

THE INSECT WING, PART III. VENATION
OF THE ORDERS¹

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ABSTRACT

The venational nomenclature derived in the previous two parts of this paper is applied to 24 orders of insects and compared to existing terminologies. Important works on the homologies and comparative morphology of the wing parts are listed and briefly discussed. Theories concerning the origins of the ephemeropteran anal brace, odonate triangle, orthopteroid anal fan, homopteran claval suture, and the so-called jugal veins are advanced.

This third of a series of four papers on the wings of insects is a brief summary of some of the major works on the venation of the various orders and an application of recommended changes in venational terminology. Certain peculiar venational problems are also discussed.

The original wing venation of insects that I have proposed (Hamilton, 1972) is illustrated in Figure 1, and its probable tracheation in Figure 25. One should not be surprised that neither this venation nor tracheation is directly evident in any recent order of insects. All these orders are highly specialized. Several have left good fossil records of the evolution of their venation; this information will be included in the analysis of the venation of the recent forms.

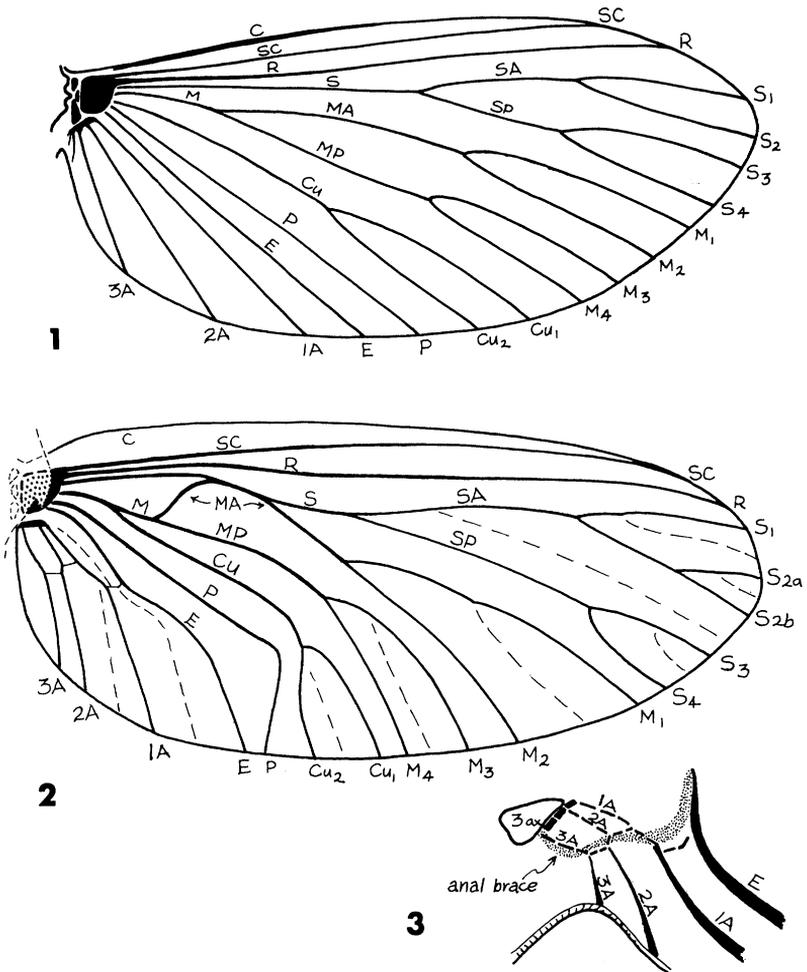
PALEOPTEROUS VENATION

Ephemeropteroid orders. The very ancient lineage represented today only by the Ephemeroptera has proven a major problem in venational studies. Comstock and Needham (1898-1899) found that tracheation data could not be applied to the Ephemeroptera with confidence, as the tracheae are strongly amalgamated basally (Fig. 26). Tillyard (1923 et al.) studied the wing fluting, and derived the most widely accepted venational homologizations for this order.

The most primitive of the ephemeropteroid orders is the Syntonopterodea (Fig. 2). Its venation is basically similar to the hypothetical ancestral venation (Fig. 1). Its three distinctive features, the extra branch of S_2 , the basal fusion of M to Cu, and the arching of MA against S, are all features peculiar to the ephemeropteroid lineage (Edmunds

