aphids R_1 was seen to be preceded by a wavering trachea in all the subfamilies except the Chermesinæ where the vein R_1 is altogether lacking. In the hind wing of none of the aphids does either the vein R_1 occur, or the corresponding trachea.

In the front wing of the psyllid and *Aleurodicus* alone for this group is R_1 a strong vein and here it is evidently the response to the mechanical necessity not otherwise provided for. Subcosta is wanting and, as the only vein present in this portion of the wing, the burden of support falls upon the radius.

It is exceedingly interesting to find the condition of R_1 as predicted for the Hemiptera† on the basis of the Cicada and Coreid, fulfilled in this group of highly specialized Homoptera.

It is interesting, too, to find the same veins, vein for vein, appear in the wing of the psyllid that we have in the wing of the aphid—the most striking difference is a very slight one,—the cubitus branched in the psyllid and unbranched in the aphid. There is experienced no difficulty, as has been seen, in homologizing either the aphid or the psyllid veins independently of each other but the fact that in doing so the conclusions arrived at with each support and bring additional evidence for the other should in no wise be disregarded.

The fact that the costal margin of the psyllid wing is strengthened in one of two distinct ways (1) by a stigma and (2) by R_1 , is very well brought out in the five psyllids which have been selected to represent the venation of this family. Of these *Euphalerus nidifex* Schwarz‡ (fig. 38) would seem to be the most generalized type so far as the radial region is concerned, R_1 in this wing extending to near the tip of the wing as the trachea preceding R_1 does in the nymphal wing pad of *Psylla floccosa* (fig. 33). In *Pachy-*

* Comstock and Needham: Wings of Insects. Page 245.

† Comstock and Needham: Wings of Insects. Page 245.

‡ For an opportunity to study and figure the wings of *E. nidifex* and *A. mori*, the writer is indebted to Dr. L. O. Howard, who kindly loaned specimens of these species for this purpose.

psylla c. mamma Riley (fig. 39) the tip of R_1 has migrated slightly toward the middle of the costal margin. In both these wings the space from the base of the wing to the tip of R_1 is evidently too long to bear the strain of flight without further strengthening. This needed reinforcement occurs in the presence of a more or less pronounced stigma the proximal edge of which is margined by a ridge which is in some species so clearly defined as to be frequently figured as a vein.

As the tip of R_1 approaches the middle of the costal margin as in *Anomoneura mori* Schwarz (fig. 40) and even more in *Psylla floccosa* (fig. 36) the need of the stigma is removed as R_1 strengthens this portion of the wing margin.

The wing of *Trioza* (fig. 37) shows an extreme case of the migration of R_1 , this vein being here scarcely longer than the stigmal ridge in *Pachypsylla* and in about the same position. Correlated with this condition are other striking departures from the more generalized psyllid wing, perhaps the most conspicuous being the origin of the free parts of media and cubitus at approximately the same point as the origin of the free part of radius,—the common stem $M + Cu$ present in most psyllids being lacking in *Trioza*.

The wing of *A. mori* is in one respect most unusual for the family, and that is in the branching of the radial sector. This is the only instance in the four families discussed in this paper where the radial sector is branched, and it throws additional evidence on the interpretation of this vein as the sector. It should be stated in connection with the discussion of figure 40, that the venation here shown may possibly be not normal for this species. The writer had access to but a single specimen and in this the radial sector of the wing on one side bore five branches as figured while the radial sector of the other side was six branched.

The purpose of this study in wing tracheation has had the vein homologies as a goal and is not intended to enter into systematic discussions. However, since the systematists of the Psyllidæ build their tables largely upon the basis of the wing veins,* it is apparent that it would be more satisfactory to apply

* Löw. Verh. g-b. Wien XXVIII.

Maskell: Transactions of the N. Z. Institute Vol. XXII, 1889, page 158.

Frogatt: Australian Insects.

Kuwayama: Trans. of the Sapporo Nat. Hist. Soc. 1907-08.

a terminology which has the same significance for not only the closely related families of Aphididæ, Aleurodidæ, and Coccidæ, but the other insect orders as well.

For instance it would certainly seem more convenient to say "M + Cu is longer than the stem of R" than to resort to the more tortuous statement of Maskell*: "the stalk of the lower branch (cubitus) of the furcation of the primary vein is longer than the stalk of the upper branch (subcosta)."

