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Wing Tracheation in Chrysopidae and Other Neuropterida (Insecta): A Resolution of the Confusion about Vein Fusion

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ABSTRACT

The wings of insects are one of their most prominent features and embody numerous characters and modifications congruent with the variety of their lifestyles. However, despite their evolutionary relevance, homology statements and nomenclature of wing structures remain understudied and sometimes confusing. Early studies on wing venation homologies often assumed Neuropterida (the superorder comprising the orders Raphidioptera, Megaloptera, and Neuroptera: snakeflies, alderflies and dobsonflies, and lacewings) to be ancient among Pterygota, and therefore relied on their pattern of venation for determining groundplans for insect wing venation schemata and those assumptions reciprocally influenced the interpretation of lacewing wings. However, Neuropterida are in fact derived among flying insects and thus a reconsideration of their wings is crucial. The identification of the actual wing venation of Neuropterida is rendered difficult by fusions and losses, but these features provide systematic and taxonomically informative characters for the classification of the different clades within the group. In the present study, we review the homology statements of wing venation among Neuropterida, with an emphasis on Chrysopidae (green lacewings), the family in which the highest degree of vein fusion is manifest. The wing venation of each order is reviewed according to tracheation, and colored schemata of the actual wing venation are provided as well as detailed illustrations of the tracheation in select families. According to the results of our study of vein tracheation, new homology statements and a revised nomenclature for veins and cells are proposed.

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INTRODUCTION

One of the most conspicuous traits among the majority of insects are their wings. The winged insects (Pterygota) comprise over 98% of hexapod diversity (Grimaldi and Engel, 2005; Engel, 2015), and their wings have allowed them to disperse effectively, locate resources, and evade predators. In addition, wings have been coopted into numerous alternative functions, ranging from protection and thermoregulation to concealment and communication, or in numerous instances have been lost outright (Grimaldi and Engel, 2005; Engel et al., 2013). Wings and flight appeared first among the insects (Engel et al., 2013), and extend deep into the early history of the class, with evidence of pterygotes in the earliest Devonian (Engel and Grimaldi, 2004). Given their comparatively flat form and durability, wings preserve well and it is therefore not surprising that the fossil record of insects is largely comprised of the remains of wings. Yet, despite their seeming simplicity, wings have left many entomologists exasperated in many regards, not the least of which has been in deducing their evolutionary origin. With their often easily discerned pattern of veins, crossveins, and markings extending through the main body of the wing, it is easy to understand why considerable attention has been given to vein homology and function. While many have sought a record of pterygote evolutionary history written out in the venation of wings (e.g., Brauer, 1885; Handlirsch, 1906, 1907, 1908; Comstock, 1918; Martynov, 1924, 1925, 1938), clear homologies and patterns have at times vexed even the most distinguished of morphologists.

The wing venation of insects has been a matter of contention and controversy for well over a century (e.g., Hagen, 1870; Adolf, 1879; Brauer, 1885; Redtenbacher, 1886; Brauer and Redtenbacher, 1888; Comstock, 1918; Lameere, 1922, 1923; Martynov, 1924, 1930; Needham, 1935; Hamilton, 1972a), and while many fundamental elements have been established an equal or greater number of details remain fiercely debated (e.g., Béthoux and Nel, 2001, 2002; Kukalová-Peck and Lawrence, 2004; Rasnitsyn, 2007; Béthoux, 2008; Engel et al., 2013; Prokop et al., 2017). In more recent history, confusion over vein homologies, combined with perceptions of either putative lability or overconservatism within a given lineage, has led some researchers to discount the systematic value of wings in favor of genitalic structures. Characters of female and particularly male genitalia are certainly effective for species-level identification, or recognition of groups of related species (e.g., Aspöck, 1986), but this does not preclude valuable information from wings. In fact, wings remain an important source of character data for estimating relationships among insects at various levels of interest.

In many insect lineages there is a disjunction between the actual venation (including fusions and losses) and what is visible across the wing, the result of total or partial fusion, or even loss of particular vein sections. It is this ambiguity between the actual and apparent venation that has resulted in difficulties in interpreting vein homology and many subsequent controversial interpretations. Apparent venation refers to the simple pattern observed macroscopically, whereas actual venation, according to one hypothesis, should take into consideration the paths and trajectories of the tracheae that form these veins internally (e.g., Needham, 1903). The use of tracheal trajectories as a proxy for actual venation has stimulated discussion about the validity and extensibility of using tracheation for homology determina-

tions (Ross, 1936; Fraser, 1938; Fennah, 1944; Whitten, 1962; Carpenter, 1966), and there are reasons why tracheae are not perfectly concurrent with the final, observed venation in a developing wing. While the complete notion of a one-to-one correspondence between tracheae and veins in the origin of wings may not be settled, nor do their courses match those of veins in every instance, some broad patterns exist and should therefore not be dismissed. Tracheae extend only through the longitudinal veins and thus provide evidence for fusion otherwise rendered hidden by the apparent venation (e.g., Fraser, 1943; Béthoux, 2005; Béthoux and Wieland, 2009).

Patterns of tracheation in insect wings, particularly by looking through various stages of wing development, were once broadly explored (e.g., Comstock and Needham, 1898a, 1898b, 1898c, 1898d, 1898e, 1898f, 1898g, 1898h, 1899a, 1899b, 1899c; Comstock, 1918; Withycombe, 1922). Such work subsequently fell out of fashion and was dismissed cavalierly primarily because a few cases blocked a comprehensive explanation for all taxa owing to tracheal capture or differences between pupal wing pads and the adult wing (e.g., Fraser, 1938; Holdsworth, 1942; Fennah, 1944; Whitten, 1962; Wootton, 1965; Carpenter, 1966). It is true that the "pre-tracheation" hypothesis (Needham, 1903, 1935; Comstock, 1918) incorrectly asserts that the tracheae form first and separate the layers in the developing wing, and thereby do not actually form the final veins, and instead run through the vein lacunae. Nevertheless, the course of the tracheae may serve as a reliable marker for ascertaining vein identities as there remains in many taxa a correlation between tracheae and the final veins. Indeed, the pattern of tracheation in many lineages largely reflects the course of sectors of the wing, and therefore remains an important body of evidence for establishing elements of vein homology, albeit not the sole source. The tracheae are particularly useful in locating sections where the longitudinal veins have changed course, with segments (abscissae) appearing like crossveins in places, and fused. In such locations, the two original tracheae can be found adjoining within the course of a single "apparent" vein (thus, demonstrating fusion at that point) (e.g., see fig. 1). As with most patterns in evolution, there are often exceptions, and universal statements require a list of examples where they do not hold; even Comstock (1918) alluded to such exceptions for tracheation. Tracheation certainly points to an exceptional case, and some of the rancor directed at Needham's "pre-tracheation hypothesis" was unwarranted. Accordingly, in those cases where there is considerable confusion over the identity of particular vein elements, recourse to tracheation may serve as an important indicator of the original homology, especially when placed in the context of other forms of evidence.

The insect superorder Neuropterida comprises the familiar lacewings, antlions, owlflies, dobsonflies, hellgrammites, snakeflies, etc. Among the hyperdiverse Holometabola, extant neuropteridan diversity seems meager, with fewer than 6500 species collectively. Nonetheless, they have some of the most spectacular wings, whose mesh of veins makes their general moniker of "lacewing" very appropriate. This netted threadwork of veins, however, has been equally frustrating to study. Vein fusion has fueled confusion relative to the "apparent" versus "actual" pattern of the sectors in the neuropteridan wing. Early entomologists assumed those wings with a large number and latticework of veins to be primitive, and therefore used "Neuroptera"

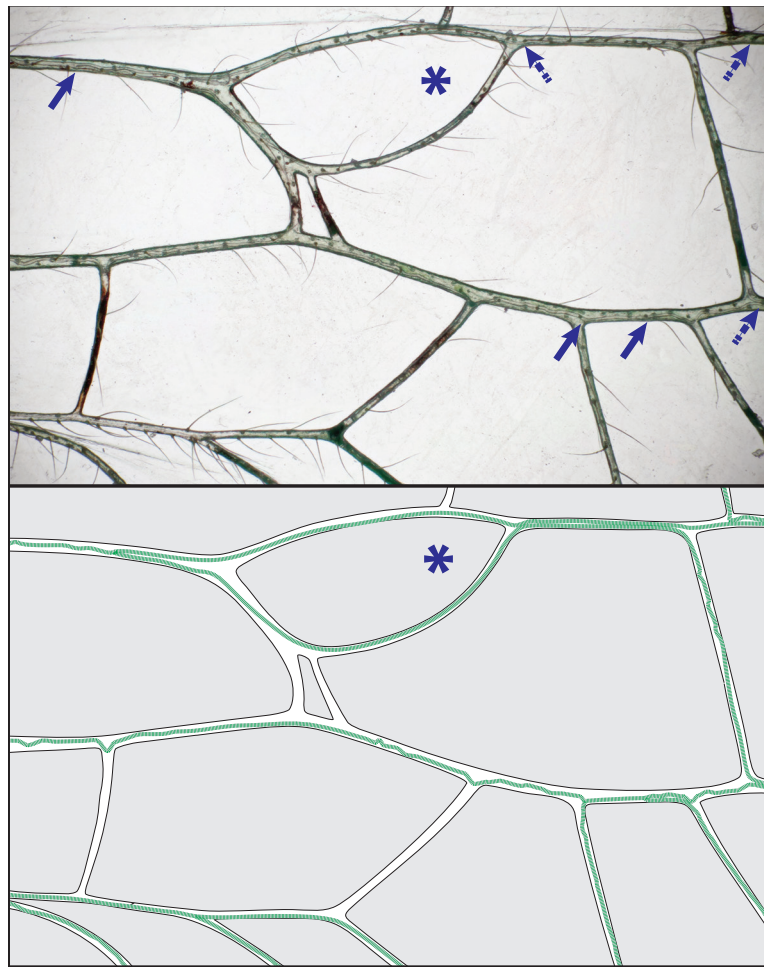

FIGURE 1. Microphotograph (above) and line drawing (below) of *Chrysopa nigricornis* Burmeister show detail of *mamp1* (first intermedial cell, indicated by asterisk) and surrounding area, illustrating the dissimilarity between apparent and actual venation, ventral view. Solid arrows indicate points of tracheal division, dashed arrows indicate fusions of veins with multiple tracheae present; course of tracheae indicated by green lines.

as a proxy for ancestral wing venation (Redtenbacher, 1886; Comstock, 1918). At the time, the order included many unrelated insect groups such those today classified as Odonata, Ephemeroptera, Plecoptera, Embiodea, Isoptera, Psocoptera, Mecoptera, and even Trichoptera, all gathered together as "Neuroptera" (e.g., Latreille, 1807, 1817; Stephens, 1835; Westwood, 1839, 1840; Rambur, 1842). In fact, the neuropterous orders as we understand them today include only Megaloptera, Raphidioptera, and Neuroptera sensu stricto (the latter sometimes referred to as Planipennia) and, as members of the derived Holometabola, Neuropterida are phylogenetically distant from the ancestral pterygote and its general wing traits. Nonetheless, lacewings have been integral in the historical development of systems of vein nomenclature and homology, and especially the green lacewings (Chrysopidae). Naturally, establishing correct vein identities in chrysopids is important for the systematics of this family, and also for interpreting

those patterns present in other neuropteran lineages, given that early work on Chrysopidae served as the basis for historical interpretations across Neuroptera.

In an attempt to resolve controversies regarding vein identities in the wings of chrysopids and homologies for use in phylogenetic studies of the family, we employed corroborating evidence from tracheation across the entire Neuropterida. We have examined a selection of chrysopids representing the spectrum of extant diversity, as well as representatives of nearly all neuropterous families and orders so as to place the pattern found in Chrysopidae within a broader context. By adopting the use of tracheation, we do not imply anything regarding wing origins as it relates to the defunct "exite" or "gill hypothesis" for overall wing homology, that is, wings as serial homologs with abdominal gills found in some crown-group naiads (e.g., Landois, 1871; Wigglesworth, 1976; Kukalová-Peck, 1978, 1983, 1991), which is in opposition to the "paranotal hypothesis" (e.g., Müller, 1873a, 1873b, 1875; Crampton, 1916; Hamilton, 1971, 1972a; Wootton, 1976; Rasnitsyn, 1981). Instead, wings have been more recently determined to be of largely notal origin with the incorporation of subcoxal elements to form an articulation at the base, also known as the dual model hypothesis (e.g., Grimaldi and Engel, 2005; Niwa et al., 2010; Engel et al., 2013; Prokop et al., 2017). In this context, the tracheae of the wing represent nothing more than similar tracheation of any body structure. We resurrect tracheation as a method for investigating wing vein identities, as an additional line of evidence. What general consequences this might have for the interpretation of venation across all Pterygota, particularly the early diverging lineages of Ephemeropterida, Triplosoboptera, Palaeodictyopterida, and Odonatoptera, is beyond the scope of the present work. Similarly, we fully recognize that there are instances where tracheae may be more labile and misleading and should not be adopted wholeheartedly in the absence of other evidence. Nonetheless, we do provide some potential implications our findings have regarding the controversial fate of the media anterior (MA) in Neuropterida.

Wings

Comprehensive reviews of insect wing structures and venation have been published over the centuries and are not repeated here. For pertinent reviews of these subjects, we direct the reader to Snodgrass (1909, 1935), Hamilton (1971, 1972a, 1972b, 1972c), Wootton (1979, 1992), Brodsky (1994), and Engel et al. (2013). Nonetheless, some details are useful to mention.

The insect wing is formed by an outgrowth of the body at the juncture of the meso- and metathoracic nota and the upper portion of their corresponding pleura. For Holometabola, wings develop from imaginal discs in the larva, forming in the pupal wing pads; in hemimetabolous insects the wing pads develop externally in nymphal stages. The wing initially extends outward as a thin, flat body cavity forming two layers (upper and lower) of the wing body sac. These membranes lay down the cuticle and elongate, tubular cavities (lacunae) form between them. Finally, tracheae enter the lacunae and provide the wing with nutrients. In the adult vein these often sclerotized lacunae are visible as the veins with the tracheae detectable within them.

