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STANDARD DRAWING CONVENTIONS AND DEFINITIONS FOR VENATIONAL AND OTHER FEATURES OF WINGS OF HYMENOPTERA

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Abstract.—Descriptions of veins and other features of wings in the taxonomic literature of Hymenoptera are usually inadequate, terms are variably applied, and figures are incomplete and not standardized. This situation leads to a deplorable loss of useful taxonomic and phylogenetic information. There is need for standard definitions and some conventions for drawing figures of venational and related features. New terms for three reductional stages of veins are defined: tubular, nebulous and spectral. Flexion lines and folds are defined as well as adventitious veins. A diagrammatical wing section is shown and five kinds of lines representing different venational features presented. Several wings are figured to show examples of the system.

Recent taxonomic works in Hymenoptera often use vague or inadequate terms to describe wing venation and furrows. Figures of wings usually lack details and also lack explanations of conventions used to depict features, resulting in a loss of useful taxonomic characters and making interpretation of such figures a matter of guesswork. This paper is intended to be a plea to hymenopterists writing taxonomic papers to introduce more precision into their descriptions and figures of wings. I wish to make suggestions toward establishing uniform and easily understood definitions and drawing conventions for venational and other features on the wing membrane. Studies of wing anatomy and vein nomenclatural systems can be found elsewhere (Rohwer and Gahan, 1916; Redtenbacher, 1886; Comstock, 1918; Ross, 1936; Carpenter, 1966; Hamilton, 1971–72; Wootton, 1979).

When I refer to veins by name I shall use the Redtenbacher (1886) system as modified by Ross (1936). It is not well known that the hypothesis of homologous venation and the naming scheme for veins that most modern entomologists call the Comstock-Needham system was invented by Redtenbacher (1886), to whom Comstock (1918) rightly gave credit. Redtenbacher's hypothesis of alternating convex and concave veins is now generally accepted, though it was rejected by Comstock, whereas Comstock and Needhams' hypothesis that the ontogeny of wing trachea determines the course of veins was subsequently disproven (Wootton, 1979). Comstock's very large production of textbooks and great reputation as a teacher have largely eclipsed Redtenbacher's sound and original contribution.

Veins and Other Features of the Wings

Although wings of generalized insects have an arrangement of alternating concave and convex veins (Carpenter, 1966), the Hymenoptera have lost all but a small remnant of the concave veins, leaving almost all members of the order with exclusively convex longitudinal veins. The only obvious concave vein is the subcosta, present in only a few small families of Symphyta. The posterior branch of the radius (Rs) although said to be primitively concave, is convex throughout the Hymenoptera. Media posterior, also a concave vein, is absent.

The cubitus posterior, also concave, is normally absent in Hymenoptera, but it may coincide with the claval flexion line, although often both are distinct in Neuroptera and Plecoptera (Wootton, 1979). One family, the Rhopalosomatidae, has an unsclerotized but strongly pigmented vein in the outer posterior section of the fore wing (Fig. 4, CuP). This vein is concave above and represents, I postulate, the distal part of cubitus posterior extending from near the claval notch to the wing margin. It is the only clear cubitus posterior that I have seen in Hymenoptera. In addition many primitive sphecoids and bees and some ichneumonids and megalyrids have an unpigmented concave crease in exactly the same place (Fig. 5), probably also a trace of CuP. The course of this trace is strongly arcuate and extends no more than half way to the wing margin. Finally, in Cynipoidea, the trace venation of the hind wing has apparently become secondarily concave, a peculiarity of this group. Except for these unusual cases, the venation in Hymenoptera is entirely convex.