At present the veins in the figures of the psyllid wings are indicated by arbitrary letters or figures with no necessary relation to symbols used by the same author for any other psyllid wing or to those of any other author for the same wing. This haphazard arrangement of lettering or numbering the figures of psyllid wings increases the confusion caused by the fact that the veins themselves are cumbered with such a system of nomenclature as the following:

"Stalk of cubitus, lower branch of cubitus, lower fork of lower branch of cubitus, upper fork of lower branch of cubitus," etc.

But by the use of a uniform system of wing terminology the abbreviation of the names of the veins become the natural and inevitable symbols to use for lettering the figures of the wings, and no confusion arises in associating Rs of the figure, for instance, with the radial-sector of the text.

The relative simplicity, ease of abbreviation and uniformity of such a system of terminology is recommendation enough aside from the homological significance it bears.†

As is stated in the discussion of Redtenbacher's homologies (see page 125) except for his interpretation of the alternate concave and convex veins his terms for the psyllid veins are in the main those applied in this present paper upon the basis of the tracheation.

ALEURODIDÆ.


Four fine but distinct tracheæ are present in the freshly emerged wing of *Aleurodes* *sp.*,—the costal, subcostal, radial and cubital tracheæ (fig. 44). All of these are uncoalesced to the

* Maskell: Trans of the N. Z. Institute, Vol. XXII, 1899, page 158.

† The Comstock-Needham system of terminology has been adopted by Handlirsch in all his recent papers dealing with venation of fossil insects and in his extended monograph of the fossil insects of the world. (*Die Fossilen Insekten und die Phylogenie der Rezenten Formen* 1906-1908). It has been with interest that the writer has noticed the application of this system of nomenclature to the group of insects with which this present paper deals, especially as the basis for his conclusion was a study of the tracheation of the wings.

base of the wing. The medial trachea is suggested merely by a very faint and delicate but constantly appearing tracing in the wing.

As in the wings of Aphididæ and Psyllidæ the radial trachea in Aleurodidæ is branched, being represented by the branches corresponding to R_1 and R_s . And as in the hind wing of all aphids and the front wing of the Chermesinæ, and the hind wing of psyllids, the *vein* radius in Aleurodes is unbranched, R_1 being lacking. The formation of the vein radius in Aleurodes is of exceeding interest. It follows the course of the radial trachea to the branching of the trachea and then proceeds along the radial sector. R_1 in the mature wing is lost and its position, if indicated at all, is suggested by the most delicate "shadowing" in the wing tissue. As has been previously stated,* the "complete absence of vein R_1 " was predicted as characteristic of the Hemiptera on the basis of the two widely separated insects,—the Cicada and a Coreid, and the phylogenetic significance of the added testimony of the weakness of this vein and the trachea that precedes it, in the remote and highly specialized group of Homoptera here under consideration seems to the highest degree interesting.

The tracheation of *Aleurodicus* I have not had an opportunity to study. On the basis of figures of the mature wing (not a safe basis for this group by any means, as has been shown), however, the additional vein found there can only be interpreted as R_1 . Its prominence is to be accounted for here doubtless, as in the case of its prominence in the forewing of the psyllid, by the rounded shape of the wing which results in a large wing expanse not otherwise strengthened. In response to mechanical necessity this vein, weak or absent when not needed, becomes more strongly developed. 

The second vein of the wing of *Aleurodes* is cubitus as will be seen by comparing figures 44 and 45 where the second vein is shown to follow the course of the cubital trachea.

The hind wing of *Aleurodes* (fig. 46) has but one trachea and one vein,—the radial sector it seems inevitable to conclude.

COCCIDÆ.

Before examining wings of freshly emerged male coccids it seemed possible only to echo the sentiment of Redtenbacher,—*"Cocciden konnte ich nicht untersuchen."*† Imagine the surprise,

* See Page 119.

† Vergleichende Studien über das Flügelgeäder der Insekten. Page 188.

then, which was caused when mount after mount of *Dactylopius* sp. on cactus showed five very delicate but perfectly distinct tracheæ. See Figure 42.

Four of these tracheæ are simple and uncoalesced to the base of the wing. They are arranged in two groups, the base of the subcostal, radial and medial tracheæ lying close together and the cubital and first anal tracheæ forming the other group at a little distance from the first.

The subcostal and radial tracheæ are both very wavy and as they lie close together, they cross and recross, often for the greater part of their length.

The medial trachea takes a median course. This consists of two interwoven branches, pursuing a common course.

The tracheæ in the wing of this coccid remain distinct until after the veins begin to form so that the relation of the two is at once discerned. One vein follows the general trail of the subcostal and radial tracheæ. This vein very evidently represents radius.

