

8'	Aedeagal subapical processes less than two thirds length of shaft	9
9 (8')	Aedeagal subapical processes arising near apex	10
9'	Aedeagal subapical processes arising at least one fifth length of shaft from apex	11
10 (9)	Aedeagal subapical processes short, one fourth length of shaft	<i>rogenhoferi</i> (Spang) (Figs. 41-45, 54, 58)
10'	Aedeagal subapical processes longer, one half length of shaft	<i>acrita</i> n.sp. (Figs. 45-49, 57, 71)
11 (9')	Pygofer spine broad, in lateral view	12
11'	Pygofer spine narrow, in lateral view	<i>basalis</i> (Osborn) (Figs. 50-53, 55, 56)
12 (11)	Aedeagal shaft broad at base in ventral view, tapered to narrow apical portion	<i>nota</i> DeLong & Freytag (Figs. 50-63, 70)
12'	Aedeagal shaft narrower at base, in ventral view, apical portion only slightly narrower than basal portion	<i>robusta</i> (Osborn) (Figs. 64-69)

THE INSECT WING, PART IV. VENATIONAL TRENDS AND THE PHYLOGENY OF THE WINGED ORDERS¹

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ABSTRACT

Evolutionary trends of dissimilarity between wing pairs in shape and venation, of fusion of vein systems, of number of anal veins, and of crossvein types are traced. It is concluded that the following are primitive characters: similar wings, the hind wing with a larger anal lobe; all vein systems separate to the base; 7 anal veins, unbranched; crossveins forming an archdictyon. Three other types of primary crossveins, representing successive grades of evolutionary advancement, are discussed: polyneurous, costaneurous, and oligoneurous. These are contrasted with secondary venational types. A phylogeny of recent orders is constructed and compared to other data recorded previously in parts I, II, and III of this series. Fossil orders are fitted to this phylogenetic scheme. This necessitates redefinition of the orders Hadenomoida, Protomecoptera, Protembiaria, and fossil Psocoptera.

The first part of this series of four papers dealt with the origin of wings, and touched on the phylogeny of the Insecta as exhibited by the wing types, nature of the basal sclerites, and methods of wing

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folding (Hamilton, 1971). This showed that the Ephemeroptera are the most archaic lineage of winged insects, and that the Neoptera are derived from a paleopterous ancestor closer to the ancestor of the Odonata. The Neoptera evolved in two monophyletic lines, the Pliconeoptera (with wings folded in a fan along the numerous anal veins) and the Planoneoptera (with wings folded flat, and few anal veins), from the extinct order Protorthoptera. The neuropteroid orders were shown to be definable by the folding of the hind wing along the jugal rather than the vannal fold.

This final contribution analyzes venational data as they apply to the phylogeny of the insect orders. Such a study is made possible by the second part of this series (Hamilton, 1972a), in which the venation of the orders was homologized, and the archetypal venation deduced. The third part (Hamilton, 1972b) grouped similar venational types among the orders into six main series: ephemeropteroid, odonatoid, orthopteroid, plecopteroid, hemipteroid and neuropteroid. These are considered to be monophyletic lineages each with specializations peculiar to themselves. The last two probably arose from a common ancestor, as they both possess a peculiar venational feature, the "jugal bar."

Venational trends

Serial identity of vein systems between the wing pairs seems the general rule in primitive insects. A greater degree of venational dissimilarity of the wings is evident in the more specialized forms. These changes are usually accompanied by increasing differences in wing shape and size. High degrees of wing disparity may be observed in Orthoptera, Dermaptera, Diptera, Coleoptera, and Hymenoptera; these orders are among the most highly specialized of the winged insects.

The insect wing apparently has greater venational stability basally than toward the apex. This is best shown by a comparison of the highly diverse venations found in the Fulgoroidea. Since the apical half of the wing passes through the greatest arc in flight motions, it bears most of the force of the stroke, is most instrumental in modifying the flight pattern, and hence is under the greatest selection pressure for divergent types of both venation and shape. For this reason, only the basal portion of the main veins will be discussed in this phylogenetic analysis of the orders.