When the wing is outstretched, three major regions can be described: the remigium takes up the majority of the wing's surface and encompasses the space with the most sectors (costa to cubitus) anterior to the claval furrow, whereas the anal and jugal areas often take up only a small portion of the posterior wing surface, especially in more derived insect lineages. The remigium is separated into two parts by the median-flexion line, which, as for all other principle folds, runs from base to apex. The claval furrow separates the remigium and anal area, while the jugal fold separates the latter from the jugum, which often forms a small lobe (jugal lobe). The anal area can be divided by an anal fold.

Winged insects are typically divided into paleopterous and neopterous forms. Paleopterous wings have different articulatory sclerites, ranging from the comparatively simple wing base of Odonatoptera (with two axillary sclerites) to the complex system of plates in the Ephemeropterida (Matsuda, 1970). These orders can only bring their wings together over the body, fully extended, but not folded flat over the abdomen and abutting the body. The exception is the extinct Diaphanopterodea, which evolved a mechanism of neopterous folding, convergent with Neoptera (Grimaldi and Engel, 2005). Neoptera have a distinctive arrangement of three axillary sclerites and median plate, the form of the third axillary sclerite being critical to the folding of the wings.

The main features in a wing are the series of longitudinal sectors, or principal veins. These are, from anterior to posterior, denoted in the Comstock and Needham (1898a, 1898b, 1898c, 1898d, 1898e, 1898f, 1898g, 1898h, 1899a, 1899b, 1899c) tradition as: costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal (A) (this original nomenclature was set forth by Redtenbacher, 1886). These sectors are formed of hollow spaces through which run extensions of the tracheal system (originally consisting of a single trachea per sector), and they are often modified through ramified branching, fusion with other sectors, or simple loss of one or more sections. These alterations reflect the interplay between historical patterns resulting from inherited transformations (i.e., phylogenetic inertia), and organization imposed by the flight mechanics peculiar to the species under investigation (i.e., functional constraints). Crossveins often occur between the longitudinal sectors, which are hollow and do not contain portions of the wing tracheae (or at most have minute, tapering portions of tracheoles). This permits comparatively easy identification of true crossveins relative to the principal sectors, even when the latter are considerably modified (e.g., Tillyard, 1916; Comstock, 1918; Withycombe, 1922). Crossveins are usually denoted by the two longitudinal sectors (or portions of those sectors) they connect, and then numbered from proximal to apical. Due to the association of each longitudinal vein with a different axillary element in the wing base, we can determine that, for example, R in one order is the same as R in another order, and thus underpinning our hypothesis of comparative homology at any taxonomic level. Therefore it follows that the costa is associated with the humeral plate, the subcosta with the first axillary sclerite, the radius with the second, media and cubitus with the median plate, and the anal veins with the third axillary sclerite. In the radius, media and cubitus there is a distinction between anterior and posterior, which can be simple branching and size differential. Different ways of naming these sectors were proposed by Kukalová-Peck (1991) and Béthoux and Nel (2001, 2002) (α and β branches) (table 1). For this study, we define the anterior and posterior branches as the branches resulting

TABLE 1. Comparison of systems of insect wing vein nomenclature as it applies to Neuropterida.

present work		Kukalová-Peck (1991)		Béthoux (2005)		Comstock (1918)	
C		C		C		C	
Sc		Sc		ScP		Sc	
R	RA	R+MA	RA	R	RA	R	RA
	RP		RP+MA		RP/RS		RS
M	MA	M	MP1+2	M	MA	M	MA
	MP		MP3+4		MP		MP
Cu	CuA	Cu	CuA	Cu	CuA	Cu	CuA
	CuP		CuP		CuP		CuP
A	A1	A	AA1	A	AA1	A	A1
	A2		AA2		αAA2		A2
	A3		AA3		βAA2		A3
	A4		AP		γAA2		A4
	...		...		...		...
J		J		J		J	

from the first split of a longitudinal vein. In the case of Hemerobiidae and Ithonidae, where multiple R branches are present we cannot make a certain assessment as to whether RA or RP is bearing the multiple branches. Historically, the determination of anterior and posterior branches was decided by examining corrugation or pleating, but in higher taxa this feature is often lost. We here assume that the bifurcation points are homologous to the observed conditions in extinct taxa in which corrugation can be observed.

Although there is a standardized way of naming veins, there is no universal nomenclature that covers the spaces between them, or cells. The names that are applied to cells are quite heterogeneous, and vary depending on the order and author. Sometimes cell nomenclature is based on their relative position to other markers, such as the submarginal cells in most Hymenoptera, or in relation to the bounding veins. In Chrysopidae there are named cells that are of importance, such as the intramedian (*im*) or the distal cubital (*dcc*) cells (fig. 16A) (e.g., Brooks and Barnard, 1990).

Entomologists working on different lineages of Pterygota sometimes use subtle modifications of the Comstock-Needham-Redtenbacher vein nomenclature, but overall the fundamentals of the present system differ little from that established by Comstock and Needham. Kukalová-Peck and colleagues (1978, 1983, 1991, 1997, 2008, 2009; Kukalová-Peck and Richardson, 1983; Riek and Kukalová-Peck, 1984; Kukalová-Peck and Brauckmann, 1992; Haas and Kukalová-Peck, 2001; Kukalová-Peck and Lawrence, 2004; Kukalová-Peck et al., 2009) have provided the most extensive recent revision of the Comstock-Needham system as well as other hexapod appendicular structures, attempting to incorporate considerable, albeit controversial (Béthoux and Briggs, 2008; Béthoux et al., 2008), evidence from paleontological data. The Kukalová-Peck venational modification effectively considers all the longitudinal sectors to have

been paired in the ancestral insect wing, and relies on an archetype with some hypothetical veins not present in any modern or fossil wing (refer to Discussion, below). This system considers each sector to have had an anterior and posterior ramus, giving costa anterior, costa posterior, subcosta anterior, subcosta posterior, and so forth. There may be some merit to ScA and ScP in some taxa, such as in Palaeodictyoptera, Odonata, and even Symphyta; however, this would require a much more extensive study across pterygotes. In Neuroptera C and Sc do not bifurcate, but all other sectors split into an anterior and posterior branch subbasally. Most neuropteran families show no to little fusion of longitudinal veins, but there are several autapomorphies in the wing venation, including fusions, with the highest degree of fusion present in Chrysopidae (refer to Results, below).

Wing Venation of Chrysopidae

Comstock (1918), summarizing his series of earlier papers with Needham, utilized the tracheation of pupal wing pads to explore vein identities across insects, and this work remains the most extensive of its kind. In that work, the forewing venation of *Chrysopa nigricornis* Burmeister was discussed, and with the same pattern of venation as that presented here. Comstock (1918) summarized information for all currently recognized families of Neuropterida and made some general conclusions about wing venation patterns, and suggested an extensive fusion in the chrysopid fore- and hind wing. In fact, the wings of Chrysopidae display the greatest degree of fusion among Neuroptera; as such, there is much difficulty in identifying the actual course of the longitudinal veins and especially of RP, MA, and MP. This difficulty results from the formation of pseudoveins in the fore- and hind wing, which appear to be single veins but are actually the product of several fused longitudinal and crossveins. Later, Tillyard (1916) undertook a similar investigation of developing pupal wings across Neuropterida, and based on this he suggested some slight modifications to interpretation of chrysopid wing venation. While his overall scheme was similar to that of Comstock (1918), not all of the veins across the remigium (i.e., each vein from proximal origin to wing margin termination) were accounted for in Tillyard's discussion. He concluded that there is less fusion in the chrysopid wing than Comstock had proposed. Eight decades would pass before the subject would be revisited in any considerable detail. Adams (1996) revived the tracheation approach and revised the homology of neuropteran wing venation, particularly basing his conclusions on the venation established by Comstock, as well as Tillyard's illustrations of pupal wings. Adams' interpretation of the chrysopid wing did not contain an inordinate degree of fusion between veins and, like Tillyard's before him, did not account for all the longitudinal veins (i.e., not every vein could be traced from its proximal origin to its termination at the wing margin).

Despite more than a century of concerted effort investigating neuropteran wing venation, the latticework of chrysopid wing veins remained a complicated matter to be unraveled. When examining many of the individual sections of veins, particularly those near the base and posterior margin and seemingly composed of the abscissae of RP, MA, MP, and CuA, it remains confusing at any given point which vein elements are involved. Accordingly, the cells with their

borders demarcated by these vein elements are unclear, particularly as one compares increasingly divergent wings. The present contribution is an attempt to revisit this important topic of establishing vein homologies. Aside from the usual means of ascertaining vein identity (e.g., position, connection, axillary sclerite articulation), we employ tracheation in mature wings as corroborating evidence and in the tradition of Comstock, Needham, Tillyard, and Adams.

We differentiate between *apparent* and *actual* wing venation. By apparent wing venation we mean the perceived venation without considering tracheae. In the actual wing venation, the longitudinal veins are defined by the paths of the tracheae. As an example, in Chrysopidae the apparent venation would include the pseudoveins such as PsM (pseudomedial) and PsC (pseudocubital) (sensu Adams, 1996; Brooks and Barnard, 1990; fig. 16A), whereas the actual venation is based on the longitudinal veins forming these composite structures (fig. 16B).

Longitudinal veins are represented by capital letters, crossveins and cells by lowercase letters. The abbreviation for crossveins is a combination of the two longitudinal veins that are connected by said crossvein and its number (numbered from proximal to apical). For example, if we address the second crossvein between MP and CuA, the abbreviation is 2mp-cua. Cells are described by italicized abbreviations without hyphenation (e.g., *im* or *mamp1*) (see Discussion for detailed description of vein and cell nomenclature, below).

MATERIAL AND METHODS

Tracheae are best visible when examining the ventral surface of the wing under high magnification and with transmitted light. Preferably, eclosed (nonteneral) adult pinned specimens with spread wings were examined to observe the entire wing and wing base. There is no special preparation necessary, rendering this process noninvasive and allowing observation of tracheae even in rare material. The wings of a few Neuroptera do not allow the easy examination of tracheae, either because they are too small or the veins are too thickly sclerotized or infuscate to see through (without removal and clearing), but overall such wings did not show any obvious abnormalities. Tracheae are visible in most, but not every specimen, possibly due to the method of fixation. Aside from other evidence, such as corrugation or pleating, especially in fossils, we mainly rely on adult tracheation for the determination of the actual venation pattern. In Neuroptera there are currently no documented cases in which the pupal and adult tracheation were not identical (e.g., Tillyard, 1916), and in all examined species we could not find discrepancies.

We examined at least two genera of each extant neuropteridan family, except for Coniopterygidae, Rhachiberothidae, and Nevrorthidae, where no or insufficient material was available. For these families we extracted information from the literature. We attempted to sample putatively basal groups for each family, but were limited by availability of suitably preserved material (i.e., wings spread, tracheation visible). Material examined is deposited in the collection of the California State Collection of Arthropods, Sacramento, California, and the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas. The presentation of taxa is loosely organized around those relationships recovered by Winterton et al. (2010, in press), at least in the sense of not recognizing suborders Nevrorthiformia, Hemerobiiformia,

and Myrmeleontiformia within Neuroptera. Instead, we use a series of monophyletic superfamilies but not in an order that matches their pattern of branching from the base of Neuroptera based on the classification proposed recently by Engel et al. (in press). The current numbers of species of the families and subfamilies were extracted from the Lacewing Digital Library (Oswald, 2017). Wings were examined with Nikon SMZ 1500 and Olympus SZX7 stereomicroscopes, using transmitted light. Line drawings were produced in Adobe Illustrator CC2015 on the basis of photographs of wings from representative species. Photomicrographs were prepared using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens as well as an Olympus DP72 digital camera attached to an Olympus SZX16 stereomicroscope, and then arranged in Adobe Photoshop and Illustrator CC2015. Abbreviations for wing veins and cells are provided in the legend to figure 2.

RESULTS

In the wings of Neuropterida, "actual" and "apparent" patterns of venation are not always identical. Tracheae are present within the longitudinal veins of all insect wings. These tracheae are visible in the adult wing and follow the same paths as those in the pupal wing pads of Neuropterida, among the taxa we examined. Tracing the tracheae allows for the determination of these "actual" longitudinal sectors, and it is possible to determine points of fusion between these due to the presence of multiple tracheae (fig. 1) within a single vein abscissa. In addition, the precise points of ramification of particular tracheal stems can be observed (fig. 1), and this branching gives rise to the broader fields of particular vein systems (e.g., the medial field encompasses the space between the various branches of the medial stem). Crossveins can appear superficially identical to longitudinal veins but differ by the lack of tracheae running through them; though minute tracheoles can enter, they rarely persist. This distinction has proven useful in detecting the actual pattern of venation in the various families of Neuropterida.

Lineages of Neuropterida

As noted earlier, the wings of many Neuropterida are comparatively simple, possessing few or no fusions among the sectors. In several families the apparent and actual patterns of venation are identical and the identity of the longitudinal veins can be determined easily without reliance on extra evidence such as tracheation. In such cases, the usual sectors can be identified by their proximal connections to individual axillary sclerites in the wing base and articulation. Each family has a unique pattern of wing venation, and some have clear autapomorphies in vein fusion, recognizable through the study of tracheae as described here.

