THE INSECT WING, PART II. VEIN HOMOLOGY AND THE ARCHETYPAL INSECT WING[1]

K. G. Andrew Hamilton[2]

Abstract

The importance of using all available data to interpret venation is stressed. Several venational peculiarities of the Paleoptera indicate that many of the vein systems of the Neoptera are in fact compound in nature. "Radius sector" of Comstock and Needham (1898–1899) is designated a separate vein system *sector*, and their first anal vein is designated the *empusal* vein; Forbes' (1943) designation of their second branch of cubitus (cubitus posterior of Edmunds and Traver, 1954) as the plical vein is upheld. The media is shown to be basically four-branched.

This is the second in a series of four papers on the morphology of the insect wing. The first dealt with the origin and development of the wing from a paranotal lobe, with special reference to the development of tracheation, axillary sclerites, and wing folding. This section discusses the methods of studying venational homology, and the results of these studies in determining the ancestral condition of wing venation. The third section will contain a detailed analysis of the venation of the orders, and the fourth will discuss phylogenetic data derived from this study.

Methods

Comstock and Needham (1898–1899) observed the relationship of the tracheae and veins in insect wings. They found that the course of the tracheae in most wings gave good evidence of the homologies of the associated veins. These homologies can be said to be based upon the theory that the first wings had as many tracheae as veins, and that these were concurrent. This theory has been generally accepted.

This is not to say that the tracheational data are always reliable. The correspondence of vein and trachea may well have been one-to-one in the first wings, but in highly evolved orders this is not always so. Ross (1936) states that the hymenopterous venation is laid down before the tracheae develop, and the latter, in effect, follow the course of least resistance. Conversely, Fennah (1944) demonstrated independent adventitious vein development around the displaced costal trachea in three different families of Fulgoroidea. Whitten (1962) showed that the tracheae may take different courses within different instars of even the same species. Moreover, the tracheae may be so highly modified (as in the Ephemeroptera) that identifying them cannot be done with

any degree of confidence. In the extreme case, the Trichoptera virtually lack wing tracheae.

Various authors have proposed other methods of establishing vein homology to circumvent these problems. Snodgrass (1909) noted the relationship of the vein bases to the axillary sclerites in neopterous insects. I have reexamined these data and expanded their usefulness to the Paleoptera as well in the first part of this paper. Wing fluting data were introduced by Lameere (1917, translated 1923), who noted the alternation of concave and convex vein systems across the wing surface in the Paleoptera. This system was elaborated and extended to the Neoptera by Edmunds and Traver (1954). I have noted the limitations of such a practice in the first part of this work, pointing out that these data are inapplicable to the branched vein systems, which are neutral in most orders, and even secondarily fluted in several unusual insects (Zalessky, 1944).

The most generally practiced system of establishing homologies of venation is by direct comparison of the vein branchings among genera thought to be related. Ross demonstrated the usefulness of this method in solving the venation of the Hymenoptera. It must be employed with care, however, to make sure that the comparison material represents a more primitive and not a more specialized or unrelated venation.

All these methods used singly have defects. They should be considered in concert to ensure the accurate homologizing of the veins. Systems based on one or two such pieces of data have often been shown to be founded on illegitimate grounds.

Venational Archetype

The generalized wing venation proposed here is composed of the most constant features in the wings of numerous orders. Features not so widespread that are incorporated here are added because their possession by the paleopterous orders strongly suggests that they were features of the ancestral venation type. The generalized venation type proposed will thus approximate the ancestral venation type.

Basal attachment. I have discussed the origin and homologies of the basal sclerites in the first part of this paper. In Ephemeroptera, as probably in the first Paleoptera, all veins except the anal veins arise from a common basal plate. When this plate broke up in the higher Paleoptera to form the subcostal, median, and cubital plates, two vein systems were associated with the subcostal plate and three with each of the others (Hamilton, 1971, Fig. 14). With the exception of the last vein before the anal system, which may become associated with the other surrounding structures as well, all these veins tend to retain their primitive connections.