The second vein follows the base of the first tracheal group to about the point where the medial tracheal separates from the subcostal and radial. The vein here takes a direct line for the middle of the caudal margin of the wing. For slightly less than one-third the length of this vein it frequently joins the path of the cubital trachea. This corresponds most closely with media.

Besides these two main veins a short spur representing the subcosta is present.

In a wing so highly specialized as the coccid wing it is not improbable that the tracheation has lost its value as a basis for the venation. Certainly in the species studied there seems no necessary connection between the tracheæ and the veins which are found later.

In *Pseudococcus citri* the tracheation was exceedingly difficult to trace. The same veins occur in this species (fig. 41) as in the preceding (fig 43).

In many species of Coccids there are shadowed portions of the wings. It is due to this fact that we find the coccids sometimes figured with apparently four long veins, alternately dark and light, as for instance, in Westwood.*

* Westwood, J. O. Arcana Entomologica. Vol. I, Plate 6.

HISTORICAL DISCUSSION.*

As is the case with other groups of insects the names applied to the wing veins of aphids were given in the first place without homological reference to the veins of other insects. That is, we have an arbitrary system which has no significance outside the family of Aphididæ. Recently several papers have appeared which rename the wing veins with this aim in view, but as the true homologies of the wing veins themselves have not heretofore been established, certain mistakes in applying the Comstock-Needham nomenclature have, of necessity, arisen. These papers will be discussed in turn. First, however, it would seem of interest to review the earlier terminology.

For convenience in this discussion attention is called to Fig. 8, in which the names are used as based upon the homologies revealed in the study of the tracheation of the wings as recorded in this paper.

The following table will show the relation of the Comstock-Needham terminology to the terminology previously in use for the wing veins of aphids:

<i>After Buckton</i>	<i>Current terminology</i>	<i>Comstock-Needham</i>
	Fore Wing	(See fig. 8)
Costal Nervure	Costal	Costa (C.)
Cubitus or post-costal nervure	Subcostal vein	Subcosta (Sc) Radius ₁ (R ₁) (together with basal portions of the remaining wing veins).
Stigmatic	Stigmal vein	Radial sector (Rs)
First furcal	First branch	Media (M ₁)
Second furcal	Second branch	Media (M ₂)
Cubital nervure	Third discoidal or cubital	Media (M) Media ₃₊₄ (M ₃₊₄)
Second oblique	Second discoidal	Cubitus (Cu)
First oblique	First discoidal	First Anal (1st A.)
	Hind Wing.	
Cubitus or post costal nervure	Subcostal vein	Radial sector (Rs).
Second oblique	Second discoidal	Media (M.)
First oblique	First discoidal	Cubitus (Cu.)

* For careful general historical discussion of studies of wing-venation see MacGillivray, A. D. ('06). Wings of the Tenthredinoidea. PP. 570-574.

The interpretation of the so-called subcostal has been* that it is a single heavy vein spreading at the distal portion into the stigma. That this interpretation is incorrect the foregoing discussion on the tracheation has made clear. It is really a composite structure bordered along the cephalic margin by the subcostal vein and containing the radius and the coalesced proximal portions of the remaining wing veins.

It will be seen by reference to the accompanying table that the first, second and third discoidals are respectively the 1st Anal, Cubitus and Media. The second anal not persisting in the adult wing (that is, it is represented only by a constantly appearing trachea which soon clears) is not shown in any published figures of aphid wings.

In the hind wings the first and second discoidals are respectively (fig. 8) the cubitus and media, and the so-called subcostal vein is the radial sector.

Redtenbacher† gives homologies of the wing veins of aphids and psyllids, which except for his interpretation of alternate convex and concave veins, come pretty close to the conclusions arrived at from the study of the tracheation. Except for Sc and vein VI in the forewing and that Sc is not accounted for in the hind wing his psyllid wings are correct. His difficulties with the aphid wings could not be settled without reference to the tracheation.

Handlirsch‡ gives the only figure of wing tracheæ for psyllids or aphids published previous to this present paper. His interpretation of the tracheæ for the wing pad of the psyllid nymph is practically the same as that given in this paper. With the freshly emerged wing of *Schizoneura langigera*, however, three mistakes occur. The line which he indicates as the subcostal trachea does not occur as a trachea but as a well defined fold of the subcostal vein. (See page 108). The unbranched trachea which he considers M is really Cu. and his Cu. is one of the anals. The question in regard to M. and Cu. however could only be settled by the testimony of the tracheation of the wing pad. (See page 113 and fig. 21).