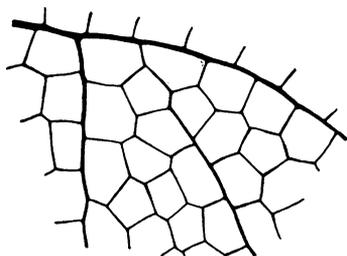
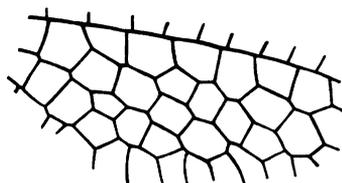
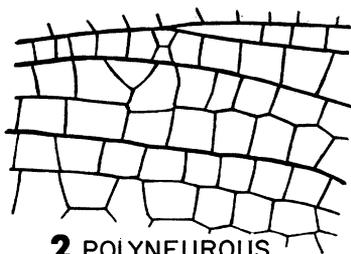
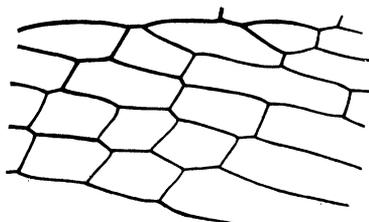
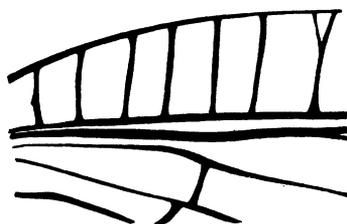
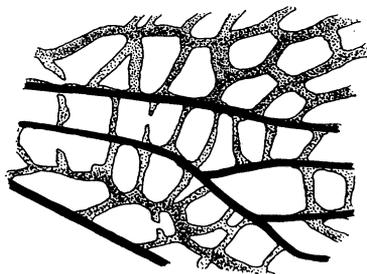
The basal fusion of vein systems gives much phylogenetic data. Radius and sector are fused (Fig. 11, R+S) in all wings except those of the most primitive orders belonging to the ephemeropteroid series. Media is fused to R+S in hemipteroid orders (Fig. 25, R+S+M), although the original connection may be lost, leaving M secondarily attached only to Cu by the crossvein m-cu. This same fusion of M to R+S is also found in the Pliconeoptera, but only on the hind wing; some Orthoptera have M of the fore wing incompletely fused to R+S, traceable to the wing base. In Odonata S and M are intimately

fused, with SA, SP, MA and MP arising pectinately. S+M is basally fused to R in these insects, but further out these separate, S+M becoming fused to Cu (Hamilton, 1971, Fig. 15). Cu is fused to M only in ephemeropteroid orders (Fig. 14, M+Cu). Cubitus is fused to the plical vein in all Planoneoptera (Fig. 34, Cu+P). The empusal vein is completely fused to the plical vein in Odonata, and is only observable by its tracheation (Hamilton, 1972b, Fig. 27). The "claval suture" of hemipteroid insects is the product of incomplete fusion of these two veins (Fig. 25, P+E); recent Psocoptera and Sternorrhyncha have P+E completely fused. E is fused to 1A by the anal brace in Ephemeroptera. The anal veins of Plecoptera arise pectinately at the wing base; those of Odonata and Dermaptera are broadly pectinate across the wing.

The number of anal veins varies from 0 to 16. The usual variation seems to be attributable to loss of veins with reduction in size of the vannal field, as in Psocoptera. Addition of anal veins is a less common phenomenon. Pliconeoptera generally have added 2 supernumerary veins without tracheae or bases after the true anal veins; there are 4 such "postanal veins" in the hind wings of crickets (Gryllidae). Branching of preexisting veins, as in the hind wings of Plecoptera, is the more usual situation. The large number of anal veins on the hind wing of Pliconeoptera is due to pectinate branching of 1A. The first 6 anal veins of most Dictyoptera do not arise from the wing base. They are unlike other anal veins, as they do not have enlarged bases (Hamilton, 1972b, Fig. 12) and do not articulate to aid in fan folding (Tillyard, 1937b, Fig. 7). They thus resemble supernumerary branches of a single vein. Together with a maximum number of 4 postanal veins (in crickets), there are thus as many as 9 extra "anal veins" in the Pliconeoptera. Since Gryllidae have 16 "anal veins," the basic number of pliconeopterous anal veins is 7. This conclusion agrees well with fossil evidence, which shows that many of the earliest paleopterous and neopterous insects had 7 anal veins on each wing.