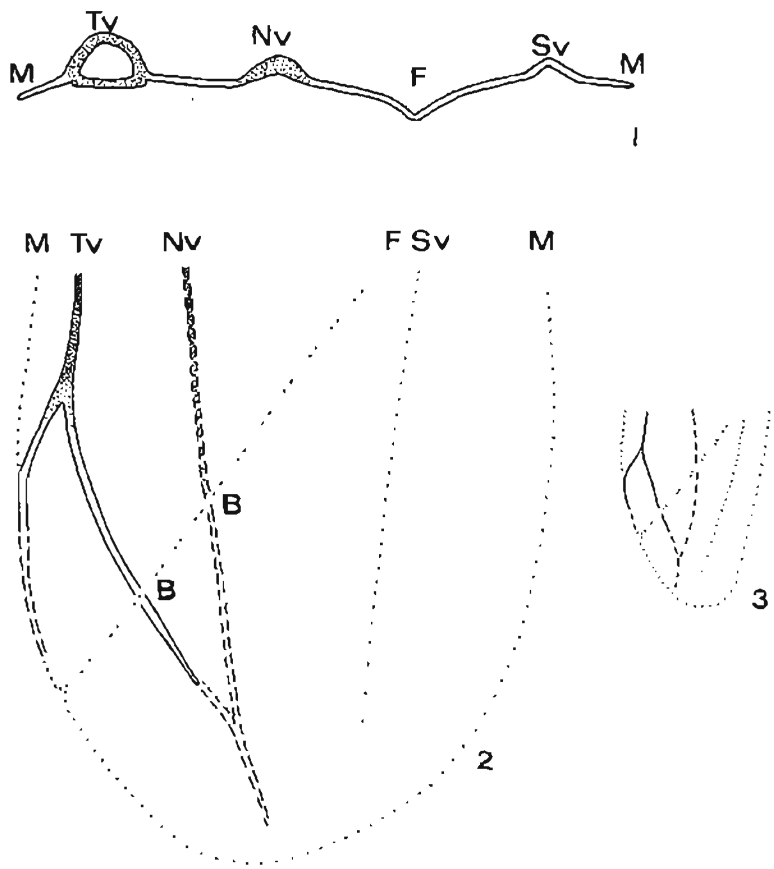
Wing membranes usually also exhibit flexion lines (Wootton, 1979), which are concave above in Hymenoptera (Figs. 1F, 2F) and represent areas of the wing membrane that flex during flight, apparently for aerodynamic reasons. Thus, with rare exceptions, all veins in Hymenoptera are convex above whereas flexion lines are concave. Being concolorous with the membrane, the flexion lines, are almost or quite invisible by transmitted light, and therefore cannot be studied or drawn in this mode of illumination. One must, instead, use diffused light reflected from the wing membrane. I must stress that trace venation (spectral veins—see definition below) and flexion lines cannot be studied from wings placed in mounting medium on a slide or even glued to a slide without a cover slip.

Finally the wings of Neoptera contain fold lines which, as the name suggests, have a function in folding of the wings (Wootton, 1979). In Hymenoptera the only fold line is found in the hind wing where the jugum meets the rest of the wing (Fig. 6). Here it is convex but is of such limited occurrence and so easily identified that it can usually be ignored in taxonomic descriptions.

Definitions of Reductional Stages of Veins

Stages of reduction of veins.—*1. Tubular vein* (Figs. 1Tv, 2Tv): a rigid tubular structure with sharply defined edges, usually yellow, brown or even black, but sometimes milky or clear. The edges appear darker, the center paler. The normal wing vein of Hymenoptera. These are sometimes called "tracheated" veins but the term is misleading because it has been repeatedly demonstrated that veins are formed independently of tracheae (summarized by Wootton, 1979; Carpenter, 1966).

2. Nebulous vein (Figs. 1Nv, 2Nv): a more or less-pigmented vein without a tubular structure, thus having ill-defined edges. These veins appear darkest centrally and fade gradually toward the edges. They are visible by transmitted light and also by light reflected from the wing membrane at an angle. The name refers to the cloudy indefinite margins.