Fluting. The paleopterous wing had each vein system alternatively concave and convex (Hamilton, 1971, Fig. 11). This was modified in the Neoptera for sculling flight, with the branched veins becoming neutral in position (Hamilton, 1971, Fig. 12). Lameere (1923) was
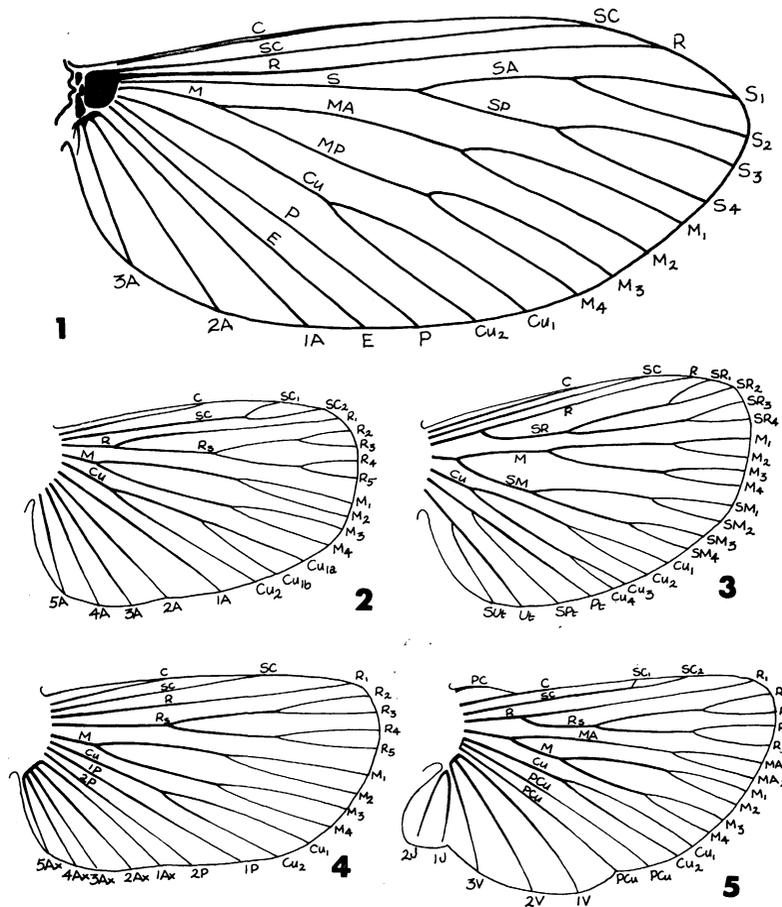
FIGS. 1–5. Archetypes of insect wings. 1, proposed system; 2, Comstock-Needham, 1898–1899; 3, Lameere, 1923; 4, Forbes, 1932; 5, Snodgrass, 1952. Rs, radial sector; SR, subradius; SM, submedia; PCu, postcubitus; Pt, penultimate; SPt, subpenultimate; Ut, ultimate; SUt, subultimate; Ax, axillaries; V, vannal veins; J, jugal veins; for other labeling, see text.

thus incorrect in postulating from fluting data that media of the Neoptera is homologous to its first main branch in the Paleoptera; Bradley (1931) similarly incorrectly regarded the neopterous media to be homologous to its second branch in the Paleoptera. There is thus no basis for supposing that more than four branches of media was the primitive condition.

Vein branches. The first three vein systems (costa, subcosta, and radius) are usually unbranched, as are the last three systems (plical, empusal, and anal veins). The three intermediate systems are dichotomously branched. Sector ("radius sector" of Comstock and Needham, 1898–1899) and media, the first two of these branched veins, have four branches; cubitus has only two (Fig. 1).

Subcosta is sometimes illustrated as being two-branched. This is based on the tracheation of the Plecoptera reported by Comstock and Needham, which has an adventitious branch of subcosta entering a costal crossvein.

"Radius sector" of Comstock and Needham is a free vein system in Ephemeroptera (Edmunds and Traver, 1954). It is basally fused to radius in the Odonata, but its trachea is still separate (Forbes, 1943). Zalessky (1944) found similar evidence for its separate identity in other insects. These facts indicate that the original venation had radius and sector separate, as I am treating them. Use of Zalessky's term "antemediana" (AM) for R_s would result in confusion with the first branch of media (MA or AM of authors).

A similar case is found in the plical vein, which is fused to cubitus in the Ephemeroptera and the Planoneoptera to form a three-branched system (Tillyard, 1919).

All the veins after cubitus have at one time or another been labeled "anal veins." Snodgrass (1935) pointed out the importance of the different features of these veins in correctly homologizing them. The first two arise from the cubital plate and lie above the vannal fold; the true anal veins arise from a common base articulating directly against the third axillary sclerite. The first of these veins is strongly concave; the others are typically weakly convex or neutral.