The number of anal veins in Neoptera is rather variable from order to order. Pliconeoptera, as already noted, have basically 7 anal veins on the hind wing, but never have more than 5 on the fore wing (those of Blattodea branch repeatedly). Dictyoptera are considered the most primitive Pliconeoptera, as other orders have at most 3 anal veins on the fore wing, and articulating branches of 1A of the hind wing that permit the entire vannus to be plectated. Planoneoptera do not have more than 2 anal veins on the fore wing, and not more than 5 on the hind wing, although these may be branched. The condition of 5 anal veins on the hind wing is found only in the Plecoptera. Hemipteroid and neuropteroid orders have at most 2 anal veins on each wing.

Venation between the main veins is perhaps the most difficult aspect of wing structure to interpret phylogenetically. This venation

**1** ARCHEDICTYON**4** FALSE ARCHEDICTYON**2** POLYNEUROUS**5** FALSE POLYNEUROUS**3** COSTANEUROUS**6** TEGMEN

FIGS. 1-3. Primary venational types, as labeled. 1, Libellulidae; 2, Acrididae; 3, Corydalidae. FIGS. 4-6. Secondary venational types, as labeled. 4, Ascalaphidae; 5, Perlidae; 6, Aetalionidae.

is usually irregular, differing between even the lateral halves of the same individual. Supernumerary branches of main veins and intercalaries give data useful only among the most closely related genera. On the other hand, the system of crossveins shows long-term phylogenetic trends.

There are six basic types of crossvenation, distinguishable by their general appearance. The first type, the *archedictyon* (Fig. 1), consists of an irregular meshwork of generally pentagonal cells between

the much heavier veins and intercalaries. This is considered the ancestral condition, both for its lack of organization and its prevalence in wings and notal lobes of early fossil insects. The second type, the *polyneurous* condition (Fig. 2), has the main veins only slightly heavier than the crossveins; the latter are more widely spaced than the crossveins of the archedictyon, and are usually parallel. The cells are thus square or rectangular with their long axis perpendicular to the main veins. The third type, the *costaneurous* condition (Fig. 3), has a row of polyneurous crossveins between C and SC (also between M and P in Plecoptera); crossveins are almost wholly lacking from the rest of the wing. It is thus similar to most highly-evolved wings (*oligoneurous*) which almost entirely lack crossveins.