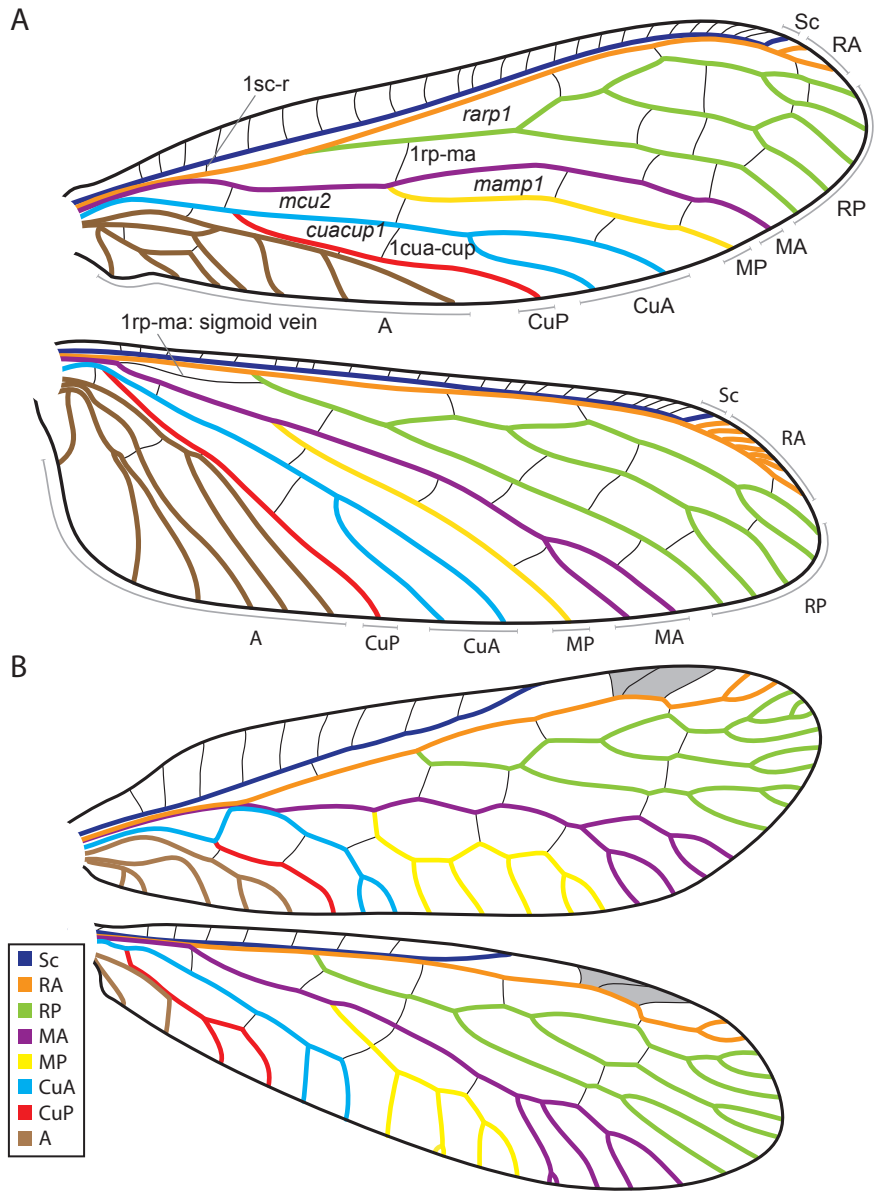

FIGURE 2. Line drawings of forewings and hind wings of Megaloptera and Raphidioptera. **A.** *Protochauliodes aridus* Maddux (Megaloptera), longitudinal veins: Sc (subcosta; dark blue), RA (radius anterior; orange), RP (radius posterior; green), MA (media anterior; purple), MP (media posterior; yellow), CuA (cubitus anterior; light blue), CuP (cubitus anterior; red), A (anal; brown); crossveins: 1rp-ma (first crossvein between RP and MA), 1cua-cup (first crossvein between CuA and CuP); cells: *rarp1* (first interradial cell); *mamp1* (first intermedial cell), *mcu2* (second medial cell). **B.** *Agulla adnixa* (Hagen) (Raphidioptera).

Order Megaloptera

Figure 2A

Megaloptera comprise 373 species in two distinct lineages—the large dobsonflies, fishflies, and hellgrammites of Corydalidae (295 species), and the diminutive alderflies of Sialidae (78 species). The megalopteran wing is slightly elongate, there are no differences between the apparent and actual venation, and the general pattern of tracheation present in corydalids is identical to that observed in Sialidae. As in Psychopsidae, Hemerobiidae, Nevrorthidae, and many Osmylidae there are no tracheal fusions in the fore- or hind wing. The longitudinal veins extend across the length of the remigium without considerable changes to their courses over this distance, and RP does not occupy a disproportionally large area of the wing. The "sigmoid vein" of the corydalid hind wing (and other neuropteridan hind wings with such a crossvein) has been a subject of discussion for the last century (e.g., Martynov, 1928; Tillyard, 1932; Carpenter, 1940). In the hind wing, the first crossvein between R and M (1r-m, 1rp-m, or 1rp-ma, depending on the lineage) can be straight or sigmoid shaped. When it is arched (as in fig. 8), the crossvein is usually elongate and more longitudinal in orientation (rather than transverse), and has traditionally been dubbed the sigmoid vein. The presence of a sigmoid vein has been used as evidence for a possible fusion of MA into R or RP (Martynov, 1928). Within this line of argumentation, the sigmoid vein is considered a vestige of MA. This means that MA's proximal origin from the stem of M is revealed by the sigmoid vein and in those taxa where this crossvein is more transverse and short, it has taken on a more typical crossveinlike appearance as part of its reduction and attachment to R or RP. The absence of tracheation in the sigmoid vein was dismissed as it was assumed that the tracheae of R and MA were proximally fused beyond recognition in extant taxa, and therefore secondarily lost in this abscissa of MA. While this is a possibility, the argument relies on a combination of absence of evidence, ad hoc supposition of complete fusion, and the peculiar reappearance of the MA trachea in the portion of its branch beyond the purported RP+MA fusion (i.e., present in the apical sector of MA beyond the sigmoid vein and after it reseparates from RP as the posteriormost branch of the radial field). The presence of the sigmoid vein (i.e., the more elongate, longitudinal, proximal crossvein between R and MA, RP and MA, or RP and M) serves as some of the primary evidence for proximal fusion of R or RP and MA, along with a reversal in corrugation (see Discussion, below). In addition, in megalopteran wings the costal crossveins are simple (not forked), there is no recurved humeral vein (i.e., first costal crossvein, which is curved toward the wing base in some families and is often pectinately forked), and trichosors (i.e., short veinlets without tracheation on the wing margin that are typical of many Neuroptera) are lacking. The pterostigma varies from absent to marked.

Species examined: *Protochauliodes aridus* Maddux (fig. 2A); other species examined but not figured: *P. cascadius* Evans, *Sialis nevadensis* Davis, and *Sialis* sp.

Order Raphidioptera

Figure 2B

Modern snakeflies comprise approximately 248 species in two comparatively similar families, Raphidiidae and Inocelliidae, that differ in the presence or absence of pterostigmal crossveins among other traits. The snakefly wing is neither strongly elongate nor rounded. Unique to Raphidioptera is a subbasal fusion of M and CuA (fig. 1B), which in its form is not present in any other Neuropterida. CuA arches anteriorly to join M, taking on a form that makes it look like the first apparent crossvein between M and CuA. CuA then shortly diverges from M. In snakefly wings R and M in the forewing are proximally fused, or nearly so, sometimes appearing as a single vein proximally, a feature also present in Sisyridae, most Chrysopidae, and Mantispoidea (i.e., Berothidae, Rhachiberothidae, and Mantispidae). In Raphidioptera this fusion is present in the fore- and hind wing; however, the individual tracheae representing R and M are distinct within the fused vein at its base. Accordingly, this fusion is not so derived as to be obscured by complete fusion of their tracheal stems. The costal crossveins are simple, a recurved humeral vein is absent, trichosors are absent, and in the hind wing crossvein 1r-m is simple. The pterostigma is strongly marked in most taxa.

Species examined: *Agulla adnixa* (Hagen) (fig. 2B); other species examined but not figured: *Agulla* sp.

Order Neuroptera

Superfamily Myrmeleontoidea

Family Psychopsidae

Figure 3

Silky lacewings are a small group with about 26 extant species in five genera; they have a disparate, relict distribution in the Oriental, Australasian, and southern Afrotropical regions (Oswald, 1993; Bakkes et al., in press). The large, broad wings of Psychopsidae are characterized by a dominant costal and radial sector, but all longitudinal veins are tracheated in correspondence with the branching pattern. No fusions are detectable in the fore- or hind wing. Apart from some Apochrysinae and Myrmeleontidae, psychopsid wings are the only Neuropterida with a gradate series in the costal field (fig. 3). Crossvein 1r-m of the hind wing is simple and not sigmoidal in shape (i.e., not forming a so-called sigmoid or sigmoidal vein). The costal crossveins are forked, sometimes dichotomously; a distinct, recurved humeral vein is present; and trichosors are present along the entire wing margin (fig. 3). The pterostigma is inconspicuous in most taxa and weakly marked in few.

Species examined: *Psychopsis insolens* McLachlan (fig. 3); other species examined but not figured: *Psychopsis illidgei* Froggatt, *P. barnardi* Tillyard, *P. elegans* (Guérin-Méneville), *P. gracilis* Tillyard, *P. mimica* Newman, and *Zygophlebius leoninus* Navás.

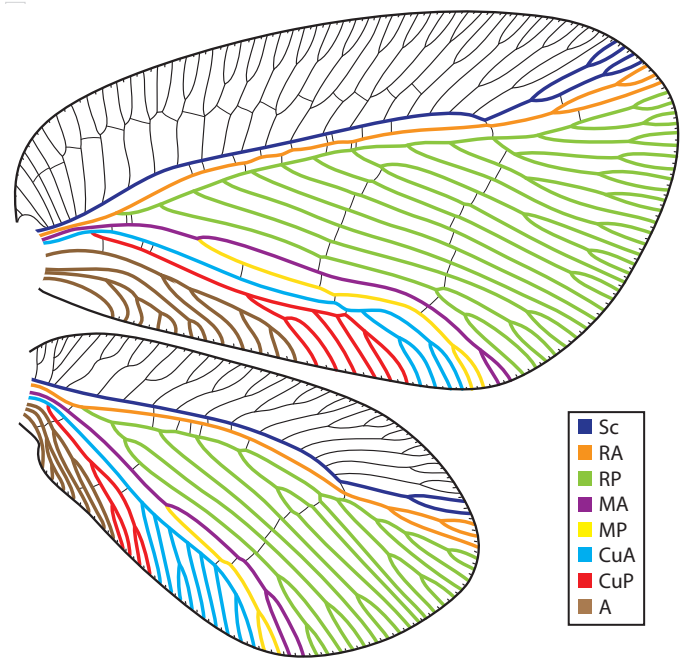

FIGURE 3. Line drawings of forewing and hind wing of *Psychopsis insolens* McLachlan (Psychopsidae); see figure 2 for explanation of abbreviations.

Family Nymphidae

Figure 4

Split-footed lacewings are a small group and comprise 35 modern species endemic to Australasia. Nymphids have elongate to ovoid wings with a rather conservative pattern of wing venation with little secondary fusion, so the tracheae reflect the apparent venation. In the forewing, MP diverges from MA apically on the wing further than in any other Neuropterida except some Osmylidae. Indeed, overall similarities between wings of distantly related Nymphidae and Osmylidae have led some authors to misplace fossil taxa in either family (e.g., Myskowiak et al., 2015). Nymphidae often have a large RP field with numerous crossveins forming a prominent reticulation (fig. 4), although this is known from other families as well. The only fusion present is Sc and RA at the level of the pterostigma. Crossvein 1rp-ma of the hind wing is short and not sigmoidal. The costal crossveins are forked, a recurved humeral vein is absent, and trichosors are present along the entire margin. The pterostigma is small, but present. A notable apomorphy for Nymphidae is the presence of thyridiate crossveins in the Sc-RA space. These crossveins originate on Sc but do not reach RA and are abbreviated presumably due to crossing the flexion line between the two longitudinal veins (Oswald, 1998; Shi et al., 2015).

Species examined: *Myiodactylus osmyloides* Brauer (fig. 4); other species examined but not figured: *Osmylops armatus* (McLachlan), *O. ectoarticulatus* Oswald, *Nesydrion nigrinerve* Esben-Petersen, and *Nymphes myrmeleonoides* Leach.

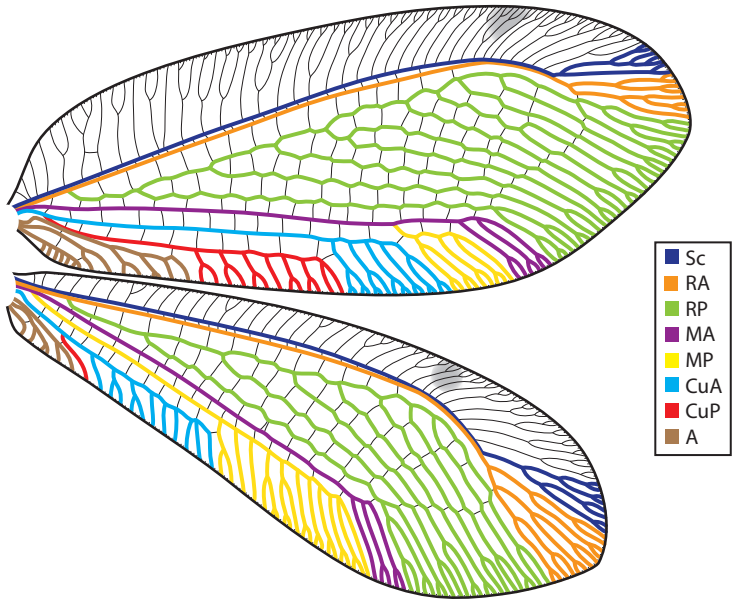

FIGURE 4. Line drawings of forewing and hind wing of *Myiodactylus osmyloides* Brauer (Nymphidae); see figure 2 for explanation of abbreviations.