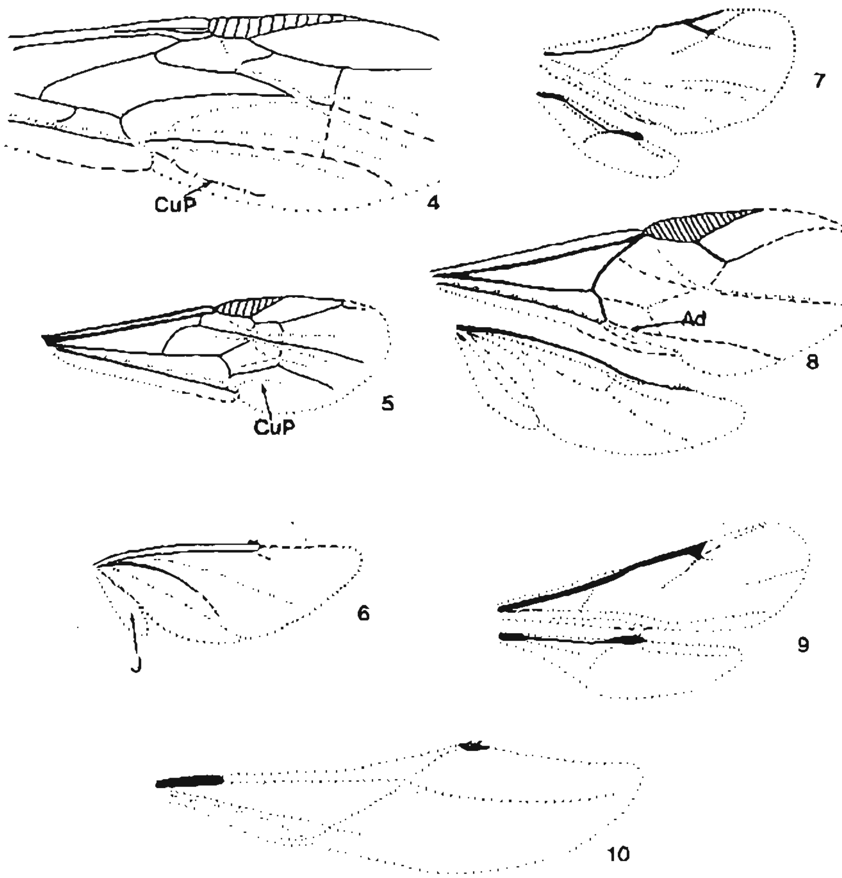


Figs. 1–3. Conventional system for illustrating various features of the Hymenopterous wing. 1, Hypothetical cross section. 2, Large scale figure. 3, Small scale figure. M = margin; Tv = tubular vein; Nv = nebulous vein; Sv = spectral vein; F = flexion line; B = bulla.

3. Spectral vein (Figs. 1Sv, 2Sv): an unpigmented vein that is normally invisible by transmitted light but can be seen by light reflected off the wing membrane because its course is marked by a ridge or furrow on the wing surface. If wings are placed in a mounting medium on a slide the spectral veins are usually no longer visible, although nebulous and sclerotized veins are still easily seen. Lines of trichiae on wings are much too variable in occurrence and position to be a reliable guide to the course of spectral veins. The name refers to the transparent, sometimes invisible nature of the veins.

Transitions.—Tubular veins often become nebulous distally or occasionally, if hyaline, they may become spectral. The change is usually abrupt, and the end of the tubular vein often appears sealed by a rounded dark line. Nebulous veins pass gradually into spectral veins, the area of change varying between individuals. The transition is almost never abrupt.

Trace veins.—This term refers indefinitely to what I have called Nebulous and



Figs. 4–10. Samples of wings showing seldom illustrated features, especially spectral veins and flexion lines. 4, Fore wing *Rhopalosoma nearcticum*. 5, Fore wing *Hylaeus ellipticus*. 6, Hind wing *Evania* sp. 7, *Eurytoma* sp. 8, *Deinodryinus atriventris*. 9, *Trimorus* sp. 10, Hind wing *Megaspilus* sp. CuP = postulated distal part of cubitus posterior, a concave vein. J = jugal lobe delimited by a convex folding line. Ad = adventitious vein.

Spectral veins but they are also called Reduced, Evanescent, Atrophied, Relict or Spurious veins. These terms, and others, have been loosely, and often interchangeably used to denote veins that are in the stages of reduction covered by my terms *nebulous* and *spectral*. The term "spurious" is misleading, since it means false, whereas the veins so named are sometimes true though weak veins homologous with normal venation and sometimes not so. The other terms have been so loosely used that they are virtually synonyms. I think it better to use completely new and unambiguously defined terms. The chief trouble with older terms (beside their vagueness) is that it is seldom possible to know whether spectral veins are included, since many illustrators work from wings mounted on slides where the mounting medium and transmitted light most often render the spectral veins invisible. It is also a common practice for taxonomists to treat strongly colored nebulous veins in the same way as tubular veins while calling weakly pigmented veins by some other term which may, or may not, include spectral veins. The worse practice is to call spectral veins "absent" as part of a 2-term morphocline in which the other term is "present."

Other Vein-Like Wing Features

Adventitious veins.—These markings appear like nebulous or even tubular veins but occur in places where they cannot be homologized with the normal venation. The name "spurious vein" is sometimes applied but is also used loosely for true spectral veins. Perhaps the best known example is the vertical curved vein anterior to the claval notch in the fore wing of *Helorus*. There is also a frequently seen adventitious vein between M+Cu and 1A in the fore wing of many *Macrocentrus* species. Another example, so far as I know not previously noted, occurs in many Aculeata in the families Dryinidae (Fig. 8Ad), Chrysididae, and Bethylidae. In these the fore wing bears an adventitious vein between Cu-a and Cu1 but on the opposite side (anterior) of the claval flexion line from 1A. In the first two of these examples the sclerotization is neutral in its dorso-ventral orientation in the membrane but the adventitious vein in Chrysidoidea is convex.

Writers should not call a vein "adventitious" merely because they believe it to be a secondary regeneration of a normal vein (e.g. the vein RS2 in Mutillidae). The apparent homology with a regular vein is clear, even though the phylogenetic history may not be understood.