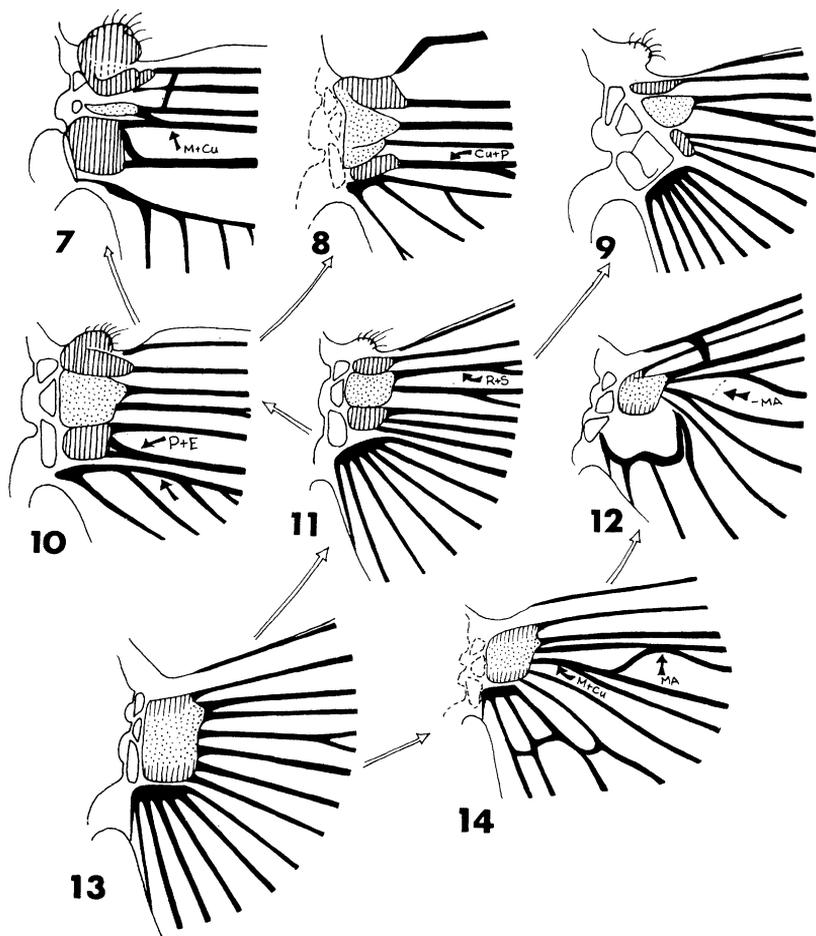
The remaining three types are not derived in any particular phylogenetic sequence. They may characterize only a part of the wing, being superimposed on the above types. The most familiar of these is the false polyneurous condition (Fig. 5), which can be readily distinguished from the polyneurous venation by the stronger crossveins, more irregularly sized cells, and the length of these cells being parallel to the main veins. Such venation is usually confined to the wing tip, or is better developed there. The false archedictyon (Fig. 4) also has the crossveins of similar size to many of the main veins; the cells are typically hexagonal, and lie in rows. Tegmina (Fig. 6) and the wings of Isoptera have the veins more prominent than the crossveins. The latter are highly irregular and often evanescent. Because these venational types may be derived from any other, and represent an increase in venational complexity, they are considered secondary to the general phylogenetic progression. Tertiary venation, the result of reduction of secondary types to resemble primary venation (as in Issidae) is so rare that it need not concern us here.

PHYLOGENY OF THE ORDERS

Comparative morphology of recent forms establishes the general outline of the phylogeny of the orders of winged insects. To attain a more detailed understanding of the evolutionary history of these orders, it is necessary to examine the fossil data as well.

The rare Hadentomoida as redefined here are generalized Planoneoptera with at most 2 anal veins on the fore wings, Cu basally fused to P, and a narrowed vannal field on the hind wings. This order includes several genera currently placed in the Protorthoptera.

Fossil Protomecoptera are costaneurous, unlike recent Mecoptera, which are all oligoneurous but may show false polyneurous venation. Their venation indicates that these fossils are distinct from recent "Protomecoptera," as does their body form (Laurentiaux, 1953, after Martynov). This conclusion was reached independently by Hinton (1958), who separated fossil "Mecoptera" from recent Mecoptera by analyzing panorpid larval types. The fossil Paramecoptera probably also belong in the Protomecoptera rather than in the Mecoptera.



FIGS. 7-14. Evolutionary sequence of paleopterous venation and basal sclerites. 7, Odonata; 8, Paleodictyoptera (after Kukulova, in Matsuda); 9, Neoptera; 10, 11, 13, hypothetical types; 12, Ephemeroptera; 14, Syntonopteroidea. R+S, etc., fusion of vein systems; -MA, loss of vein base.