Family Nemopteridae

Figure 5

Spoon-wings and thread-wing lacewings comprise 146 extant species in two subfamilies, Crocinae and Nemopterinae, distributed in most biogeographical regions except the Nearctic. Nemopteridae have ovoid forewings, but are unique in their extremely elongate, petiolate hind wings; concomitantly the hind-wing venation is greatly reduced (fig. 4). In the forewing there is only one major fusion of the longitudinal veins, whereby MP originates basally and then almost immediately merges with CuA for a short distance (MP+CuA usually has a length bordering 4–5 ma-mp[+cua] crossveins) (fig. 5). The forewing RP originates near the middle of the wing, while MA is unbranched and comparatively unremarkable. By contrast, after its separation from CuA, MP produces a series of pectinate branches, creating a wide MP field along the posterior wing margin. Once MP and CuA diverge again, CuP has one principle fork. CuP has multiple marginal branches. The hind wing of Nemopteridae is greatly elongate and there is uncertainty about the identity of the veins. Three major longitudinal veins are present of which Sc can be identified easily, but the constitution of the two posterior veins cannot be assessed by examining the tracheation. These two veins are most likely a result of several fusions containing parts of R, M, and Cu. Due to the extensive amount of fusion in most of the hind wing further detailed examination of the wing venation, tracheation, and development is needed to determine homology. The costal crossveins are simple, there is no recurved humeral vein, and trichosors are lacking. The pterostigma is very small, but present.

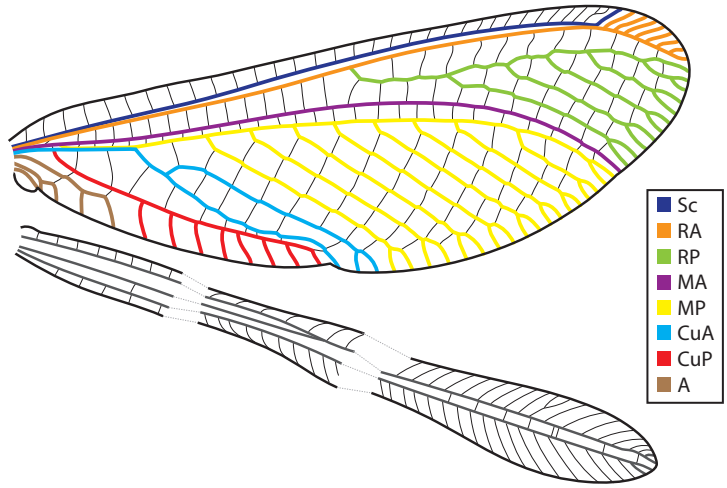

FIGURE 5. Line drawings of undetermined nemopterine genus (forewing) and *Nemoptera sinuata* Olivier (hind wing) (Nemopteridae); see figure 2 for explanation of abbreviations.

SPECIES EXAMINED: Undetermined genus (fig. 5, forewing), *Nemoptera sinuata* Olivier (fig. 5, hind wing); other species examined but not figured: *Halter halteratus* (Forskål), *Nemia costalis* (Westwood), and *Nemoptera coa* (Linneaus).

Family Ascalaphidae

Figure 6A

Owlflies comprise 431 extant species in three subfamilies, two of which are distributed worldwide. Ascalaphid wings are elongate and the forewing is characterized by a complete intermingling of MP and the anterior branch of CuA, thus forming an elongate MP+CuA. In the forewing MP diverges from MA, and is present as an apparent transverse crossvein; it then immediately fuses with CuA just apical to the first fork in CuA (fig. 6A). Two intermingled tracheae extend to the wing margin in MP+CuA and the branches originating from this sector can variably be assigned to MP or CuA; that is, the origin of the individual branch trachea are often visible and can confidently be assigned to either MP or CuA. Thus, in any given ascalaphid wing a particular branch of MP+CuA may either originate from the trachea of MP or from that of CuA, without a consistent pattern (hence the dotted pattern of colors used in figure 6A). As far as we have been able to observe, this is the most significant derivation in tracheation pattern among the lineages of Neuroptera. Otherwise, the apparent venation is similar to the closely related Myrmeleontidae, although the latter lack the overlapping and intermingled tracheae of MP+CuA. Like nemopterids, Ascalaphidae often have a simple MA, without branches, and this, along with the close association of MP+CuA, might be apomorphic for the Nemopteridae + (Ascalaphidae + Myrmeleontidae) clade. In the hind wing MP and CuA overlap only briefly in the marginal area and first MP branches (fig. 6A). The costal crossveins are simple, there is no recurved humeral vein, trichosors are lacking, and in the hind

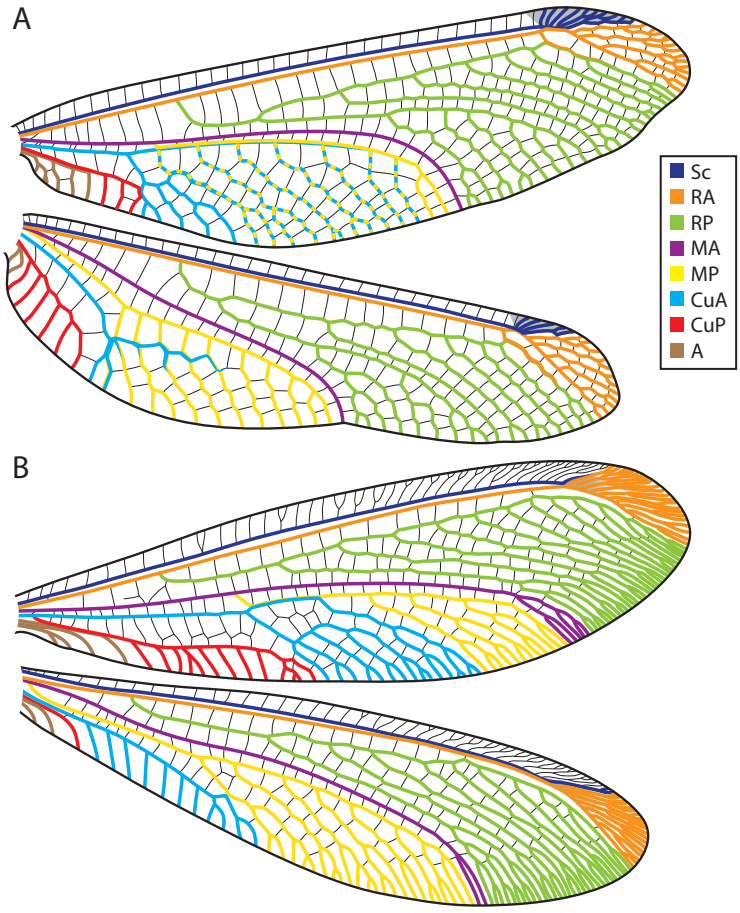

FIGURE 6. Line drawings of forewings and hind wings of an antlion and owlfly. **A.** *Acheron trux* (Walker) (Ascalaphidae). **B.** Undetermined species of Dendroleontini (Myrmeleontidae). See figure 2 for explanation of abbreviations.

wing crossvein 1rp-ma is slightly curved. The pterostigma varies between almost unmarked to strongly marked.

Species examined: *Acheron trux* (Walker) (fig. 6A); other species examined but not figured: *Ascalobyas microcerus* (Rambur), *Libelloides italicus* (Fabricius), *Ululodes arizonensis* Banks, *U. bicolor* (Banks), and *Ululodes* sp.

Family Myrmeleontidae

Figure 6B

Antlions are the largest group in Neuroptera with 1659 species and numerous subfamilies, although the classification is far from natural, with rampant paraphyly likely. The wings of Myrmeleontidae are elongate and similar to those of Ascalaphidae but lack the extended fusion of MP and CuA present in the latter family. They appear to represent an intermediate between

the plesiomorphic basal fusion of MP+CuP in Nemopteridae and the more distal intermingling found in Ascalaphidae. As in Ascalaphidae, MP and CuA do come together, at the base of MP, but then separate and extend to the wing margin forming separate medial posterior and cubital anterior fields. Similar to some Psychopsidae and Apochrysinae, representatives of Myrmeleontidae can have a gradate series present in the costal field (e.g., *Acanthaclisis* Rambur). The crossvein 1rp-ma of the hind wing is simple and not sigmoidal, and in all wings the costal crossveins can be at times forked, there is no recurved humeral vein, and trichosors are lacking. The pterostigma is marked in most taxa; often it is small and not clearly bordered.

Species examined: Dendroleontini undetermined (fig. 6B); other species examined but not figured: *Brachynemurus abdominalis* (Say), *Dendroleon* sp., *Distaleon* sp., *Froggattisca* sp., *Heleoclisis* sp., *Palpares* sp., and *Stilbopteryx* sp.

Superfamily Ithonoidea

Family Ithonidae

Figures 7A, 8

The moth lacewings and giant lacewings comprise 39 species in two main genus groups. The family now incorporates the families Polystoechotidae and Rapismatidae (Winterton and Makarkin, 2010). Ithonid wings are variable in shape from elongate-ovoid, falcate to slightly pointed apically, but in general they are broad with reticulated venation; in one genus (*Adamsiana* Penny) the female is apterous. They are characterized by the presence of up to three radial sectors (RP) in the forewing (although most commonly one) and in which the distalmost sector is more greatly developed than the basal sectors (fig. 7A). The only other Neuropterida with multiple origins to RP are Hemerobiidae. There is little fusion present among the veins except the subapical fusion of Sc and RA. In comparison to Coniopterygidae, in which a branch of Sc joins RA through the apparent crossvein, the ithonid vein fusion is due to a branch of RA joining Sc through an apparent crossvein below the area of the pterostigma. The hind wing 1rp-m is sigmoidal. Costal crossveins can be forked, particularly in the apical half of the wing; trichosors are present on the margins, and a recurved humeral vein is present (fig. 8). The pterostigma is inconspicuous.

Species examined: *Ithone fulva* Tillyard (figs. 7A, 8); other species examined but not figured: *Fontecilla graphicus* Navás, *Oliarces clara* Banks, *Platystoechotes lineatus* Carpenter, *Polystoechotes punctata* (Fabricius), and *Rapisma cryptunum* Barnard and New.

Superfamily Coniopterygoidea

Family Coniopterygidae

Figure 7B

Dustywings comprise 571 extant species in three subfamilies, two of which are cosmopolitan in distribution. They are particularly distinctive for the presence of a whitish wax layer on

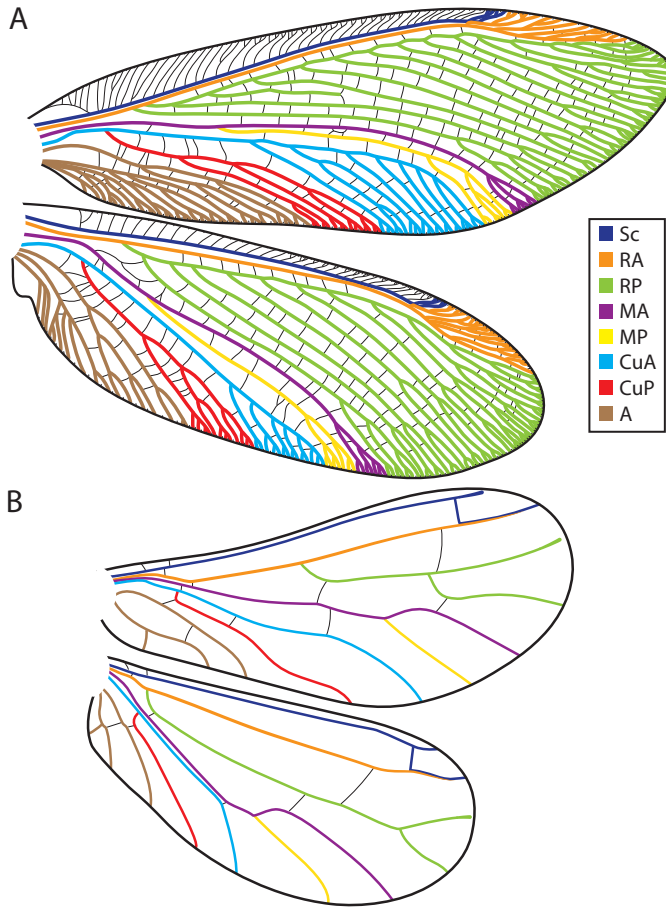

FIGURE 7. Line drawings of forewings and hind wings of a moth lacewing and dustywing. **A.** *Ithone fulva* Tillyard (Ithonidae). **B.** *Aleuropteryx juniperi* (Ohm), re-drawn from Meinander (1972) (Coniopterygidae). See figure 2 for explanation of abbreviations.

the wings and body, as well as a generally reduced venation relative to all other Neuropterida. The wing shape is typically ovoid, although some species have the hind wing greatly reduced. Owing to their exceptionally small size, we were not able to observe tracheation in specimens available to us. Based on studies by Withycombe (1922), it appears that the actual wing venation does not vary dramatically from the apparent venation. There are apparently no fusions present in the fore- or hind wing, except for the partial overlap of Sc_2 and RA. Withycombe (1922) examined the pupal tracheation of Coniopterygidae and noted the apical descent of a second branch of Sc (Sc_2) into the path of RA. At this point RA terminates or partially overlaps the base of the apical Sc_2 abscissa, but it is Sc_2 that terminates at the wing margin, despite appearing as RA. This condition would be analogous to the fusion in Ithonidae, but there the latter RA joins Sc through an apparent crossvein. The branches of the longitudinal veins are often simple apically, although forking does occur in various genera, and some of the Cretaceous dustywings have additional branching not known to occur within the modern fauna (in

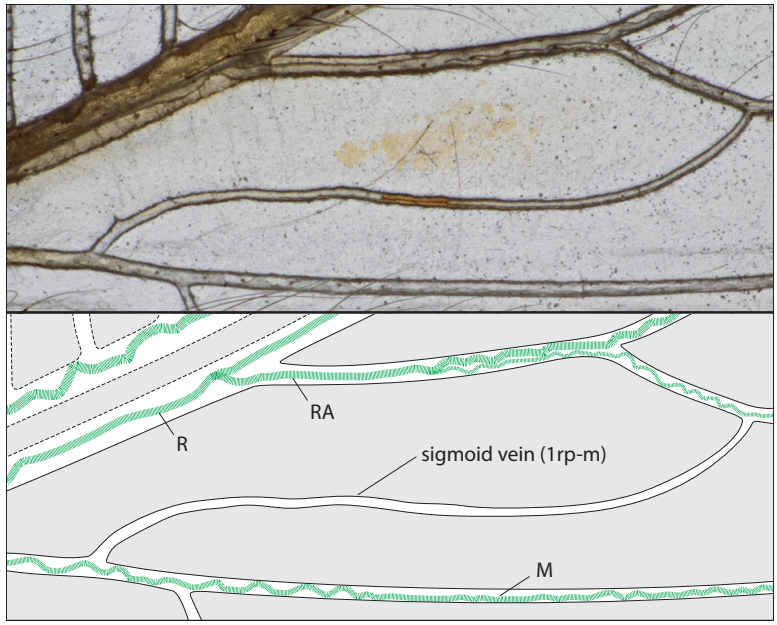

FIGURE 8. Microphotograph (above) and line drawing (below) of the proximal radial and medial sector of the hind wing of *Ithone fulva* Tillyard (Ithonidae), showing the elongate 1rp-m (sigmoid vein) in ventral view. Tracheae demarcated in green.