Flexion lines.—These furrows are defined and discussed by Wootton (1979). They are linear zones of flexibility that seem to govern the changes in airfoil shape during flight. In the Hymenoptera they are, for practical purposes, all concave above, resembling the unpigmented spectral veins but with opposite profile and different function. In wings with dark membranes, however, all the venation, including the spectral veins, is dark but the flexion lines are often much paler, even hyaline. In Hymenoptera with well-developed venations a flexion line immediately anterior to the first anal is a constant feature (here called the claval flexion line [Wootton, 1979]) and it serves as a useful landmark in reduced venations. There are other flexion lines near or between the media and radial sector veins. These are not constant in form or position and are often forked apically. They are generally called medial flexion lines and give well-developed venations of many Hymenoptera a secondary system of flutings apically (Figs. 4, 5).

Bullae.—Where flexion lines cross veins there are short sections of clear, flexible chitin unlike the rest of the veins (Fig. 2B). These areas have received the names Bulla, Fenestra or Thyridial Area but the first name seems most used nowadays. Bullae have been often used as taxonomic characters and their presence or absence should be accurately noted.

Conventions for Wing Drawings

To achieve accurate delineation of wing features some standard conventions are needed but standardization in Hymenoptera wing figures is lacking, not only between different authors but even within a single paper. There is a concordance in using continuous double or single lines for tubular veins and one or more kinds of broken lines or stippling for trace veins, sometimes also for flexion lines. The latter are frequently not represented at all and even if indicated there is seldom more than the claval flexion line drawn. About half the time the same symbol is used for both flexion lines and trace veins, a practice that can lead to serious confusion (Fig. 6). Lastly, wing margins are usually drawn as a single continuous line, a convention that can at times make it impossible to interpret the presence or length of the costal vein, a character of considerable taxonomic use.

A drawing of a wing should have the following features:

1. Parts of the margin with and without a marginal vein should be distinguishable (Figs. 2, 7, 9, 10).

2. Three stages of vein reduction, tubular, nebulous and spectral, should be represented by different symbols that also depict obviously, the differing degrees of visibility. I think it important to distinguish nebulous from spectral veins because different lighting techniques are required to see them. On the veins bullae should be indicated.

3. Flexion lines should be represented by a symbol different from those used for veins.

4. An option should be, when needed, special symbols for such occasionally important features as the convex jugal fold (Fig. 6), concave veins (Figs. 4, 5) and adventitious veins (Fig. 8).

The above requirements come closest to being met by the scheme adopted by Richards (1956) whose conventions sometimes fail to distinguish nebulous from spectral veins. The conventions used by Evans (1978) are almost as good but the symbolization is not consistent within the paper. Neither Richards nor Evans explain their symbols for veins and flexion lines and both have inconsistencies among their figures. Quite recently Day (1984) introduced a new system for naming wing features but did not explain the symbolization in his figures. I find his definitions of various stages of vein reduction too indefinite to adopt for practical use and in addition, he groups both nebular and spectral veins under the term "relict." The latter grouping is defensible but I prefer to keep the two distinct for reasons discussed above. Other works on Hymenoptera have many imperfections in symbolizations and most authors appear not to have given serious consideration to accurate depiction of all wing features or, even less desirable, to have left it entirely in the hands of an artist.

The system I propose is closest to that of Richards (1956) but has some improvements. Tubular veins are indicated by continuous lines: nebular veins by dashed lines: spectral veins by dotted lines. All the vein symbols may be used singly or doubly depending on the size of the figure and width of the vein; furthermore the tubular and nebulous vein symbols may, if doubled, be filled by stippling to indicate degree of pigmentation should it be desirable (Fig. 2). Concave flexion lines are represented by tandem paired dots, i.e. a dotted line with every 3rd dot missing or an alternating pattern of 2 dots present, 2 missing. For the convex jugal fold I suggest a line of alternating dots and dashes (Fig. 6). Wing edges, which should not be confused with spectral veins, can be represented by a dotted line if veinless, solid or dashed line if occupied by a tubular or a nebulous vein. If confusion between spectral veins and wing margins is feared, then smaller and more closely spaced dots could be used for veinless margins or hairs could be added. Special, but different symbols should be used for seldom seen features such as adventitious veins (Fig. 8) or concave veins (Figs. 4, 5).

Conclusions

Careful observation and careful description of trace venation and flexion lines will result in keys that are much easier to use accurately. In phylogenetic studies, trace venation can help settle questions of relationships. More important, perhaps, taxonomic characters can be found also in the course of flexion lines. It should be recalled that bullae, which are traditional taxonomic characters, mark where flexion lines cross veins so their presence is correlated and can be helpful in tracing weak flexion lines. Finally one should remember that concavity or convexity of veins and flexion lines is reversed when they are observed from the underside of the wing.

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