* Oestlund, O. W. Aphididae of Minnesota, p. 4. 1887.

Comstock, J. H. Introduction to Entomology, pp. 158-159. 1888.

† Redtenbacher, Josef. Ann. k. k. Naturh. Hofmus., I. 1886.

‡ Handlirsch, Anton. Die Fossilen Insekten und die Phylogenie der Rezenten Formen. 1906-08.

Handlirsch homologizes the veins of the Phytophthires which he figures and also names what tracheæ he figures.

In Woodworth's discussion of the wing veins of Phytophthires* the veins of these insects are homologized to the extent that the statement is made that the front wing of Aleurodidæ is the same in its maximum condition of venation as the maximum of the hind wings of Aphidæ, and the hind wings the same as the minimum of Aphidæ, and that the venation of the front wing of Coccidæ is the same as the minimum of the front wing of Aleurodidæ. This author figures wings of all the Phytophthires he discusses but as the wing veins are not labeled and it is not apparent from the text which of the "independents" he interprets the media and the cubitus to be either with the psyllids or aphids it is not possible to homologize them from his figures. The meaning of his statement that in only the Psyllidæ is the venation extensive enough to show clearly their affinity to the higher Homoptera is not apparent, as his maximum number of veins for the aphids according to his figures exceeds the maximum for the psyllids; and the number when the minimum is taken is the same for both wings except for one extra branch for the psyllids. Exception, moreover should be taken to his diagram of the venation of the Aphididæ, for the "additional independent and the cross vein at the tip" which he states are very rarely present, are never present in fact in the normal venation of any species of aphid. And if abnormal or freak veins are to be included in the venation of aphid wings there would be no reason to stop at these two, for cubitus might be branched, any of the branches of media have an extra fork and "cross-veins" might be almost indiscriminately located as between cubitus and the first anal.

In a very convenient classification of some of the external characters of Aphididæ Mr. Vickery† attempts a homology of the wing veins of aphids with those of other insects, stating that the names he gives, based upon Comstock's system, were decided upon from a study of other reduced wings such as Psocus, and from a study of the abnormal venations found so frequently in plant-lice. Mr. Vickery's homologies are based upon the comparison of mature wings and the misinterpretations which have

* Woodworth, C. W. ('06). *The Wing Veins of Insects*. pp. 124-125.

† Vickery, R. A. ('08). *A Comparative Study of the External Anatomy of Plant-lice*.

arisen are readily explained by this fact. Perhaps in no other family could be found a clearer demonstration of the value of the study of the tracheation in this connection.

SUMMARY.

The introductory discussion outlines the reasons for undertaking this study of wing vein homologies, states the conditions under which the study has taken place, and mentions some of the difficulties involved in the manipulation of this sort of material.

Attention is called to the coalescence of tracheæ both the normal occurrence and some unusual instances.

All the veins present in the four families discussed are homologized, each being taken up for detailed consideration and the tracheal basis for the homologies being carefully stated.

The historical discussion includes a notice of all such published work as has any direct bearing upon this present paper.

All the main features of venation or tracheation discussed are illustrated by the accompanying figures.

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EXPLANATION OF PLATES.

The figures submitted have been selected from numerous ones prepared in the progress of this study. In their preparation two methods were employed. The figures showing tracheation are from camera lucida sketches verified or corrected by examination of each significant point through a high power lens,—oil emersion when necessary. The figures giving venation (except Fig. 29) are ink tracings of photographs,—the blue prints which were used being bleached after the drawings were made in order that black and white figures uniform with the camera lucida sketches might be secured.

PLATE XVI.

FIG. 1. *Lachnus strobi* (Fitch). Tracheation of wing of newly emerged aphid. See page 111.

FIG. 2. *Melanoxanthus* sp. Wing of newly emerged individual showing an unusual case of coalescence of tracheæ. See page 107.

FIG. 3. *Myzus cerasi* (Fab.) Tracheation of wing of newly emerged aphid. See page 110.

FIG. 4. *Aphis* species. Tracheation of wing of newly emerged aphid showing connection with the body trachea. The region of the costal vein and also the main vein channel of the wing indicated here. See page 108.

FIG. 5. *Callipterus ulmifolii* Monell. Tracheation of wing of newly emerged aphid.

FIG. 6. *Chaitophorus nigræ* Oestlund. Tracheation of wing of newly emerged aphid. See page 116.