MA) (Meinander, 1975; Grimaldi, 2000; Engel, 2002, 2016). Otherwise, the generally simple venation is a seemingly unique trait within Neuropterida. The costal crossveins are simple or lacking entirely, no humeral vein is present, trichosors are lacking, and in the hind wing crossvein 1r-m is simple and not sigmoidal. The pterostigma is inconspicuous.

Species examined: *Aleuropteryx juniperi* (Ohm) (redrawn from Meinander, 1972) (fig. 7B).

Superfamily Osmyloidea

Family Osmylidae

Figure 9

Lance lacewings comprise 212 species in 30 genera. Osmylid wings vary from short and ovoid to elongate and falcate. They are characterized by the distal separation of MA and MP in the forewing, a trait only present elsewhere in Nymphidae. The separation in Osmylidae is not always as easy to see as in the species illustrated here (fig. 9), where MP and CuA are not fused. In some Osmylidae (e.g., *Stenosmylus* McLachlan) fusion of MP and CuA occurs in the distal part of the wing, and some authors have suggested an apparent absence of MP in the forewing (e.g., Shi et al., 2012, Cousin and Béthoux, 2016). Winterton et al. (2017) showed that while MA-CuA fusion does occur in some derived osmylid species of Stenosmylinae, the absence of MP in the osmylid hind wing was in fact based on incorrect interpretation of incomplete published figures, and examination of species revealed that MP is in fact small but pres-

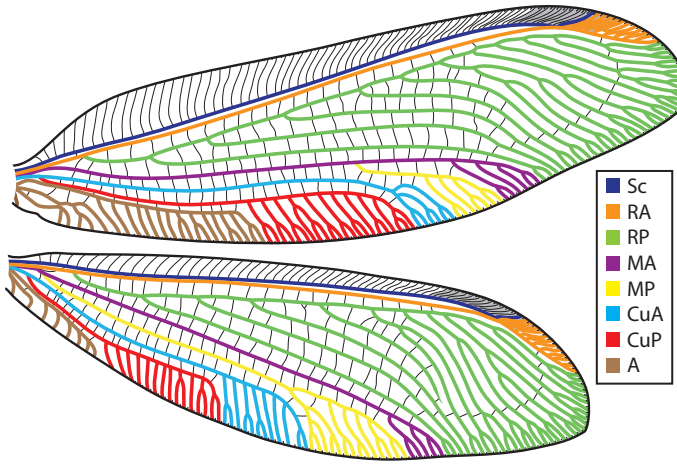

FIGURE 9. Line drawings of forewing and hind wing of *Oedosmylus* sp. (Osmylidae). See figure 2 for explanation of abbreviations.

ent. When tracing the tracheation it is possible to detect the split of the two medial sectors and the fusion of MP with CuA. Examination of representatives of additional Osmylidae genera is required to fully elucidate the extent of wing vein fusion in this heterogeneous family. As in many other Neuroptera, Osmylidae have numerous crossveins in the radial field and have only a single origin to RP. The RP field is enlarged in Osmylidae and numerous crossveins are present (especially in the proximal two-thirds of the wing). Crossvein 1r-m of the hind wing can be curved in some taxa but is simple in most. The costal crossveins can be forked, a recurved humeral vein is absent and trichosors are present on either part or the entire margin. The pterostigma is weakly marked in most taxa.

Species examined: *Oedosmylus* sp. (fig. 9); other species examined but not figured: *Australysmus* sp., *Eidoporismus pulchellus* Esben-Petersen, *Gryposmylus pubicosta* (Walker), *Kempynus acutus* New, *K. maculatus* New, *Lysmus harmandinus* Navás, *O. latipennis* Kimmins, *Stenosmylus stenopterus* McLachlan, *S. tenuis* (Walker), and *Thyridosmylus paralangii* Wang, Winterton, and Liu.

Family Sisyridae

Figure 10A

Spongillaflies comprise 71 species in four genera, with two genera largely cosmopolitan. The small sisyrid wings are rounded and tracheae are rarely visible, and when discernible are often so only in the base of the wing. Therefore, we could not confirm all details of the actual venation, but it seemingly does not vary from the apparent pattern. As in the wings of Raphidioptera, Mantispoidea (Berothidae, Rhachiberothidae, and Mantispidae) and most Chrysopidae R and M are fused at the base. We assume that the veins are fused but not the individual tracheae, as in all other taxa where this character is present. The costal crossveins can be forked,

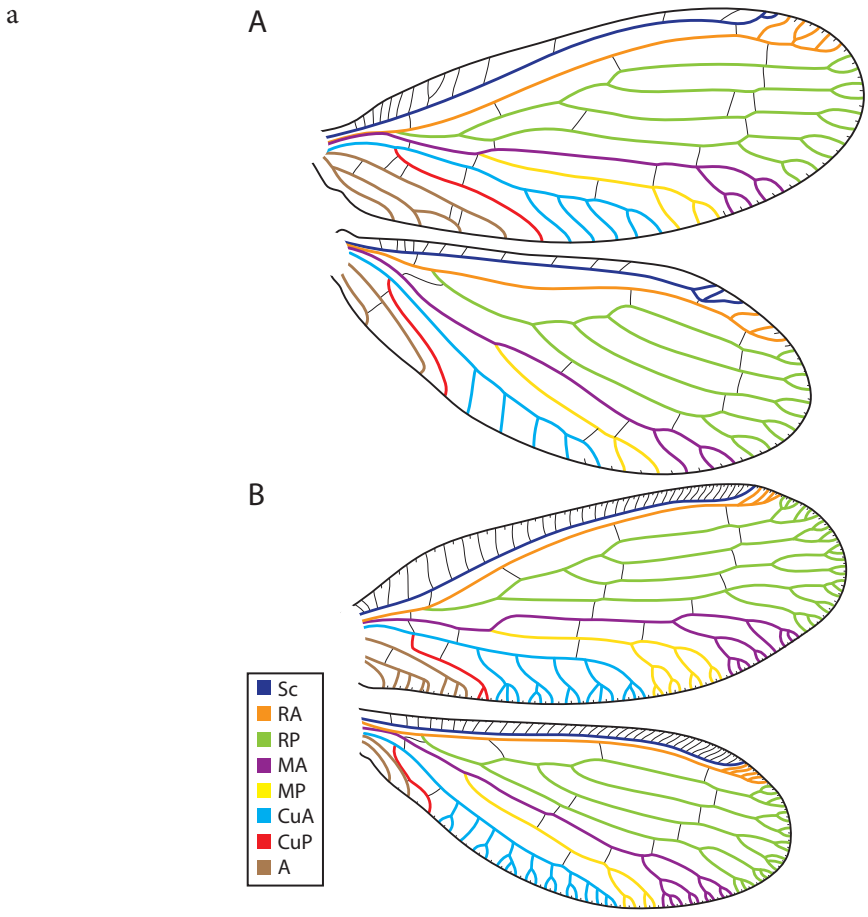

FIGURE 10. Line drawings of forewings and hind wings of a spongillafly and aquatic lacewing. **A.** *Sisyra* "*flavicornis*" (redrawn and modified from Comstock, 1918; likely a misnomer for *S. fuscata* [Fabricius]) (Sisyridae). **B.** *Nevrorthus reconditus* (Montserrat and Gavira) (redrawn from Montserrat and Gavira, 2014) (Nevrorthidae). See figure 2 for explanation of abbreviations.

recurved humeral vein is absent, trichosors are present on the apical margin, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma is inconspicuous.

Species examined: *Sisyra* "*flavicornis*" (redrawn and modified from Comstock, 1918; likely a misnomer for *S. fuscata* [Fabricius]) (fig. 10A); other species examined but not figured: *Climacia ariolaris* (Hagen).

Family Nevrorthidae

Figure 10B

Nevrorthidae are one of the smallest families of Neuroptera, with only 19 extant species in four genera. Suitably preserved specimens of Nevrorthidae were not available for this study, but

based on the wing images of Montserrat and Gavira (2014) (fig. 10B) we can assume that the actual venation does not vary from the apparent venation. The rounded wings of Nevrorthidae are very similar to Sisyridae and yet also show some similarities with closely related Osmylidae, belying their intermediate phylogenetic position between the two families. There are no fusions present in the fore- or hind wing, as is the case in Megaloptera, Psychopsidae, most Osmylidae, and Hemerobiidae. Nevrorthidae lack the basal fusion of R and M. The costal crossveins are simple, a recurved humeral vein is lacking, trichosors are present on the entire margin, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma is inconspicuous.

Species examined: *Nevrorthus reconditus* (Montserrat and Gavira) (redrawn and modified from Montserrat and Gavira, 2014) (fig. 10B).

Superfamily Dilaroidea

Family Dilaridae

Figure 11A

Pleasing lacewings comprise 77 species in six genera (Liu et al., 2017). Dilarid wings are short and rounded and in some taxa the hind wing is reduced. The forewings have only a single discernible fusion, which is the partial merging of MP and CuA (fig. 11A), a condition clearly convergent with that of Nemopteridae, Ascalaphidae, and Myrmeleontidae. Shortly after its divergence from MA, MP joins CuA and they then diverge roughly around the wing's midpoint. The costal crossveins can be forked, there is no humeral vein, trichosors are present on the entire margin, and in the hind wing crossvein 1rp-m varies from simple to sigmoidal. The pterostigma is inconspicuous.

Species examined: *Nallachius americanus* (McLachlan) (hind wing redrawn from Carpenter, 1940) (fig. 11A); other species examined in literature but not figured: *Dilar* sp.

Superfamily Mantispoidea

Family Berothidae

Figure 11B

Beaded lacewings comprise 113 species in 25 genera. Berothid wings vary from short and rounded to elongate and even falcate, and in some taxa the hind wing is reduced. As in Raphidioptera, Sisyridae, Mantispidae, Rhachiberothidae, and most Chrysopidae, R and M are fused at the base in the forewing, with both tracheae evident within the composite vein. In each of the aforementioned taxa, M diverges from R basal to the origin of RP. Aside from this area of basal fusion, all other tracheae follow the apparent wing venation. The costal crossveins are forked, trichosors are present on the entire margin, a recurved humeral vein is present, and in the hind wing crossvein 1rp-m is simple and not sigmoidal. The pterostigma varies from inconspicuous to marked.

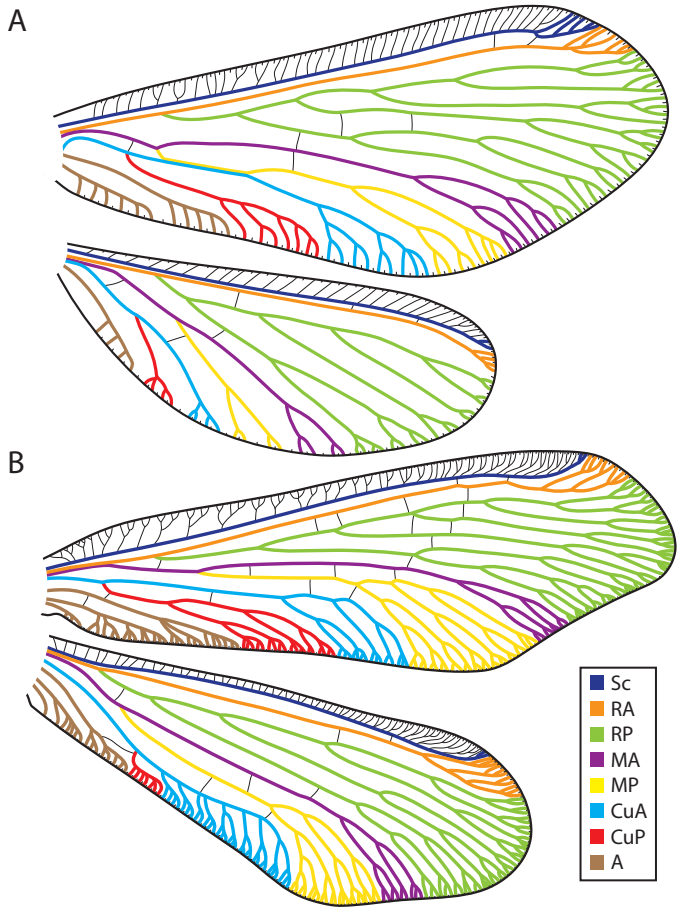

FIGURE 11. Line drawings of forewings and hind wings of a pleasing lacewing and a beaded lacewing. **A.** *Nallachius americanus* (McLachlan) (hind wing redrawn from Carpenter, 1940) (Dilaridae). **B.** *Trichoma* sp. (Berothidae). See figure 2 for explanation of abbreviations.