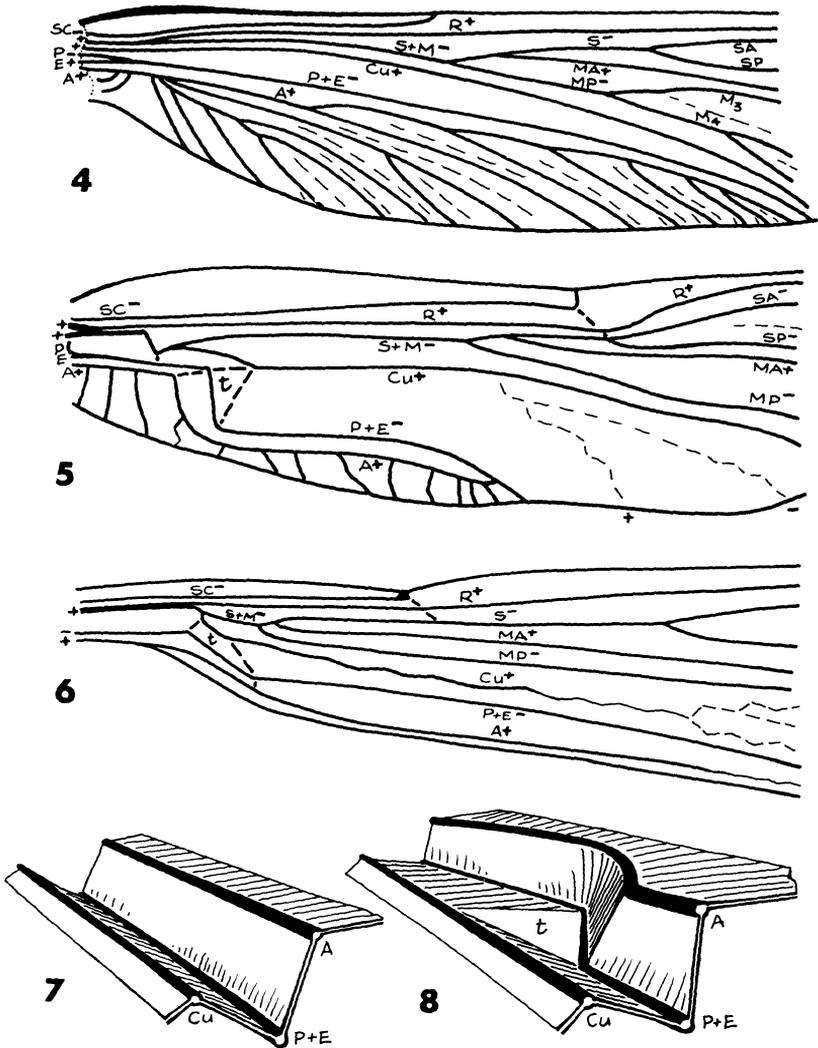
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FIGS. 1-3. 1, Hypothetical ancestral venation; 2, wing of *Lithoneura* (Syn-tonopteroidea) (redrawn from Ross, 1965); 3, hypothetical origin of the mayfly anal brace (stippled) from the syntonopteroid venation.

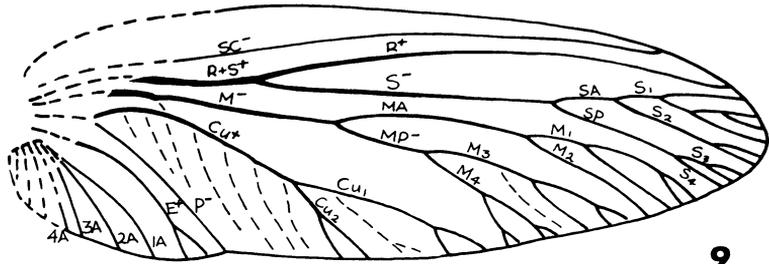
and Traver, 1954). The next step in the evolution of the Ephemeroptera is illustrated by the Protephemeroidea, which gained costal and anal vein braces. The former is simply an enlarged crossvein pair; the latter is the product of the fused crossveins of the anal vein system (Fig. 3) which replaces the original vein bases. This order differs from the Ephemeroptera in having a wide wing base, fully developed hind wings, and MA still connected to MP.



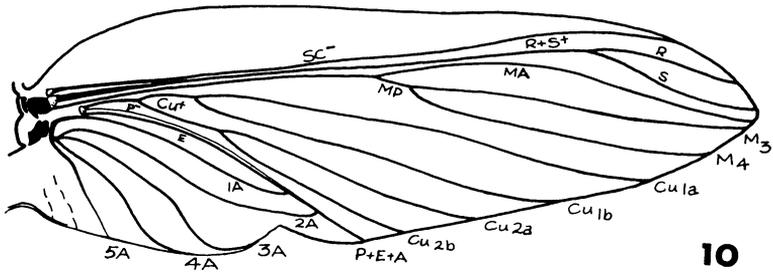
FIGS. 4-8. 4, *Triadotypus* (Protodonata) wing (redrawn from Laurentiaux); 5, wing of *Macromia* (Anisoptera); 6, wing of *Lestes* (Zygoptera); 7, model of protodonate wing fluting at plical furrow, basal aspect; 8, same, of odonate wing.

In all these orders, E ("1A" of authors) is basally divergent from the anal veins. It arises from the basal plate, separate from the true anal veins, in the Syntonopteroidea (Fig. 2).

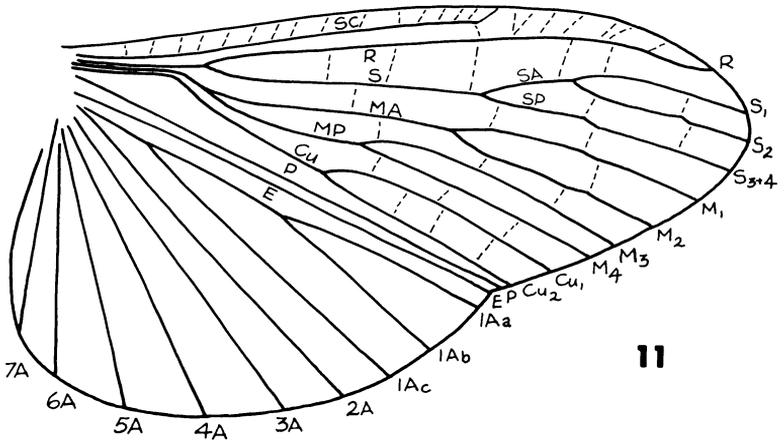
Odonatoid orders. Comstock and Needham identified the first three



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FIG. 9-11. Forewing of *Liomopterum* (Protorthoptera) (redrawn from Brues, Melander and Carpenter); 10, same, hind wing; 11, forewing of *Stagmomantis* (Dictyoptera).

veins of Odonata as SC, R, and M, stating that "Rs" crosses M apically (Fig. 27, Ri). Martynov (1930) and Fraser (1938) attempted to apply the fluting data to determine the vein homologies without regard to the evidence of tracheation. Forbes (1943) derived an homologization of

the venation that agrees with tracheation, fluting, basal attachment, and fossil evidence equally. Needham (1951) restated his tracheation studies in an effort to refute this venation terminology, pointing out that the crossing of the tracheae remains to be otherwise explained.