The nomenclature of these veins is difficult to unravel. Forbes (1932) designated three veins from different systems as the plical veins. When this term is used for only one of these veins, it always designates the first one. "Plical" in this context is descriptive of this concave vein system, as the furrow in which it lies has often been confused with the vannal fold in the Neoptera. Its abbreviation (P) is similar to that for "postcubitus" (Snodgrass, 1935, 1952), which also refers to this vein, and hence will not cause confusion. The term "cubitus posterior" of Edmunds and Traver (1954) erroneously suggests that this vein is a branch of cubitus. Zalessky's (1944) nomenclature uses "cubitus" for P and "antecubitus" for Cu.

The second of these veins has been confused with both the adjacent systems, and has never had a distinctive name. I am therefore designating it the "empusal vein" in reference to its distinctive features having been overlooked for so long.

The last system is a cluster of veins with a common base and usually also a common tracheal trunk stem. These "anal veins," as they have long been known, are comparable to Forbes' "axillary veins," and to Snodgrass' "vannal veins." The so-called "jugal veins" are one or two

spurlike extensions of a basal sclerite of dubious origin, and are probably not homologous with veins at all. I term this unit the "jugal bar."

The vein systems are labeled as in the Comstock-Needham system, with S, P, and E representing sector, plical and empusal veins respectively (Fig. 1). Numbers represent the typical terminal vein branches; lower case letters supernumerary branches. If there are more than two main branches, the primary branches are labeled with the postscript anterior (A) and posterior (P). This resembles the terminology applied to the Paleoptera, but is of sufficient utility to justify its more widespread use (see Ross, 1936).

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FOOD PREFERENCES OF GRASSHOPPERS IN SIX PLANTED PASTURES IN EASTERN KANSAS[1]

J. D. Lambley[2], John B. Campbell[3], and Herbert Knutson[4]

Abstract

The crop contents of 8,535 grasshoppers representing 31 species were collected and analyzed in the Flint Hills region of Kansas during the frost-free seasons of 1965 and 1966 in 6 planted-pasture sites. Sites were predominantly (1) western wheatgrass–Korean lespedeza; (2) smooth brome–sweetclover–alfalfa; (3) Kentucky bluegrass–Japanese brome–downy brome–sideoats grama–big bluestem; (4) smooth brome–bindweed; (5) smooth brome–ironweed–ragweed; and (6) reed canarygrass–smooth brome. Total plant species were: 17 perennial grasses, 8 annual grasses, several species of *Carex*, a *Typha,* 33 perennial forbs, 5 biennial forbs, 17 annual forbs, and 8 woody plants. Ingestion of both the planted forage plant species and the native plant species was determined at each site by percentage of plant fragments in crops of each grasshopper species.

The weather during 1965 was normal, but the spring of 1966 was cool, followed by a hot, dry summer.

Grass-feeding grasshoppers predominated and ingested the most grasses in sites planted with grasses. Some forb-feeding grasshoppers were abundant in the western wheatgrass–Korean lespedeza site, where this lespedeza was ingested by *M. differentialis, M. femurrubrumfemurrubrum, M. keeleri luridus,* and *M. sanguinipes;* normally, predominantly grass-feeding *C. viridifasciata, H. rugosus,* and *P. nebrascensis* also ingested lespedeza in significant amounts.

Smooth brome was ingested in significant amounts by all species except *M. keeleri luridus.*

Western wheatgrass was ingested significantly by *C. viridifasciata, H. rugosus, O. speciosa,* and *P. nebrascensis* and was not ingested in proportion to prevalence by *M. femurrubrumfemurrubrum* and *M. sanguinipes.*

Sweetclover was ingested significantly by *M. femurrubrumfemurrubrum, M. keeleri luridus, M. packardii,* and *M. sanguinipes.*

Reed canarygrass was ingested significantly by *M. differentialis, M. femurrubrumfemurrubrum,* and *P. nebrascensis,* and was not ingested in proportion to prevalence by *O. speciosa.*

Kentucky bluegrass was significantly ingested by *M. femurrubrumfemurrubrum, M. sanguinipes,* and *O. speciosa* but was not by *S. admirabilis.*

Japanese brome, a weed grass, was not ingested in proportion to prevalence except in one site where smooth brome was not present. Downy brome was not ingested in proportion to prevalence by *O. speciosa.*