SPECIES EXAMINED: *Trichoma* sp. (fig. 11B); other species examined but not figured: *Naizema mendozina* (Esben-Petersen), *Stenobiella variola* Winterton, and *Trichoma gracilipenne* Tillyard.

Family Rhachiberothidae

Figure 12A

Thorny, or raptor, lacewings are a small group of 13 species in three genera, and their modern diversity is restricted to sub-Saharan Africa. Rhachiberothids have rounded wings, although rarely narrowly elongate in one species. Due to their small size, the tracheae are not visible in many species (often only at the wing base). Consequently, we were unable to confirm details for Rhachiberothidae but assume that the actual wing venation does not vary from the apparent venation in most details, as is the case for the closely related Berothidae. As in Raphidioptera, Sisyridae, Berothidae, most Chrysopidae, and Mantispidae, the bases of R and M are

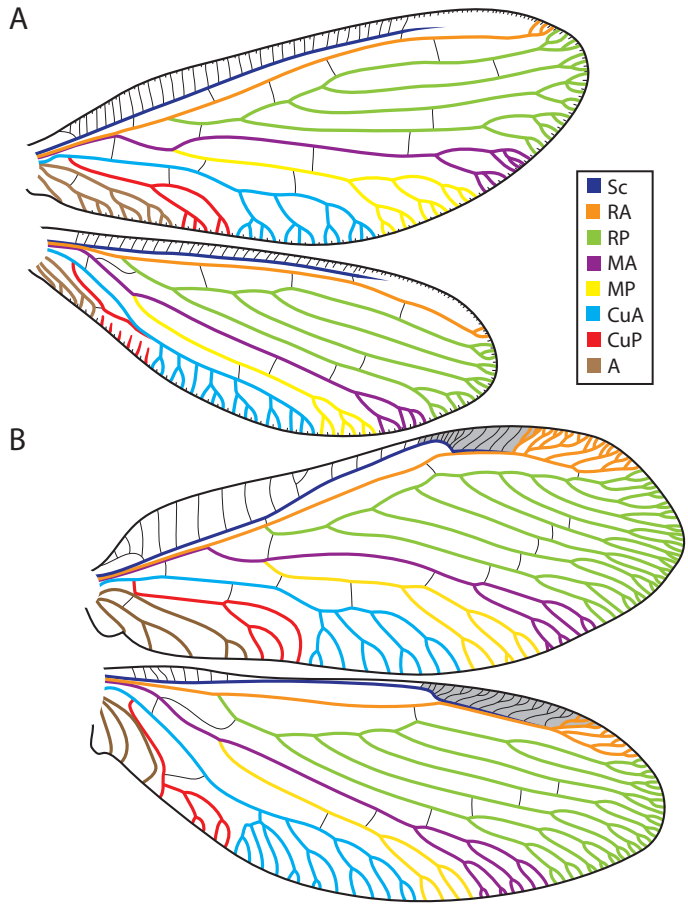

FIGURE 12. Line drawings of forewings and hind wings of a thorny lacewing and a mantispid lacewing. **A.** *Mucroberotha* sp. (Rhachiberothidae). **B.** *Plega* sp. (Mantispidae). See figure 2 for explanation of abbreviations.

fused in the forewing. There is an apical fusion of CuA and CuP in the hind wing, thereby forming a cubital loop (fig. 12A). The costal crossveins are simple, trichosors are present on the entire margin, a recurved humeral vein is present, and in the hind wing crossvein 1rp-m is sigmoidal. The pterostigma varies from inconspicuous to marked.

Species examined: *Mucroberotha* sp. (fig. 12A).

Family Mantispidae

Figure 12B, 13

Mantidflies are a large group of 395 species in 44 genera. Mantispid wings are rounded and slightly elongate and there are some fossil taxa in which the hind wing is shortened or even absent. R and M are fused at their base, as is also the case in Raphidioptera, Sisyridae, Berothidae, most Chrysopidae, and Rhachiberothidae. Apart of this one area of fusion, and

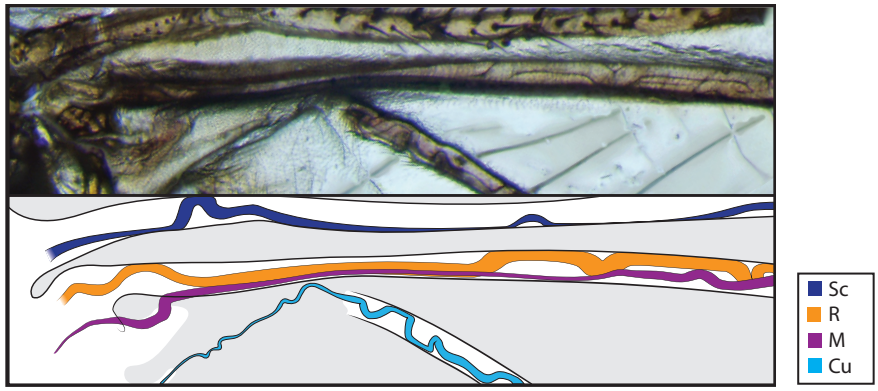

FIGURE 13. Microphotograph and line drawing of the wing base of *Plega* sp. (Mantispidae), showing the basal fusion of R and M, ventral view.

a short fusion of Sc and RA below the pterostigma in some mantispids, all other tracheae follow the apparent wing venation. Some genera of Mantispidae (e.g., *Climaciella* Enderlein) have an additional abscissa of R and M fused in the forewing, which results in the formation of a small cell where M rejoins R. Shortly after this second fusion, M diverges from R and descends toward the wing margin. This second point of fusion has at times served as further evidence for the notion of complete fusion of MA with R, but this does not seem to hold when considering the tracheation (see Discussion, below). The costal crossveins can be forked, a recurved humeral vein may be present, trichosors are present on the apical margin, and in the hind wing crossvein 1rp-m is strongly sigmoidal. The pterostigma varies from weakly to strongly marked.

Species examined: *Plega* sp. (fig. 12B, 13); other species examined but not figured: *Dicromantispa* sp., *Ditaxis biseriata* (Westwood), *Drepanicus chrysopinus* Brauer, *Climaciella* sp., and *Gerstaeckerella* sp.

Superfamily Chrysopoidea

Family Hemerobiidae

Figure 14

Brown lacewings are a large group of 591 species in 28 genera. The shape of hemerobiid wings is highly variable with short, elongate, rounded and falcate forms present and in some taxa the hind wing is reduced. The wing is characterized by the presence of multiple radial sectors, a character state approached only by the occurrence of up to three radial sectors in Ithonidae. Whether this is a duplication of RA or RP branches is uncertain, but the tracheation does not imply a difference between the multiple R branches. It was suggested that the multiple R sectors of Hemerobiidae are an argument in favor of MA basally fusing with R.

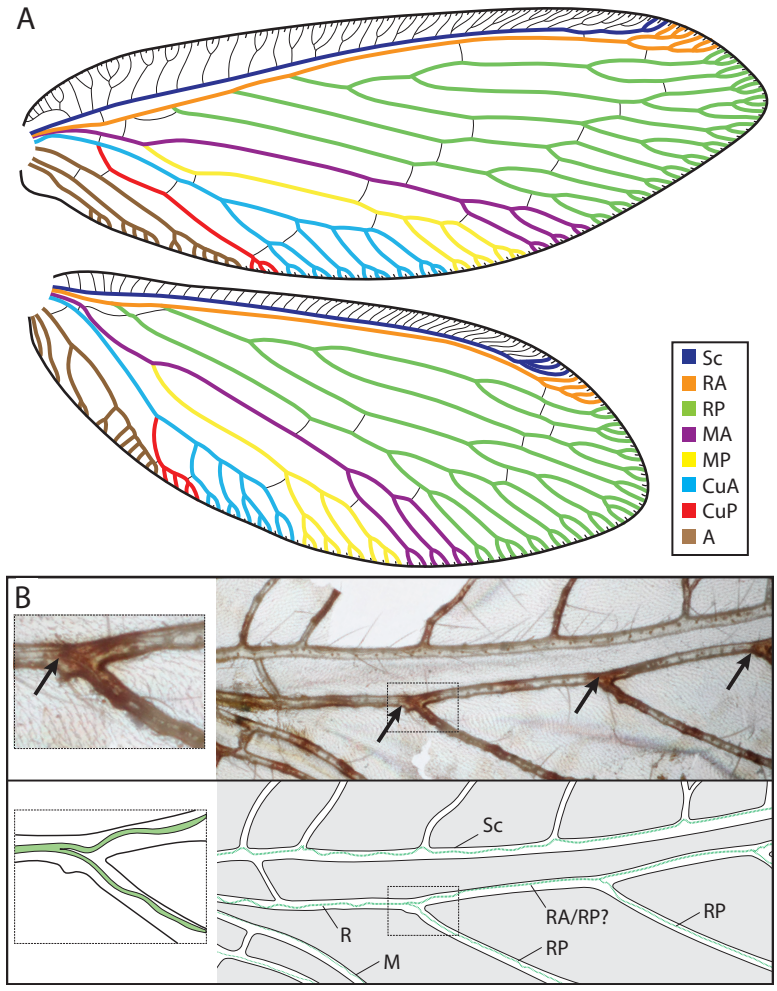

FIGURE 14. Forewings and hind wings of brown lacewings (Hemerobiidae). **A.** Line drawings of forewing and hind wing of *Hemerobius* sp. **B.** Microphotograph and line drawing of detail of multiple radial sectors of *Micromus posticus* (Walker) in ventral view; tracheae in green. See figure 2 for explanation of abbreviations.

The basalmost abscissa of R bears a single trachea and each split of the R branches is clearly detectable, with a trachea of equal size (fig. 14B), and therefore does not favor this view. As in Megaloptera, Psychopsidae, Nevrorthidae, and many Osmylidae, there are no fusions present in the fore- or hind wing. The costal crossveins are largely forked, trichosors are present along the entire or only apical margin, a recurved humeral vein is present and in the hind wing the crossvein 1rp-m is sigmoidal. The pterostigma varies from inconspicuous to marked.

Species examined: *Hemerobius* sp. (fig. 14A), *Micromus posticus* (Walker) (fig. 14B); other species examined but not figured: *Notiobiella* sp. and *Sympherobius* sp.

Family Chrysopidae

Figures 15–20

Green lacewings are the second largest family in Neuropterida, comprising 1415 species in three subfamilies. Most chrysopid wings are rounded to slightly elongate, although there are taxa with very broad wings. The venation of the chrysopid wing is one of the most variable and derived within Neuroptera, and the extent of fusion in the forewing and hind wing is unique among Neuropterida. Extensive fusion led to the formation of a pseudomedial (PsM) and pseudocubital (PsC) veins (fig. 16A), which appear as single longitudinal veins, but actually are composites of several longitudinal veins, and for some abscissae also of crossveins, even from different sectors. Due to this extreme fusion it is important to consider both the longitudinal sectors as well as crossveins in further detail. PsM is formed by RP and MA, although these are not completely fused or neither are present over the entire course of PsM. MA always forms a principal component of PsM, whereas MP is integrated into PsM for only one or two abscissa when a triangular intramedian (*im*) cell is present (figs. 1, 16B, 17A). PsC is formed by abscissae of RP, MA, MP, and even CuA. The amount of overlap between the longitudinal veins in PsM and PsC varies between the three subfamilies of Chrysopidae (below).

Fusion of these longitudinal veins progresses gradually from a relatively small degree in Nothochrysinae to greater complexity among the more derived Chrysopinae. As such, many nothochrysines lack some of those fusions leading to the formation of PsM and PsC (fig. 15A), whereas Apochrysinae and Chrysopinae display highly developed pseudoveins (figs. 15B, 16).

There is a general pattern to chrysopid, and especially chrysopine, wing venation. While C and Sc are simple with one branch each and no fusions, R, M, and Cu each have an anterior and posterior branch and are involved in several fusions. The number of RP branches varies greatly across each lineage, while wings have two MA, two MP, four CuA and two CuP branches. In rare cases, one or more of the longitudinal veins lack one of their branches. Because this general pattern is relatively consistent, it is possible to "estimate" the actual wing venation with the proposed system by simply looking at any given chrysopid wing, even in the absence of the tracheation. All RP branches can be traced from the origin of RP to the margin, and by tracing these branches one by one from the most distal RP branch back to the RP stem, it becomes apparent where along the margin the first branch of MA appears (i.e., the next marginal branch toward the base of the wing proximal to the posteriormost branch of RP). In the great majority of chrysopids this technique leads to a correct determination of the wing venation and each vein is accounted for from its origin to the wing margin.