Comparative studies of the venation within the order have been conducted by Munz (1919) and Needham and Broughton (1927).

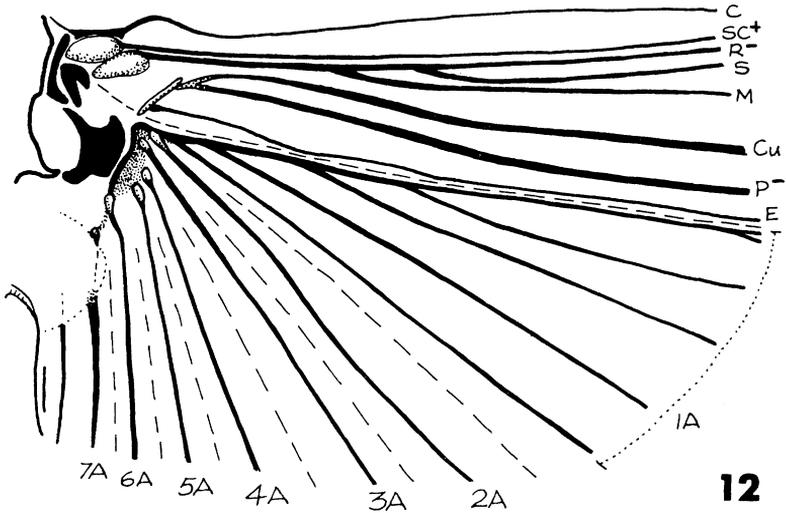
Most workers agree that the Protodonata (or Meganisoptera) is either the immediate ancestor of the Odonata or very close to such an ancestor. Its venation (Fig. 4) lacks the subnodus (R_s of Needham). The tracheation of this structure, therefore, has no significance in the ancestry of the wing venation, being merely an adventitious branch of the radius trachea that serves the subnodus and one of the intercalary veins.

The triangle (t , Figs. 5, 6) is a feature confined to the recent Odonata, although it is lacking in the Agrionidae. Its form is rather irregular in the other Zygoptera; it has thus been confused with the quadrilateral, which is not involved in the fluting. Fraser (1942) expressed the opinion that this triangle represents an aligning of cross-veins. I consider it an extension of the basal fluting of the odonate wing, a product of the curving of the main veins in the anal region. P lies in the plical furrow in both Odonata and Protodonata (Fig. 7). This vein is straight in the latter, but is angled backward and then curves outward in the Odonata. This results in a difference of slope of the membrane between P and Cu near the base, and of that further distad (Fig. 8). This causes two folds to develop at an acute angle to each other, a process which can be demonstrated easily by folding a paper model in the same way. Sclerotization along these lines of bending, for strength, would result in the formation of the triangle. This theory explains the function of the triangle, which Fraser's theory does not. Woodworth (1906) proposed a similar theory, but based it on the highly modified venation of *Archilestes*, without explanation of the origin of the venation of this insect.

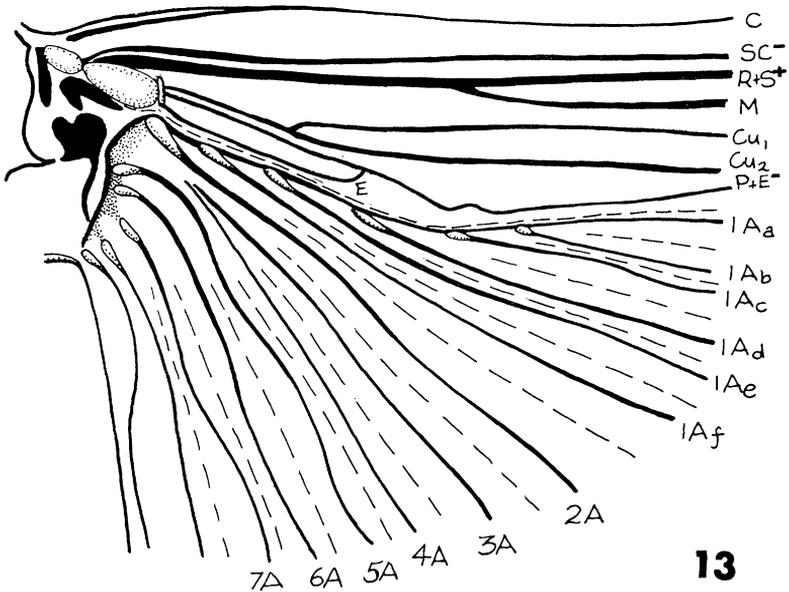
Tracheation shows two branches of P (Fig. 27), suggesting that E has fused with this vein. Further evidence for this conclusion is found in the Protodonata (Fig. 4), in which P and E are separate at the base, and distinctly fluted. These vein bases are also separate in recent Odonata (Hamilton, 1971, Fig. 15), but are more firmly united and have lost their fluting at that point.