FIG. 7. *Chaitophorus populicola* Thos. Tracheation of hind wing of newly emerged aphid. Typical, showing connection with body trachea. See page 116.

FIG. 8. *Macrosiphum solanifolii* Ashmead. Venation of both wings.

FIG. 9. *Macrosiphum pisi*. Tracheation of hind wing of newly emerged aphid. Very exceptional. See page 116.

PLATE XVII.

FIG. 10. *Microparsus variabilis* Patch. Venation of both wings. Venation of this species very unstable. The type figured is a common one.

FIG. 11. *Toxoptera graminum* Rond. Venation of both wings.

FIG. 12 and 13. *Pemphigus acerifolii* Riley. Tracheation of fore and hind wings of newly emerged aphid. See pages 109 and 117.

FIG. 14. *Pemphigus venafuscus* Patch. Venation of both wings.

FIG. 15. *Hamamelistes spinosus* Shimer. Tracheation of wing of newly emerged aphid. See page 114.

FIG. 16. *Hamamelistes spinosus* Shimer. Venation of both wings.

FIG. 17. *Tetraneura* sp. Venation of both wings.

PLATE XVIII.

FIG. 18. *Mindarus (abietinus)* Koch (?). Tracheation of wing pad of nymph. See page 115.

FIG. 19. *Mindarus (abietinus)* Koch (?). Tracheation of freshly emerged wing.

FIG. 20. *Mindarus (abietinus)* Koch (?). Venation of both wings. See page 114.

FIG. 21. *Schizoneura rileyi* Thomas. Tracheation of wing pad of nymph. See page 114.

FIG. 22. *Schizoneura rileyi* Thomas. Tracheation of freshly emerged wing. See page 114.

FIG. 23. *Schizoneura americana* Riley. Venation of both wings.

PLATE XIX.

FIG. 24. *Chermes abietis* (Linn.). Tracheation. Note how the branches of the radial trachea weave along the margin. See page 110.

FIG. 25. *Chermes abietis* (Linn.). Tracheation. An extraordinary case in which the first anal trachea is distinct to the base of the wing. See page 107.

FIG. 26. *Chermes pinifoliæ* Fitch. Tracheation. An unusual case of coalescence. See page 107.

FIG. 27. *Chermes pinifoliæ* Fitch. Tracheation. An unusual case of coalescence. See page 107.

FIG. 28 and FIG. 29. *Chermes pinifoliæ* Fitch. Two camera lucida drawings of the same identical wing. Fig. 28 shows the tracheation of the freshly emerged wing, and Fig. 29 shows the course of the veins Rs, M, Cu and 1st A, twenty-four hours after Fig. 28 was drawn and after the tracheæ had all become invisible. See page 111.

FIG. 30. *Chermes pinifoliæ* Fitch. Normal tracheation of hind wing. See page 116.

FIG. 31. *Chermes*. Venation of both wings.

PLATE XX.

FIG. 32. *Phylloxera* sp. Venation of both wings.

FIG. 33. *Psylla floccosa* Patch. Tracheation of wing pad of nymph.

FIG. 34 and FIG. 35. *Psylla floccosa* Patch. Tracheation of freshly emerged fore and hind wings.

FIG. 36. *Psylla floccosa* Patch. Venation of fore wing.

FIG. 37. *Trioza* species. Venation of both wings.

PLATE XXI.

FIG. 38. *Euphalerus nidifex* Schwarz. Venation of fore wing. See page 119.

FIG. 39. *Pachypsylla celtidis* Riley. Venation of both wings. See page 119.

FIG. 40. *Anomoneura mori* Schwarz. Venation of forewing. See page 120.

FIG. 41. *Pseudococcus citri*. Venation. See page 123.

FIG. 42. *Dactylopius* species. Tracheation of freshly emerged wing. See page 123.

FIG. 43. *Dactylopius* species. Venation. See page 123.

FIG. 44. *Aleurodes* sp. Tracheation of freshly emerged fore wing. See page 122.

FIG. 45. *Aleurodes* sp. Venation of forewing. See page 122.

FIG. 46. *Aleurodes* sp. Tracheation of hind wing. (Venation is identical with this). See page 122.



Patch, Edith M. 1909. "Homologies of the Wing Veins of the Aphididae, Psyllidae, Aleurodidae, and Coccidae." *Annals of the Entomological Society of America* 2, 101–129. <https://doi.org/10.1093/aesa/2.2.101>.

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