Certain crossveins are always present in similar positions. In the forewing the first vein originating from RP is always a crossvein (often 1rp-m or 1rp-ma). This initial radial-medial crossvein descends most commonly from RP and only rarely from R (in which case it is 1r-m) (e.g., *Berchmansus* Navás), and joins M slightly proximal to, slightly apical to, or bordering the *im* cell. Two crossveins are present at the base of the forewing between M and Cu (1m-cu or 1m-cua and 2m-cua or 2mp-cua; figs. 15–17), although in some the second crossvein appears forked as it is actually borne by MP where the sector diverges from and then reattaches to MA (fig. 17C). In chrysopids

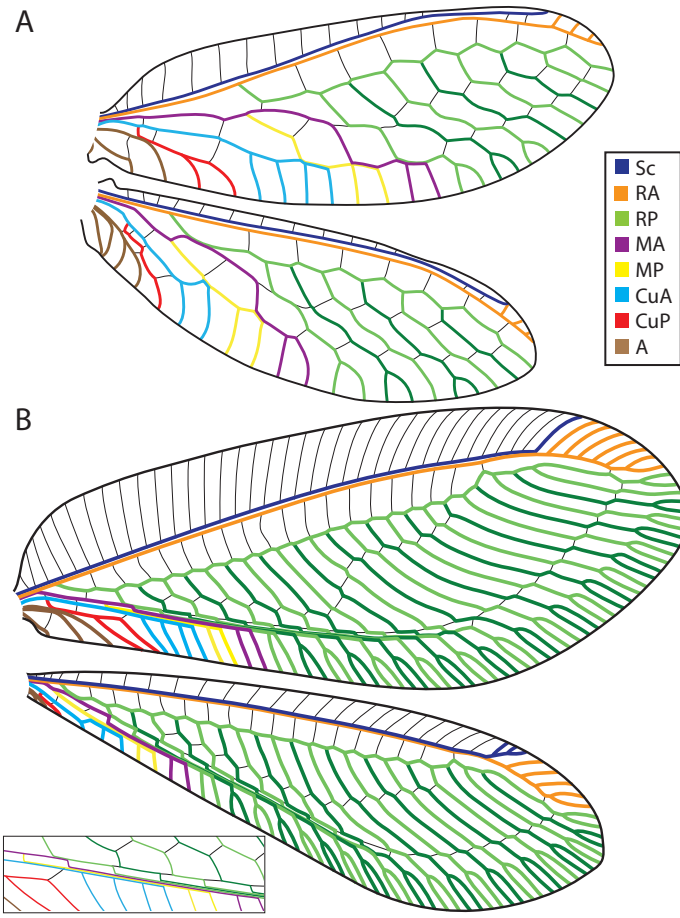

FIGURE 15. Line drawings of forewings and hind wings of green lacewings (Chrysopidae). **A.** *Hypochrysa elegans* (Burmeister) (Nothochrysinae). **B.** *Apochrysa lutea* (Walker) (Apochrysinae), with a detail of fusion in PsM (pseudomedial) and PsC (pseudocubital) (inset). See figure 2 for explanation of other abbreviations.

the apparent third crossvein between what is then PsM and PsC is not a crossvein at all but instead MP. The course of MP determines the shape of the *im* cell, with three principal shapes:

1. Triangular, with a crossvein forming one of the cells boundaries (here dubbed pseudotriangular); MP originates apical of 2m-cua and the boundaries of the triangular cell are formed by MA, MP, and 1ma-mp (fig. 17B). In this shape, common in primitive nothochrysines, MA and MP first fuse in PsC.

2. Triangular without a crossvein forming a portion of the cell (fig. 17A); MP originates proximal to 2m-cua, which is positioned against the *im* cell (and is therefore more properly an mp-cua crossvein); MP first fuses with MA in PsM at the apex of the *im* cell, hence its triangular form and is bounded completely by abscissae of M (here dubbed eutriangular).

3. Quadrangular; MP originates proximal to 2m-cua and is connected to CuA by that crossvein (thus properly an mp-cu crossvein); MA and MP are connected by a crossvein (1ma-

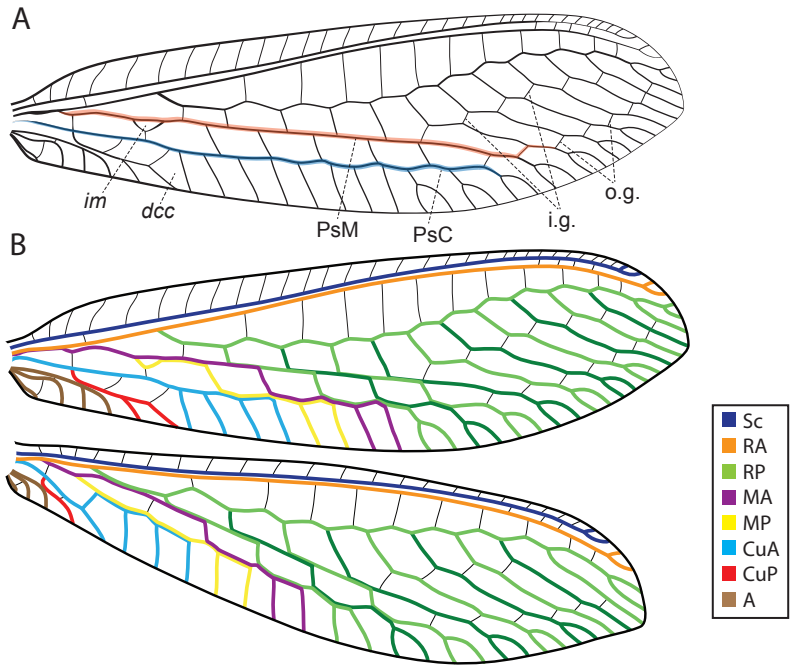

FIGURE 16. Line drawing *Cryptochrysa chloros* Freitas and Penny (Chrysopidae: Chrysopinae) **A.** Apparent wing venation of forewing, including traditional terminology. **B.** Forewing and hind wing, using revised, current vein terminology. Abbreviations: ***im***, (intramedian cell); ***dcc*****,** (distal cubital cell); **PsM,** (pseudomedial); **PsC,** (pseudocubital); **i.g.,** (inner gradates); **o.g.,** (outer gradates). See figure 2 for explanation of other abbreviations.

mp) and first fuse on PsC; the *im* cell is composed of MA, 1ma-mp, and two abscissae of MP. Of course, there are instances where the *im* cell is absent (fig. 17C).

There are always two crossveins between CuA and CuP, except for a few apochrysine wings, in which more crossveins are present. CuP diverges from CuA at a position at or near to 1m-cu, and immediately curves toward the wing apex, rendering CuP one of the veins easiest to detect, even in chrysopid wings with a complex pattern of venation. The traditional *dcc* cell is formed by the posteriormost branch of CuA, the anteriormost branch of CuP, and 2cua-cup (fig. 16A).

Although the forewing pattern varies across the subfamilies, the general pattern of tracheation in the hind wing is the same across these lineages. It is characterized by the partial fusion of MA with RP as well as MP with CuA (figs. 15, 16B, 17). MA and RP are fused shortly after RP diverges from R. Within this short fusion of RP and MA both tracheae are clearly visible. By comparison with the forewing, there is only one crossvein between M and Cu, and the apparent second crossvein is actually CuA arching forward to join MP. Both PsM and PsC are present but not as pronounced as in the forewing. MA and MP diverge relatively basal and always rejoin in PsC. CuP is rarely branched. An *im* cell is absent in the hind wing and the cell that appears as the traditional *dcc* is not formed by CuA and CuP, as in the forewing, but solely by abscissae of CuA.

In most chrysopids the costal crossveins are simple, but in some species they are forked, trichosors are always absent, a recurved humeral vein is absent, and in the hind

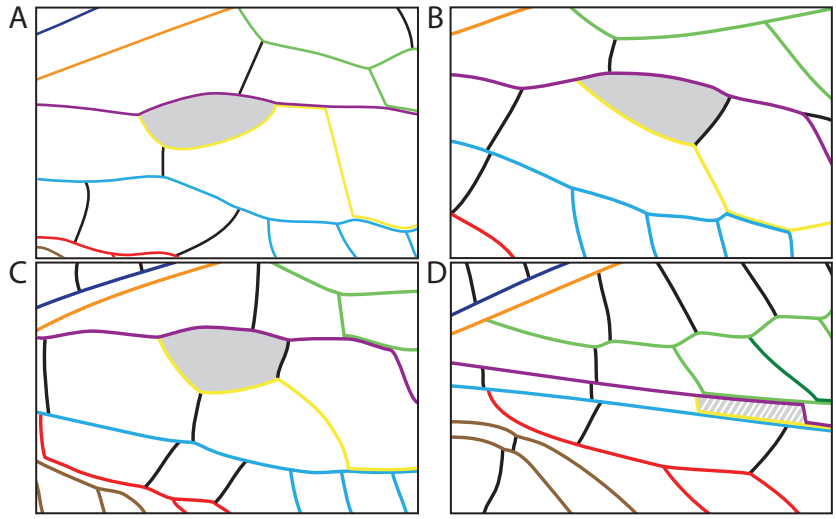

FIGURE 17. Line drawings of the variation of *mamp1* (first intermedial cell) in Chrysopidae; *mamp1* shaded in grey; refer to figure 16B for color legend. **A.** Eutriangular, *Chrysopa perla* Linnaeus. **B.** Pseudotriangular, *Hypochrysa elegans* (Burmeister). **C.** Quadrangular, *Nacarina balboana* (Banks). **D.** Absent, *Apochrysa leptala* (Rambur).

wing the crossvein 1rp-m is simple and not sigmoidal. The pterostigma varies from inconspicuous to marked.

Subfamily Nothochrysinae

Figures 15A, 17B, 18

Nothochrysinae comprise 19 species in seven genera with a circumtemperate distribution. The wing venation of this subfamily is the least derived within Chrysopidae. *Nothochrysa* McLachlan are the only nothochrysines with a strongly developed PsM and PsC, and therefore more greatly resemble the other chrysopid subfamilies (e.g., Brooks and Barnard, 1990). The remaining nothochrysine genera have a less developed venation in which there is little to no overlap of veins in the pseudoveins, rendering them less prominent (fig. 15A). The *im* cell is always present and is either pseudotriangular (fig. 17B) or quadrangular. A tympanal organ (see below) is absent in all Nothochrysinae (fig. 18).

Species examined: *Hypochrysa elegans* (Burmeister) (figs. 15A, 17B), *Nothochrysa californica* Banks (fig. 18); in addition, we examined representatives of all genera of Nothochrysinae except *Triplochrysa* Kimmins and *Leptochrysa* Adams and Penny.

Subfamily Apochrysinae

Figures 15B, 17D, 19

Apochrysinae comprise 26 species in six genera that have a pantropical distribution. Apochrysines have up to four overlapping longitudinal sectors in PsC (multiple RP branches, MA,

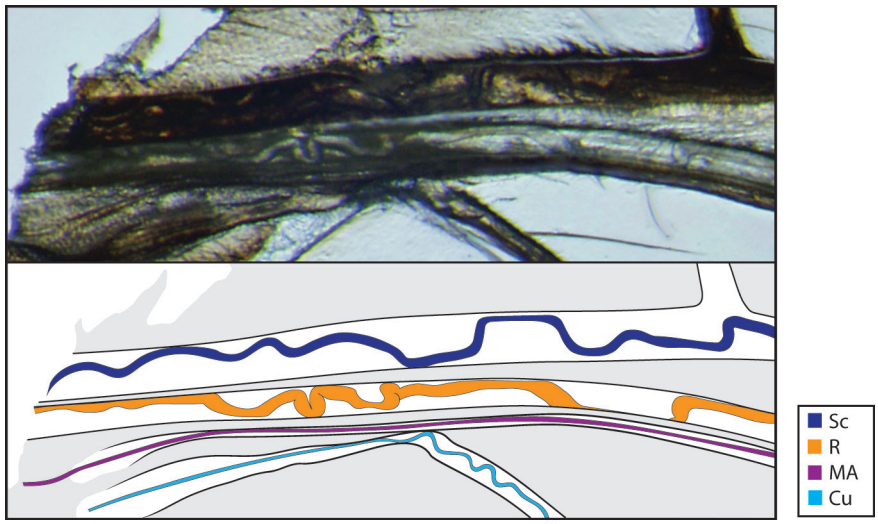

FIGURE 18. Microphotograph and line drawing of the wing base of *Nothochrysa californica* Banks (Chrysopidae: Nothochrysinae), showing that R and M are not fused, ventral view.

MP, and CuA), with up to six tracheae in one vein, thus making this subfamily appear to have the most-derived venational scheme among Chrysopidae. Although PsC is the product of many fused veins, PsM can be largely composed of augmented crossveins between longitudinal branches of RP (a condition never present in Chrysopinae, in which PsM is mainly composed of overlapping RP branches). The traditional *im* cell is always lacking in Apochrysinae (fig. 17D), with *mamp1* occupying the entire cell between PsM and PsC. Contrary to statements of earlier authors (Brooks and Barnard, 1990, Winterton and Brooks, 2002), we have not found a tympanal organ (see Chrysopinae, below) in Apochrysinae (fig. 19). R is only slightly thickened, as is Sc, and this condition is similar to that of the wing base of Nothochysinae (fig. 18), in which the tympanal organ is lacking. During this study we were not able to find any of the characteristic features of the chrysopine tympanum (fig. 20), but a further examination with histology would be valuable, and could more appropriately address this issue.

Species examined: *Apochrysa lutea* (Walker) (figs. 15B), *Apochrysa* sp. (fig. 19), *A. leptalea* (Rambur) (fig. 17D); in addition, representatives of all genera of Apochrysinae were examined.

Subfamily Chrysopinae

Figures 1, 16, 17A, 20

All other green lacewings fall within the largest subfamily, Chrysopinae. Although they are a diverse taxon, the wing venation among the group is fairly uniform. As in Raphidioptera, Sisyridae, Berothidae, and Mantispidae, the bases of R and M are fused in the forewing. Both PsM and PsC are consistently composed of fused longitudinal sectors. The *im* cell is most commonly eutriangular (figs. 1, 17A), sometimes quadrangular (fig. 17C), and in rare instances lacking. Chrysopinae are the only subfamily with a tympanal organ (fig. 20). This organ is

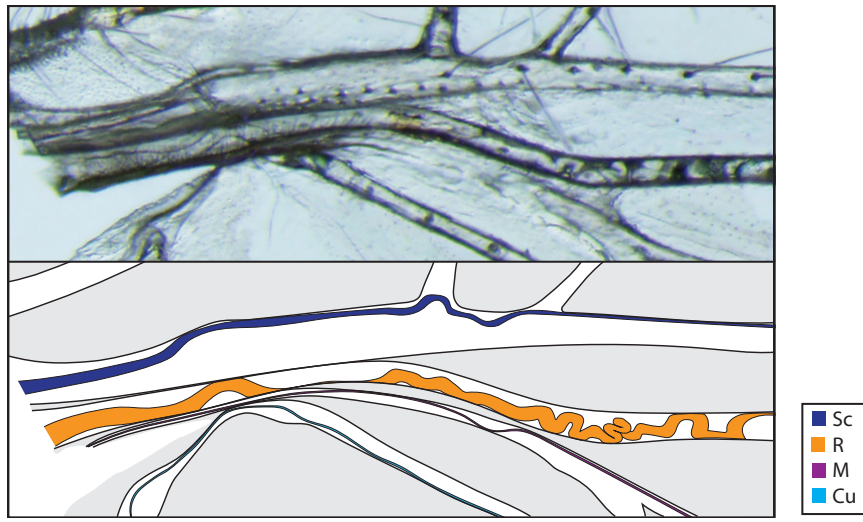

FIGURE 19. Microphotograph and line drawing of the wing base of *Apochrysa* sp. (Chrysopidae: Apochrysinae), showing that R and M are not fused, ventral view.

composed of R and M and is positioned at the base of the forewing. Both tracheae of the veins are visible within the organ, with R anterior and M (very thin) posterior. The four tribes of Chrysopinae (Ankylopterygini, Belonopterygini, Chrysopini, and Leucochrysini) show a uniform general pattern of tracheation.