NEOPTEROUS VENATION

Orthopteroid orders (Pliconeoptera). The work of Comstock and Needham on the orthopteroid orders was challenged in 1932 by Forbes, who designated three vein systems between "Cu" and "1A" as plical veins, in spite of their separate origins, separate tracheation, and differing basal attachments. Snodgrass (1935) termed these same veins "Cu₂, PCu, 1A," and (1952) "PCu, PCu, 1A." Ragge (1955a) desig-

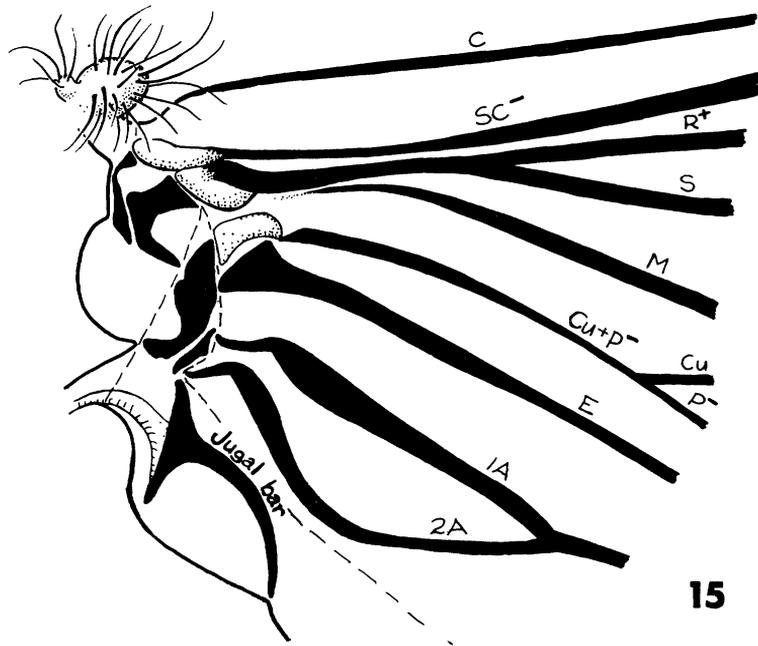
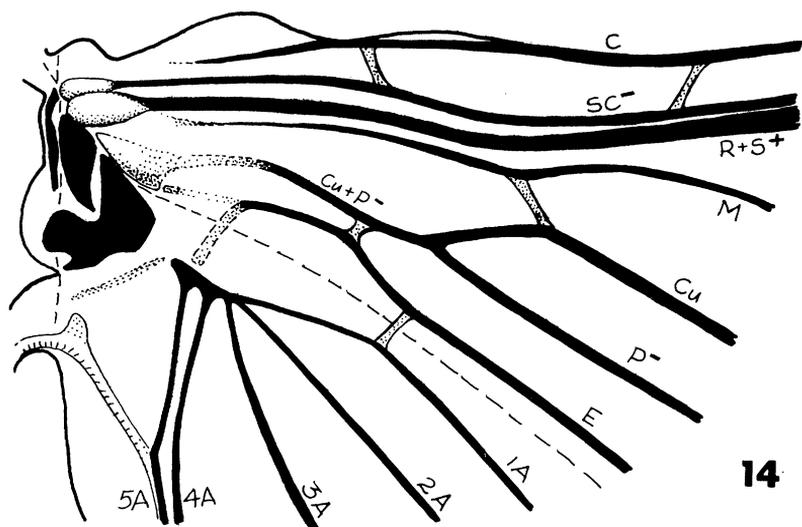


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FIGS. 12-13. 12, Base of hind wing of *Stagnomantis* (Dictyoptera); 13, same, of unidentified Phasmatodea. Dashes represent wing folds.



FIGS. 14-15. 14, Base of hind wing of *Acroneuria* (Plecoptera); 15, same, of *Rhyacophila* (Trichoptera).

nated them "Cu₂, 1A, 2A." These veins correspond exactly to P, E and 1A of other insects in all features.

Comparative studies of the wings of the Blattodea, Gryllidae, and Phasmatodea have been made by Rehn (1951), Chopard (1935), and Rague (1955b), respectively. The Orthoptera *sensu stricto* were treated in detail by Rague (1955a).

The coachroach wing has been used for establishing venational homologies (Snodgrass, 1935, 1952). I consider it to be a highly specialized form within the Dictyoptera. Fossil data show that it can be traced back to a venational pattern similar to that of the mantid (Fig. 11), which resembles that of true Orthoptera more closely. The "vannal dividens" is found only in this order. It is a weakly sclerotized band along the vannal fold, and is not tracheated. It is therefore considered not to be a true vein.

The venation of the primitive family Mastotermitidae of the Isoptera is similar to that of the Dictyoptera, differing chiefly in the great reduction of the vannal field, and the corresponding enlargement of the cubitus fan. The loss of the vannal field in the wings of other termites leaves three main veins apparent: S, M, and Cu.