Most fossil "Psocoptera" (Tillyard's Permopsocida) are distinctive in having M basally free, lacking any trace of a clavus, lacking an inflated clypeus, and having 5-segmented tarsi and segmented cerci (Tillyard, 1926). All these features are more primitive than those of any recent hemipteroid order. These insects seem to be closely allied to the Protombriaria of Tillyard (1937a). Carpenter (1950)

synonymized *Protombia* with the protoperlarid *Telactinopteryx*, and placed it in the Protorthoptera. Both these actions seem without sufficient justification in light of the features clearly visible in the photograph of *Protombia* accompanying the original description. I therefore retain the name *Protombiaria* for this order, including in it the Permopscoidea and Embiopsocida (Tillyard, 1928b) as well.

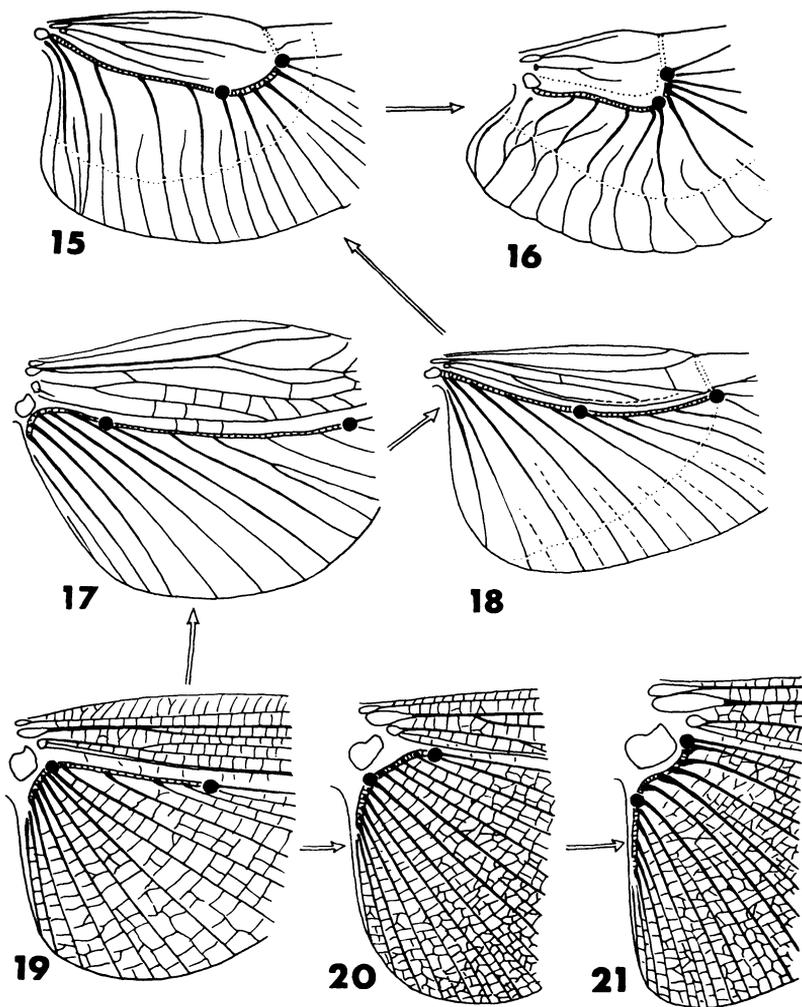
Paleoptera. The most archaic lineage of the winged insects is undoubtedly the ephemeropteroid series. Its retention of a free radius agrees well with the many other primitive features already cited. The Syntonopterodea possessed 3 specialized venational features (Hamilton, 1972b), a greatly reduced vannal area, and polyneurous wings. These facts indicate that the ephemeropteroid lineage was already highly specialized when it appeared in the Upper Carboniferous fossil record. Edmunds and Traver (1954) traced its subsequent evolution.

The Paleodictyoptera and Megasecoptera are two closely related orders in which Cu, P and E are basally fused into a common unit. Their pectinate anal system and dorsally attached wings ally them to the Odonata and Protodonata. The basal plates of the paleodictyopterid *Ostrava* (Fig. 8) show a similar configuration to those of the Odonata (Fig. 7), as pointed out by Matsuda (1970). *Triadotypus* retains a free cubital stem (a feature more primitive than that of other Protodonata, or of Odonata), but has cubitus unbranched, as in the Odonata. It thus seems likely that the Odonata evolved from some primitive Protodonata.