Species examined: *Cryptochrysa chloros* Freitas and Penny (fig. 16), *Chrysopa nigricornis* Burmeister (figs. 1, 20), *Chrysopa perla* Linnaeus (fig. 17a), *Nacarina balboana* (Banks); in addition, we examined representatives of all chrysopine genera except *Himalochrysa* Hölzel, *Neula* Navás, *Nuvol* Navás, *Sinochrysa* Yang, *Tibetochrysa* Yang, and *Turnerochrysa* Kimmins.

DISCUSSION

Identifying actual vein homologies has an enormous impact on the interpretation of the evolution of lacewings. Because only true homologies should be the base for phylogenetic hypotheses, comparing structures that appear similar but are not truly homologous inevitably leads to erroneous results. Hypotheses of insect wing venation have repeatedly been revised over the past century (see Introduction, above), including debates over the utility of tracheation (Kukalová-Peck, 1983; Rehn, 2003; Béthoux, 2005, 2008). In Neuroptera, the tracheation of wing veins appears to be a useful tool for determining the actual paths of the longitudinal sectors. The results presented here give insight into the evolution of lacewings and on that basis, we propose a revised system to identify and name these veins in Neuropterida. Each wing examined showed a similar overall pattern and we could not find differences in tracheation between conspecific specimens.

Based on our observation of representatives of almost all neuropterid families we propose a revised nomenclature for veins and cells. Only veins with tracheation are longitudinal sectors (i.e., C: costa, Sc: subcosta, R: radius, M: media, Cu: cubitus, A: anal). These veins can be simple or branched and in the latter case these branches will be named,

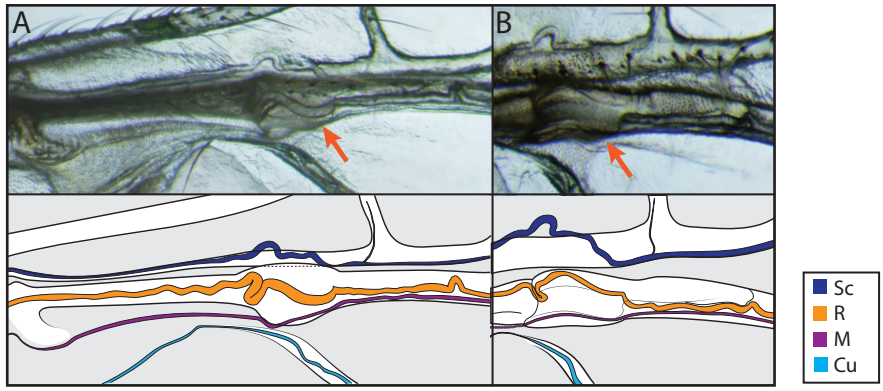

FIGURE 20. Microphotograph and line drawing of the wing base of *Chrysopa nigricornis* Burmeister (Chrysopidae: Chrysopinae), showing the tympanal organ and the associated basal fusion of R and M. **A.** Ventral view, tympanal organ indicated by arrows. **B.** Dorsal view.

according to their position, anterior or posterior. Thus, the single media, called M basally, splits into the media anterior (MA) and media posterior (MP). At the point of the first split in M the anterior portion becomes convex and the posterior portion concave, but this is not easily detectable in most modern taxa. For the sake of consistency, we advocate the use of RP over Rs for Neuropterida, rather than singling this sector out and using a different notation relative to other longitudinal veins. Rs was singled out largely given its more dramatically enlarged field, but this seems insufficient for an isolated change in vein nomenclature. In accordance to the revised system the two main branches of the radius are now named RA and RP. As is standard, further branching within the anterior and posterior sectors are denoted by a subscript number (in order from anterior to posterior) and following the abbreviation, such as MA_4 for the fourth branch of the media anterior.

The crossveins are named for the longitudinal sectors they connect and are numbered from proximal to apical. As is customary, they are denoted with lowercase letters and a hyphen between the two longitudinal vein abbreviations. In this manner, the first crossvein between R and M would be 1r-m, or the third crossvein between Sc and R is 3sc-r. For clarity, crossveins within a single field include the full name of that branch, e.g., 2ma-mp for the second crossvein between MA and MP, or $1ma_2$-ma_3 for the first crossvein between the second and third branch of MA. These very specific names will rarely be used, because the crossveins of descriptive and phylogenetic importance are most often the basal ones, but it is nonetheless an aid to workers if there is consistency in application. In the case of fused veins, the combined veins are employed, such as first crossvein between Sc and R+M being 1sc-r+m, while the first crossvein between R+M and Cu would be 1r+m-cu.

An analogous system for the naming of cells can be employed. The field of a longitudinal vein is thus defined as the area posterior to the longitudinal vein up to the next longitudinal vein of a different field. The denotation of cells depends on the two bordering longitudinal veins and the number of the cell within this field, from proximal to apical. The name is formed

by the italic lowercase abbreviation of these two longitudinal veins, without a hyphen, followed by the number of the cell. In this manner the second cell between R and M would be named *rm2*, and the first cell between MA and MP *mamp1*. Just as the naming system for crossveins, this can be extrapolated for all other longitudinal veins and all their branches. With names that are easier to grasp, these abbreviations can be applied more intuitively. The respective field is used for cells that are bordered by two longitudinal veins of two fields and "inter-" is added to the name when the cell is between branches of the same field, such as "second radial cell" for *rm2* or "first intermedial cell" for *mamp1*.

The great degree of fusion in the chrysopid wing adds difficulty to the consistent naming of veins in this taxon. The use of pseudomedia (PsM) and pseudocubital (PsC) should be maintained to correctly describe the path of the fused longitudinal veins. Most apparent crossveins between PsM and PsC are actually longitudinal veins and only the first two crossveins lack tracheation. The third apparent crossvein between PsM and PsC (or 3psm-psc) is actually MP, while the fourth is MA and the fifth is a branch of RP. The concept of PsM and PsC should not be extended to the naming of cells as to do so would complicate phylogenetic comparisons. Thus, in a typical wing of *Chrysopa* Leach the cell formerly known as *im* (intramedian) will be denoted as the first intermedial (*mamp1*), and the second intermedial cell is located between PsM and PsC (fourth cell between these two pseudoveins), but will simply be called *mamp2* so as to correctly denote the homologous veins it resides between. Accordingly, Apochrysinae, which lack the traditional *im* cell, do have a *mamp1*, which merely appears as a cell between PsC and PsM (fig. 17D).

The Controversy of 'MA'

One of the challenges in the venation of Neuropterida, and other insect lineages, is the basal path of the media anterior. The two competing hypotheses are that MA is either basally fused with R and therefore its path is encompassed within the first branching point within RP (i.e., RP's posteriormost branch), versus the notion that MA is not fused with R at the base but instead splits off from M at the same point as MP. Most entomologists have adopted the notion of basal fusion of R and MA (e.g., Orthoptera: Béthoux and Nel, 2001; Odonata: Rehn, 2003, Mantodea: Béthoux and Wieland, 2009, Holometabola: Haas and Kukalová-Peck, 2001) including Neuroptera (Riek, 1970; Aspöck et al., 1980; Adams, 1996; Nel et al., 2005). However, the evidence supporting these two alternative hypotheses leaves much to be desired.

Resolution of the actual path of MA has a significant influence not only over the nomenclature of particular veinal elements in the wing, but also the interpretation of homologies and recognition of shared character states and therein relationships among major lineages within Neuropterida. Fusion of MA with R has been advocated based on the paired nature of longitudinal veins, the pattern of corrugation (fluting), and the course of longitudinally oriented "crossveins" such as the sigmoid vein or arculus (interpreted thereby as abscissae of longitudinal sectors rather than as an augmented crossvein) (e.g., Kukalová-Peck, 1983). In the hypothetical primitive insect wing presented by Kukalová-Peck and Lawrence (2004)

(itself based on the earlier works of Kukalová-Peck as cited in the Introduction, above), each sector has paired veins originating from their associated axillary sclerite. The lack of MA as an individual branch at the wing base in most modern insects was therefore interpreted as the result of a fusion with R, with MA reappearing at the first branching of RP.

The sigmoid vein (fig. 8) in the hind wing of Neuropterida has traditionally served as one of the most compelling pieces of evidence for the fusion of MA into R (e.g., Megaloptera, Ithonidae, Hemerobiidae, Rhachiberothidae, Mantispidae, etc.: refer to individual family accounts, above). The sigmoid vein is an elongate, arched vein between R or RP and M (figs. 2A, 7A, 8, 10, 12B and 14A), i.e., 1r-m, 1rp-m, or 1rp-ma. It has been argued that its curved form and longitudinal orientation indicate it to be an abscissa of a longitudinal sector, specifically a portion of MA (Adams, 1996; Kukalová-Peck and Lawrence, 2004). However, in several families the same vein appears as a typical, transverse crossvein (e.g., Nymphidae, Ascalaphidae, Berothidae, Chrysopidae: refer to individual family accounts, above). The absence of tracheation favors the conclusion that the sigmoid vein is nothing more than a distorted and elongate crossvein in certain lineages. Moreover, the sigmoid crossvein would have little bearing on reconstructing a hypothesis for the groundplan venation of the insect wing as Neuropterida are highly derived pterygote insects, well removed from the base of Paraneoptera, let alone Neoptera or Pterygota as a whole.

In opposition to the R+MA hypothesis are our observations here, which found dual tracheation in those places where M (not just MA) is basally fused with R, and the absence of such dual tracheation in taxa where MA is supposedly fused with R and RP. Most importantly, there is no trachea running through the sigmoid vein, revealing it to be nothing more than a modified crossvein. We also could not find a trachea running from the medial plate to the base of R as would be supposed under the R+MA hypothesis.

Inferring modern wing-venation homologies from the notion of a basally fused R+MA raises two difficulties. The first is a minor point but of some significance: M is not the only vein that is formed of a singular stem at the base in the modern wing, at least the more derived wings of Neoptera. Like the media, all of the major veins are single stems at their base rather than paired anterior (convex) and posterior (concave) stems.

The second point and, in our opinion, the most difficult for the R+MA hypothesis is the original evidence itself for the notion of paired stems at the wing base. This scheme was based on purported characters in the prothoracic "wing" of the Carboniferous *Stenodictya lobata* (Brongniart). This species belongs to the Palaeodictyoptera, one of a series of orders in the extinct superorder Palaeodictyopterida (Grimaldi and Engel, 2005). Palaeodictyopterida, while certainly more basal among Pterygota than any Neoptera are still rather phylogenetically divorced from the pterygotan ancestor, a hypothetical taxon that would have existed in the earliest Devonian or even latest Silurian (Engel and Grimaldi, 2004; Engel et al., 2013). There is no reason to surmise that *S. lobata* embodies venation identical to the groundplan for Palaeodictyopterida, let alone Pterygota. Most importantly, there is no reason to believe the venation of prothoracic winglets is more reflective of the groundplan wing, particularly as the presence of prothoracic winglets is not clearly plesio-

morphic, although such immoveable winglets are present in putatively primitive forms of Odonatoptera, Palaeodictyopterida, and even some Neoptera. Any pattern of venation in these winglets may be autapomorphically augmented relative to their particular function. Moreover, the actual meso- and metathoracic wings of such extinct taxa do not demonstrate clear evidence for paired stems at the wing base. Indeed, in *S. lobata* the meso- and metathoracic wing venation is congruent with other insects, with singular stems at the base. In fact, no extinct or extant taxa are documented in which there are paired stems at each axillary point (i.e., paired stems at the base for each longitudinal vein system). Moreover, recent evidence from the nymphal pads of Palaeodictyoptera (Prokop et al., 2017) tends to support Hamilton's (1972a) hypothesis regarding the groundplan venation for insect wings, one that does not include paired, basal stems.

The combination of the above tends to refute the hypothesis that MA is fused into the stem of R at its origin from the axillary sclerite. Instead, tracheation and the lack of convincing evidence for the "paired stems hypothesis" concurs with a more likely origin of MA from the stem of M.

An enigma remains in that there is a change in fluting within the posteriormost branch of RP, and the corrugation (convexity versus concavity) of the longitudinal sectors has served as convincing evidence for vein identities (e.g., Redtenbacher, 1886; Kukalová-Peck, 1983; Béthoux and Nel, 2001; Rasnitsyn, 2007). Such evidence has been used to identify and trace the course, loss, or fusion of particular longitudinal sectors. In several modern insects the corrugation has become modified or lost. Given the derived position of Neuropterida as well as the numerous other observations we have outlined above, it seems most likely that this is merely a derived feature within RP rather than definitive evidence for MA's presence within this sector. While we cannot absolutely demonstrate such a hypothesis at the moment, it remains more convincing than the alternative R+MA hypothesis owing to the lack of any observational support for the latter. Accordingly, we conclude that there is presently no compelling evidence in favor of the R+MA hypothesis, and that instead MA appears to have a simpler course than previously surmised. It is hoped that advances in developmental biology and an understanding of vein formations during ontogeny may provide further insights, and, it is hoped, corroborate the patterns we have documented here.

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