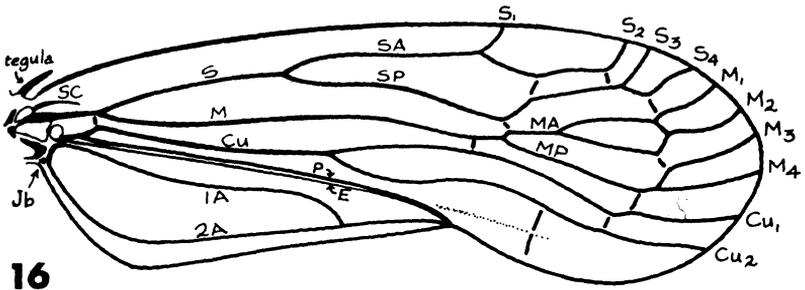
The venation of Phasmatodea (Fig. 13) is peculiar in lacking sector. Rague (1955b) incorrectly designated the two branches of Cu as "MA" and "MP" because he did not recognize this fact. Comparison with other orthopteroids shows that M is always fused basally with R + S on the hind wing, and S is not differentiated before the apical third of the wing, and is often weakly developed when the remigium is narrow. The vein arising near the base of R + S, then, must be M. The attachment of cubitus and the strong concavity of the next vein system (P) all support my interpretation.

The Dermaptera have only the vannus well developed, with numerous anal veins arising from a flexible band that runs across the wing below the remigium.

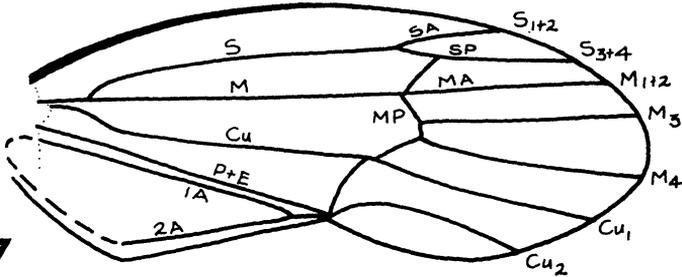
Plecopteroid orders. The Plecoptera appear to stand alone on venational evidence. The studies of Comstock and Needham are in agreement with the bulk of available data, but differ from the proposed system in designating P and E as "Cu₂" and "1A." The strongly concave nature of the plical vein is distinctive. The empusal vein appears on first sight to be indeed an anal vein, as it attaches to the anal vein base (Fig. 14). Its position above the vannal fold and its separate tracheal trunk (Fig. 28) show its true nature. The connection to the anal veins is probably achieved by a crossvein.

Forbes' (1932) venational homologies are unacceptable for the same reasons that are discussed under the Orthoptera.

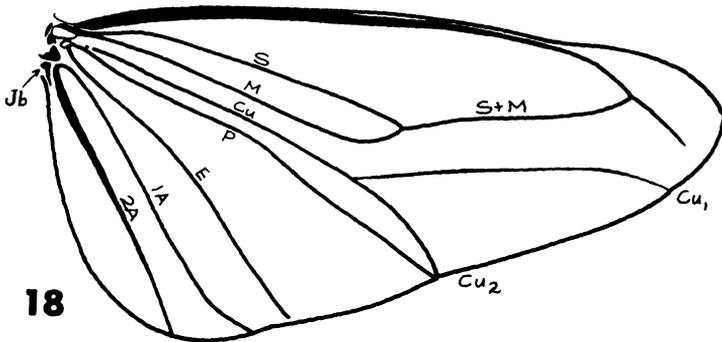
The anal vein fan of the Plecoptera (Fig. 14) is quite different from that of the Pliconeoptera (Fig. 12). There are only four or five anal veins, although these may branch several times. The hind wing folds along the vannal fold, with the large vannus rolled beneath the remigium rather than folded along distinct ridges.



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FIGS. 16-18. 16, Forewing of *Eiptera* (Homoptera); 17, forewing of *Heteroscytina* (Hemiptera) (from Evans, 1956); 18, hind wing of *Lethocerus* (Hemiptera).

Hemipteroid orders. The venation of most hemipteroid orders is very reduced or obscure. Homoptera are an exception to this general rule, and so will receive the bulk of discussion.

Evans (1946, 1956) designates the first two branches of R + S as

R₁, purely on the slight convexity of the system. The tracheation of both the Cicadidae (Comstock and Needham) and the Cercopidae (Metcalf, 1917) show that R is atrophied, leaving only sector. This data agrees well with the observed branchings of the veins in most Homoptera (Fig. 16).

Subcosta is absent in most Homoptera, being represented in most forms by a short spur arising from the subcostal plate. The trachea, however, is often well developed, and takes an anomalous course through the wing (Fig. 29). This has caused considerable confusion in the studies of the Fulgoroidea cited below.

Comparative studies of the venation have been done on the Sternorrhyncha (Patch, 1909), Membracidae (Funkhouser, 1913), Cicadellidae (Metcalf, 1913a; Oman, 1949), Fulgoroidea (Metcalf, 1913b), Cercopidae (Metcalf, 1917), Reduvidae (Davis, 1961), and Peloridiidae (China, 1962).

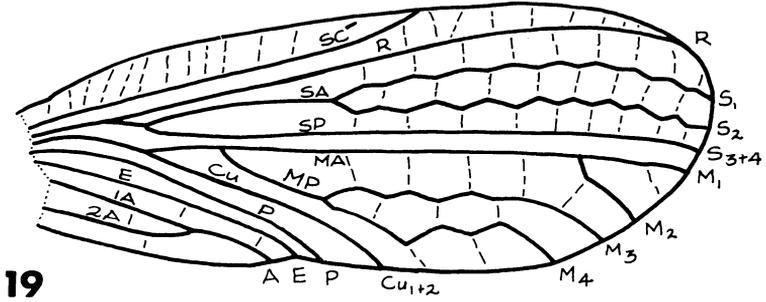
Several manifestly unsatisfactory systems have been proposed. That of Fennah (1944) for the Fulgoroidea attempted to associate the tracheae of one family, Flatidae, with the veins of another, Cixiidae. Those of Hoke (1926), Leston (1954), Slater and Hurlbutt (1957), and Davis and Usinger (1970) for the Hemiptera rely entirely upon the highly modified tracheae of the specialized forms with reduced venation.