The Diaphanoptera (=Protohymenoptera in part; Paraneoptera in part) superficially resemble Megasecoptera but lack the basal fusion of Cu, P and E in the more primitive forms. They had the ability to fold their wings flat over their backs, in an attitude similar to that of the most primitive Neoptera. The exact folding mechanism is not known. Carpenter (1963) is of the opinion that the Diaphanoptera are related to the Paleodictyoptera, and that this folding mechanism was independently acquired from that of the true Neoptera.

The "Protohymenoptera" are Paleoptera belonging mostly to the order Megasecoptera. Their venation is only superficially similar to that of the Hymenoptera. "Protohemiptera" are Paleodictyoptera, and are not similar to Rhynchota (Hemiptera and Homoptera), differing most clearly in wing venation (Crampton, 1927). Their "beak" has long palps, and it not homologous with the beak of true bugs. Similar mouthparts are found in nymphs of Odonata, where the labium is very long, but fitted for seizing prey.

Protorthopteroid orders. Probably the most primitive known Neoptera are the Protoblattoidea (=Protoptera). These alone among the Neoptera possess both a true archedictyon and 7 anal veins on both wing pairs, in addition to having retained the most complete



FIGS. 15-21. Evolutionary sequence of pliconeopterous venation. 15, 20, hypothetical types; 16, Dermaptera; 17, *Apachelytron* (Protelytroptera), redrawn from Carpenter & Kukalova, with base of anal fan restored; 18, *Protelytron* (Protelytroptera), redrawn from Tillyard; 19, Phasmatodea; 21, Orthoptera. Dots represent bases of 1Aa and 2A.

fluting of any Neoptera (Hamilton, 1972b, Fig. 9). These are the only winged insects yet found from the Lower Carboniferous (Sharov, 1966). They are not closely related to roaches at all; this presumed similarity lies only in the great venational complexity of many of the fossils.

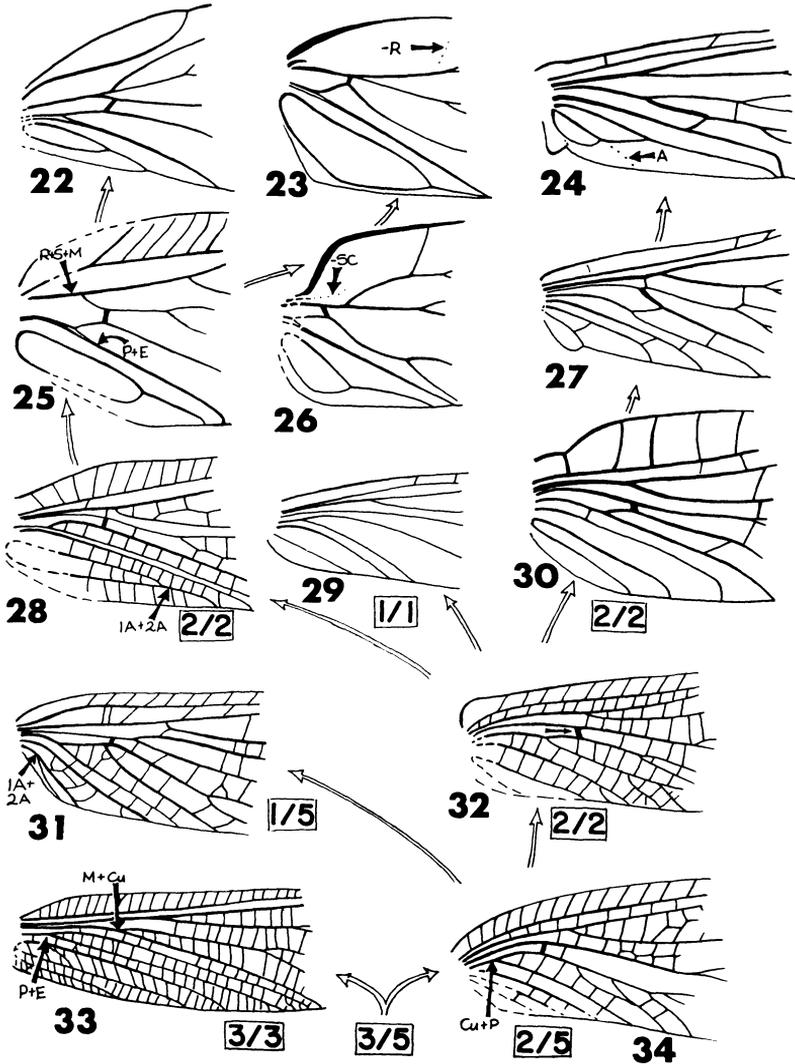
Protorthoptera (=Paraplecoptera) are polyneurous, like most Pliconeoptera, and the most primitive Planoneoptera. Since the major evolutionary changes leading to the two lineages occur on the hind wings (Hamilton, 1971), and most fossils retain only the fore wings, many of the Protorthoptera are difficult to place with accuracy. *Liomopterum* probably represents an early stage in the evolution of the Pliconeoptera. This insect possesses 5 anal veins on the fore wing, 7 anal veins and 3 branches of 1A on the hind wing (Hamilton, 1972b, Fig. 10), separate origin of media on both wings, and apparently folded its vannus flat, without plications.

The origins of the Planoneoptera can be traced to the protorthopterid *Spaniodera* and related genera that have the anal veins reduced to 3 on the fore wings and 5 on the hind wings. This particular genus shows a basal fusion of M and Cu. Caloneurodea (Fig. 33) are derived from this group, as they also have M+Cu; their wings are similar in shape, with only 3 anal veins on each, and both pairs show basal fusion of P and E.

Pliconeoptera. As demonstrated by the structure of the anal fan, the Dictyoptera are the most primitive pliconeopterous order. Isoptera are similar to Dictyoptera in possessing numerous supplementary branches of Cu (Hamilton, 1972b). Tillyard (1937c) illustrated the probable evolutionary sequence of the origin of this order from the Lower Permian blattoid *Pycnoblattina*.

Higher Pliconeoptera show the peculiar feature of migration of the anal veins (Figs. 15–21). Phasmatodea (Fig. 19) retain a primitive fan similar to that of the Dictyoptera in vein arrangement. Orthoptera (Fig. 21) have all the branches of 1A drawn basad, so that each arises close to the third axillary sclerite, as do the true anal veins. Dermaptera, on the other hand, have the flexible anal base crossing the entire wing (Fig. 16). Only its extreme end touches the third axillary. The Protelytroptera show intermediate conditions of the anal fan (Figs. 17, 18). This order also demonstrates that the dermapteran elytra evolved from polyneurous wings similar to those of the Phasmatodea. The relationship between these two orders is also shown by the short cubital stems of their hind wings. It is possible that the Cheleutoptera (=Aeroplanoptera), which are considered ancestral to the Phasmatodea (Laurentiaux, 1953), gave rise to the Protelytroptera as well.

“Protocoleoptera” are Protelytroptera (Carpenter and Kukalova, 1964). The possession of elytra is not good evidence for suggesting



FIGS 22-34. Evolutionary sequence of planoneopteran venation. 22, Pso-coptera; 23, *Scytinoptera* (Rhynchota); 24, Trichoptera; 25, undescribed fossil (X in Fig. 35); 26, *Coleoscyta* (Rhynchota); 27, *Belmontia* (Protomecoptera); 28, *Perrnoberothis* (Glosselytrodea); 29, *Dichentomum* (Protetnibiaria); 30, generalized Megaloptera; 31, *Artinska* (Protoperlaria); 32, *Haploptera* (Hadentomoida); 33, *Caloneura* (Caloneurodeia); 34, *Hadentomum* (Hadentomoida); fossils redrawn from various sources. 3/5, etc., probable number of anal veins on fore wing/ hind wing. Veins labeled as in Figs. 7-14.

that the Coleoptera evolved from this order. Coleoptera are planoneopterous, and fold their hind wings along the jugal fold, as do other endopterygote orders.