Primitive Hemiptera (Figs. 17, 18) resemble Homoptera (Fig. 16) in venation, but have all the vein systems except Cu unbranched on the hind wing. This similarity of venation and the basal attachment of the veins are the only reliable evidence of the vein homology. Unlike the Homoptera, they retain one feature in its primitive form: the vannal fold of the hind wing lies between the empusal and anal vein systems, while it crosses 1A in Homoptera to lie between the anal veins.

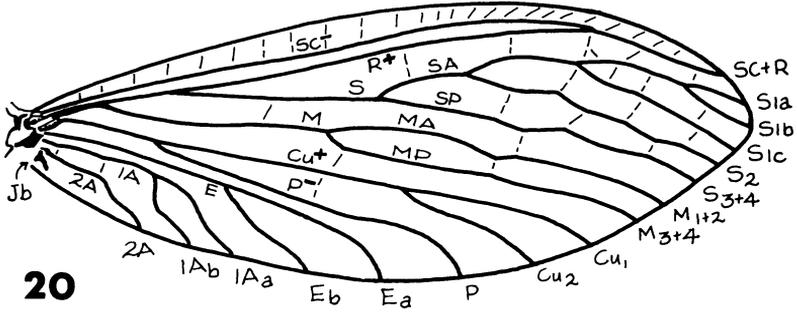
All the current works on the venation of Homoptera fail to explain one venational feature: the double vein, or "claval suture" of the tegmina. This is a close association of P and E, similar to that in the Dictyoptera (Fig. 10). The plical trachea (Fig. 29) is distinct from the empusal trachea (Fennah, 1944).

Neuropteroid orders. Betten (1934) pointed out that "1A" of Comstock and Needham in the order Trichoptera is actually homologous with "Cu₂" in hemimetabolous insects, a position later upheld by Martynova (1960) in the Lepidoptera. This is generally true of the neuropteroid orders as a whole, and also for the hemipteroid orders (Fig. 16) and for the Plecoptera (Fig. 14). In other respects, the venational homologies of Comstock and Needham have been accepted for most orders, with the exceptions of the Coleoptera and Hymenoptera. These have highly modified wings that these authors could not adequately treat.

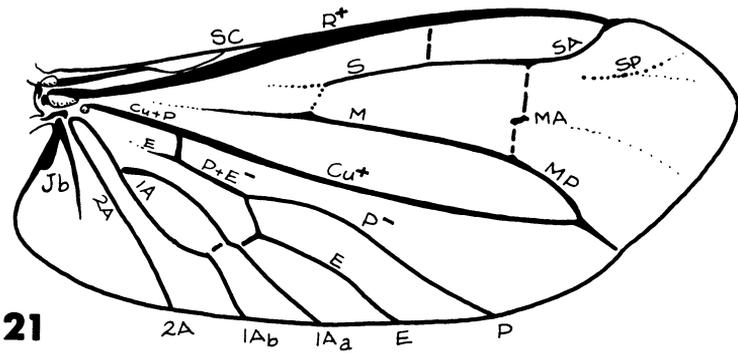
The hind wing of the Coleoptera has given rise to various interpretations in several early works. Those of Comstock and Needham, and of Graham (1922), have never gained acceptance. Forbes (1922) presented the most acceptable theory on the venation homology, which was



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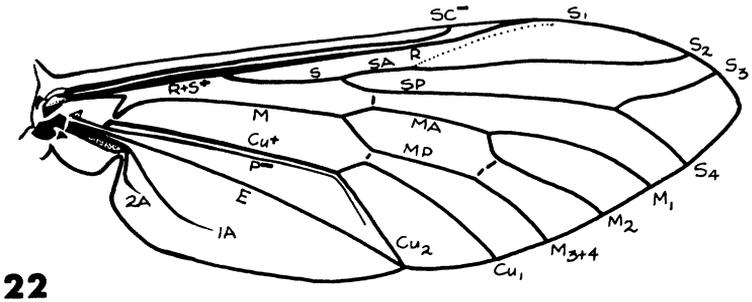


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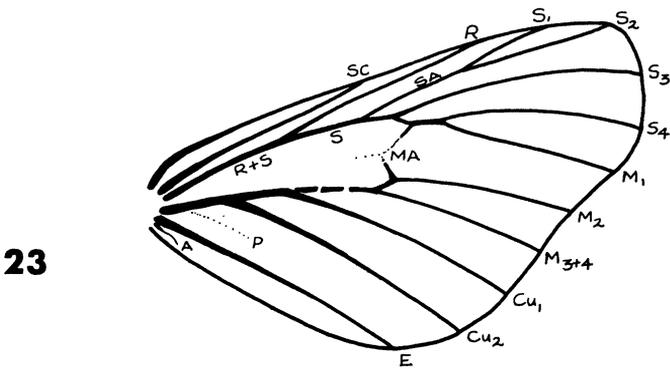


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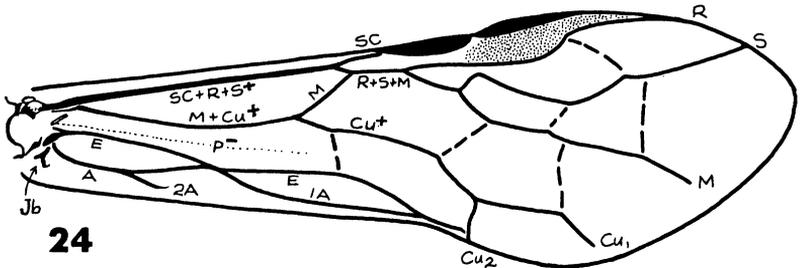
FIGS. 19-21. 19, Forewing of *Permoberoetha* (Glosselytrodea) (redrawn from Laurentiaux); 20, forewing of *Nigronia* (Megaloptera); 21, hind wing of *Hemicrepidius* (Coleoptera).



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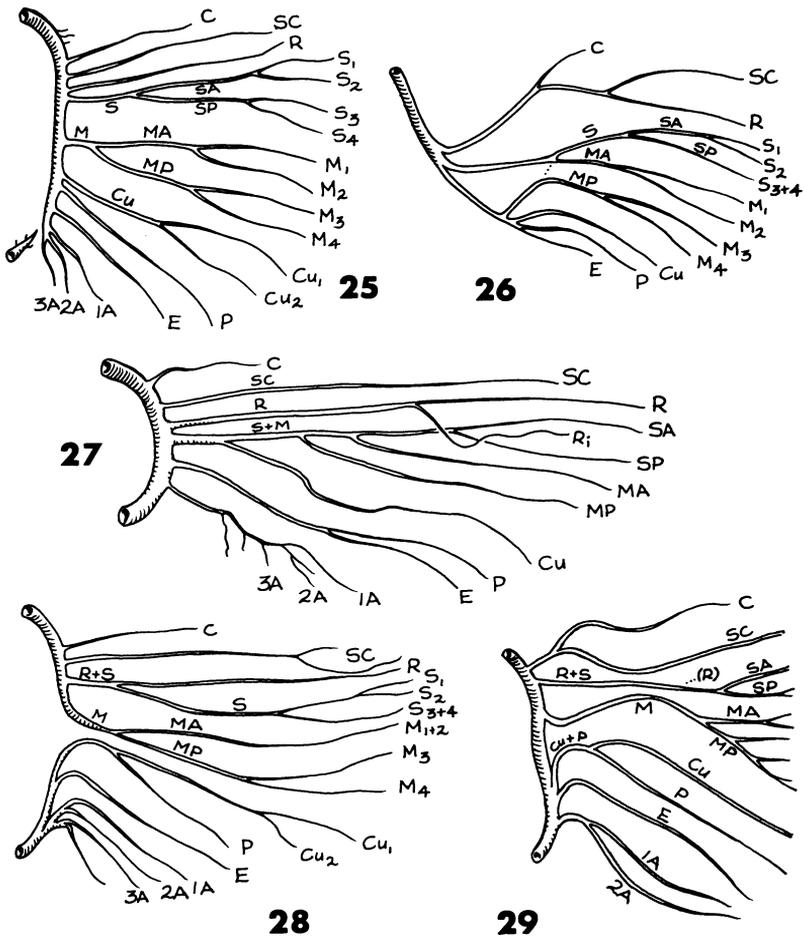


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FIGS. 22-24. 22, Forewing of *Tabanus* (Diptera); 23, forewing of *Malacosoma* (Lepidoptera); 24, forewing of *Macrophyta* (Hymenoptera).

slightly modified by Wilson (1934) in the identity of MA. The latter seems the most justified scheme.

Similar studies of venation have been made on the Buprestidae (Good, 1925), Cucujidae (Wilson, 1930), Chrysomelidae (Wilson, 1934), and Lymexylonidae (Selander, 1959). The only detailed comparative study known to the author is that of Saalas (1936) on the Cerambycidae.



FIGS. 25-29. Wing tracheae. 25, Hypothetical ancestor; 26, Ephemeroptera; 27, Odonata, Ri, intercalary branch of radius; 28, Plecoptera; 29, Homoptera (redrawn from Fennah). (Figs. 26-28, redrawn from Comstock and Needham.)

Like that of the Coleoptera, the modified venation of the Hymenoptera has proven difficult to explain. The works of Comstock and Needham, MacGillivray (1906), and Forbes (1925) that relied upon tracheation studies were never accepted. Ross (1936) showed conclusively that the evidence of the axillary sclerites and comparative venational studies contradicted the earlier interpretations, and his proposed system has been generally accepted.

Lanham (1951) made a comparative study of hymenopterous venation. Others have worked on sawflies (MacGillivray, 1906; Ross, 1937), Chalcidoidea (Burks, 1938), and Formicidae (Brown and Nutting, 1949). Comments on venational homology have been contributed by Gibbons (1935) and Caltagirone (1966). The work of Rohwer (1916) should be consulted for pre-Comstock terminology.

The order Trichoptera lacks wing tracheation. Betten (1934) was able by comparison with other orders to derive a venational homology that has been generally accepted. Venational works on Trichoptera since then have been numerous. Some major comparative studies are those of Betten, Mosely (1939), and Ross (1944, 1956).

Comparative studies on lepidopterous venation are legion. I mention only a few of the early papers on the more primitive groups: Hepialidae (MacGillivray, 1912), Micropterygidae (Braun, 1919), and Microlepidoptera (Braun, 1933). Sharplin (1963) studied the basal sclerites of the wings, but identified the cubital plate as a median plate.