Planoneoptera. The Planoneoptera are descended from Haden-tomoida (Fig. 34) as previously defined. The earliest offshoot of this lineage, the Protoperlaria, retained 5 anal veins on the hind wing (5A may be small, as in *Lemmatophora*; Tillyard, 1928a, Fig. 10). These veins are arranged in the identical pectinate condition found in recent Plecoptera (Hamilton, 1972b, Fig. 14). There seems little doubt that the Protoperlaria gave rise to the Plecoptera.

Higher Hadentomoida probably had at most 2 anal veins on each wing, and gave rise to both the hemipteroid and neuropteroid lineages.

The hemipteroid lineage probably begins with the ancestors of the Glosselytrodea (Fig. 28). In these insects P and E lie close together, and 1A and 2A are apically fused to form a "Y vein"—the two features characteristic of the clavus of Rhynchota (Fig. 26). No venational features are known to me that indicate that the Glosselytrodea are neuropteroid insects, as currently believed.

Modern hemipteroid orders are all oligoneurous, although some Fulgoroidea seem to have costaneurous wings. Fennah (1944) showed that the "costal" crossveins are actually precostal, and hence secondary structures.

A single costaneurous hemipteroid fossil is known to me. This is an undescribed fossil (Fig. 25) from the Permian beds of Oklahoma. It retains a fully developed clavus and complete venation, unlike either Psocoptera (Fig. 22) or Rhynchota (Fig. 23). On the other hand, it is more specialized than the Glosselytrodea, having P and E fused to form the "claval suture," and M basally fused to R+S.

The neuropteroid orders show quite diverse wing venation, but no obvious evolutionary trends are found among the orders. The venation of Megaloptera is in most respects the primitive one for the whole group of orders, being essentially an unmodified costaneurous type; the oligoneurous members of the Protomecoptera (Paramecoptera) are probably the ancestors of the Lepidoptera, Trichoptera, Diptera and Mecoptera.

Coleoptera probably evolved from the Megaloptera. These two orders are linked by two curious venational features: the hind wing has 1A branched, and Cu+P is neutral, with P descending into the plical furrow. In other orders P is concave throughout its length.

Lepidoptera and Trichoptera are associated on both the degree of simplification of their venation, and by their "anal loops" on the fore wing (retained in Lepidoptera by only the most primitive families). The anal loop is evidently produced by aligning the connecting crossveins, as in the unrelated protomecopterid *Platychorista*, followed by loss of the apices of the anal veins.

from venation of fossil orders without critical examination of the more complete data obtainable from recent insects. Sharov (1966) in turn based his phylogeny of the orders largely on Martynov's work.

This phylogenetic analysis has covered all the winged orders but four: Hymenoptera, Thysanoptera, Embioptera, and Zoraptera. Their highly modified venations make it necessary to rely upon morphological characters of the body for accurate phylogenetic placement. Ross (1955) associated the Embioptera with the orthopteroid series, placed the Thysanoptera near the Rhynchota, and put the Hymenoptera and Zoraptera at the base of the neuropteroid and hemipteroid series respectively. Thysanoptera retain a rudimentary clavus (Essig, 1942), and Hymenoptera have a venation basically similar to the Megaloptera (Ross, 1936), thus supporting these placements.

The Protembriaria closely resemble Zoraptera in both body and wing form. Their venation suggests that they rose from the higher Hadentomoida. Thus the venation of the Protembriaria supports the placement of the Zoraptera given above.

If Embioptera are related to the orthopteroid orders, they must represent the earliest lineage in this group. R+S on both wing pairs is very short, a more primitive character than the very long R+S of the orthopteroid fore wings.

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