Neuroptera and Diptera were treated well by Comstock and Needham, and need no further comment. Henning (1954) discussed the venation of recent and fossil Diptera in detail.

Relabeling the venation of these orders to designate correctly S, P, and E as in other orders (Figs. 20-24) is the only change recommended. It is to be noted that the anal veins are somewhat modified in the neuropteroid orders. The base of these veins is freely movable against them (Fig. 15). The empusal vein is extended below the cubital plate and also articulates against the third axillary. The "jugal veins" of authors is actually a single structure. It is an untracheated rod or T-shaped strut on the jugum, which I designate the "jugal bar." This strut is likely to be a specialized portion of the axillary cord.

SUMMARY

The following are the basic characters of the venation of the main wing types. Where the venation of a particular order may cause difficulties in interpretation, the order is also discussed. The proposed venational homologies (H) are compared with the Comstock-Needham terminology (C-N).

Ephemeropteroid orders. Syntonopteroidea, Protoephemeroidea, Ephemeroptera: paleopterous; wings of Ephemeroptera dissimilar in size, venation similar. Basal fusion of M and Cu; MA arched against S, with loss of original base in the Ephemeroptera. Three anal veins.

Main vein systems:

(H): C, SC, R, S, MA, MP, Cu, P, E, 1A, 2A, 3A

(C-N): C, SC, R₁, R_s, M, Cu, 1A, 2A, 3A, 4A, 5A, —

Odonatoid orders. Protoodonata, Odonata: paleopterous; wings usually similar, venation similar. Basal fusion of S and M, together fused basally to R and (in Odonata only) to Cu further out; P completely fused to E; anal veins probably four in number, arising pectinately, resembling crossveins in Odonata.

Main vein systems:

(H): C, SC, R, SA, SP, MA, MP, Cu, P+E, A

(C-N): C, SC, R₁, M₁, M₂, R_s, M₃, M₄, Cu₁, Cu₂

Orthopteroid orders. Dictyoptera, Isoptera, Phasmatodea, Orthoptera, Protelytroptera, Protoperlaria, Dermaptera: pliconeopterous; wings dissimilar to extremely different, venation dissimilar. Basal fusion of R and S on both wings, of M and S on hind wings. Forewings with 5 (Dictyoptera) or 3 anal veins (all others); hind wings generally with 7 tracheated and 2 untracheated anal veins, the first highly rebranching, arising pectinately.

Main vein systems:

(H): C, SC, R, S, M, Cu, P, E, 1-7A

(C-N): C, SC, R₁, R_s, M, Cu₁, Cu₂, 1A, 2-8A?

Plecopteroid orders. Plecoptera: planoneopterous; wings dissimilar, venation similar except for anal veins. Basal fusion of R and S, and of Cu and P. Forewings with two anal veins, hind wings with 4 or 5 anal veins, several often rebranching.

Main vein systems as in orthopteroids.

Hemipteroid orders. Psocoptera, Hemiptera, Homoptera: plano-neopterous; wings similar to dissimilar, venation similar. Basal fusion of R and S, of M to either S or Cu, and of Cu and P; often other fusions when venation very reduced. Clavus differentiated on forewings. Two anal veins; jugal bar present.

Main vein systems:

(H): C, SC, R, S, M, Cu, P, E, 1A, 2A, jugal bar

(C-N): C, SC, R₁, R_s, M, Cu₁, Cu₂, —, 1A, 2A, — (forewings)C, SC, R₁, R_s, M, Cu₁, Cu₂, 1A, 2A, 3A, — (hind wings)

Neuropteroid orders. Hymenoptera, Neuroptera, Megaloptera, Coleoptera, Trichoptera, Lepidoptera, Diptera, Mecoptera: planoneopterous, wings similar to extremely dissimilar, both folding on jugal fold; venation similar. Basal fusion of R and S, and of Cu and P. Two anal veins; jugal bar present.

Main vein systems:

(H): C, SC, R, S, M, Cu, P, E, 1A, 2A, jugal bar

(C-N): C, SC, R₁, R_s, M, Cu₁, Cu₂, 1A, 2A, 3A, 4-5A

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HISTOLOGY AND MORPHOLOGY OF THE ABDOMINAL SCENT APPARATUS IN THREE ALYDIDS¹

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ABSTRACT

The histology of the abdominal scent gland-reservoirs in nymphs of 3 alydids: *Alydus eurinus* (Say), *Alydus pilosulus* (Herrich-Schaeffer), and *Megalotomus quinquespinosus* (Say) is described. The abdominal scent gland-reservoir, abdominal cuticle, odor of the scent fluid, scent emission, and associated behavior are similar for the 3 alydids studied. Protective adaptations of the 3 alydids against their own scent secretions are discussed including histology of the gland-reservoir, modifications of abdominal cuticle, and behavior.

This study examines the histology of the abdominal scent apparatus in nymphs of 3 alydid species: *Alydus eurinus* (Say), *Alydus pilosulus* (Herrich-Schaeffer), and *Megalotomus quinquespinosus* (Say). Other observations on the abdominal scent apparatus and its function, including the nature of the abdominal cuticle and behavior associated with scent emission, were made. The scent apparatus adaptations facilitate the dissemination of scent while protecting the insect from toxic substances in the secretion.

METHODS AND MATERIALS

Adults and nymphs of each alydid species were field-collected and reared in laboratory growth chambers on soybean seeds (Yonke and

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