
Phylogeny of the Hymenoptera: a reanalysis of the Ronquist *et al.* (1999) reanalysis, emphasizing wing venation and apocritan relationships

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Ronquist *et al.* (1999) recoded Rasnitsyn's (1988) analysis to effect an explicit numerical cladistic analysis of his data. Here we examine their analysis and reveal that much of the resolution obtained for apocritan relationships is dependant on reductional wing characters. The wing characters in their matrix are replaced with a revised set of wing characters and reanalysed using strict parsimony. For apocritan taxa the resulting strict consensus tree is considerably less resolved, but perhaps preferable as a more conservative starting point in the continuing investigation of higher level hymenopteran relationships.

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Introduction

Rasnitsyn (1988) proposed a revamping of higher level hymenopteran classification based on an 'intuitive' cladistic methodology. Ronquist *et al.* (1999) recoded Rasnitsyn's data in an explicit manner and conducted numerical cladistic analyses. The strict consensus tree of their parsimony analysis of extant taxa is modified and redrawn in Figs 1, 2. Although they did not present a comparable tree for symphytan relationships (Fig. 1), the comparable tree for apocritan relationships is illustrated in their fig. 7 (Ronquist *et al.* 1999). Using their matrix and settings, namely, 1000 random addition sequences, retaining one tree in each step, followed by tree-bisection-reconnection swapping (PAUP version 4.0d65; Swofford 1999), the senior author (MJS) reanalysed the matrix and obtained identical results (Figs 1, 2) except that the Austroniidae + Monomachidae clade and the Pelecinidae + Proctotrupidae clade are reversed. Ronquist (personal communication) agrees that a mistake was made in their publication and he concurs that the topology presented here for the Apocrita (Figs 1, 2) is correct with respect to their data set.

When wings are mapped on to this cladogram (Fig. 2) it is apparent that the topology suggests a progressive loss of wing venation that parallels the appearance of higher taxa. The primary question that this paper asks is: is this correlation a product of the phylogeny of the Apocrita, or is the topology dependent on erroneous coding of wing characters, most of which are reductional? The goal is to improve the Ronquist

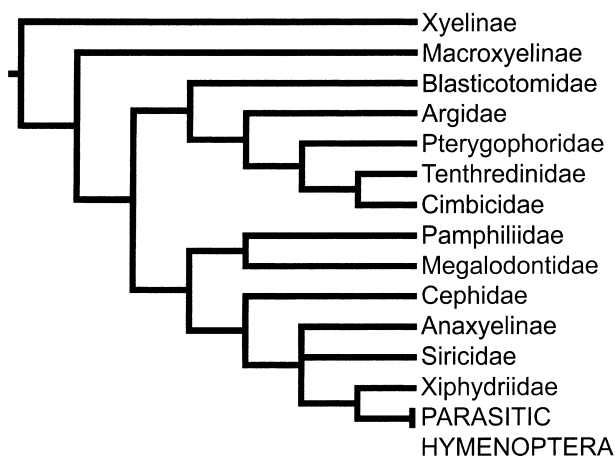


Fig. 1 Strict consensus tree for the Symphyta except Orussidae, based on the matrix of Ronquist *et al.* (1999).

et al. matrix such that it can be employed as a base for further investigations into the phylogeny of the Hymenoptera.

Methods

To address this question, the Ronquist *et al.* matrix was re-analysed using the same software and settings they employed (see above), but with their 39 wing characters deactivated (characters 72–110). The wing characters constitute only

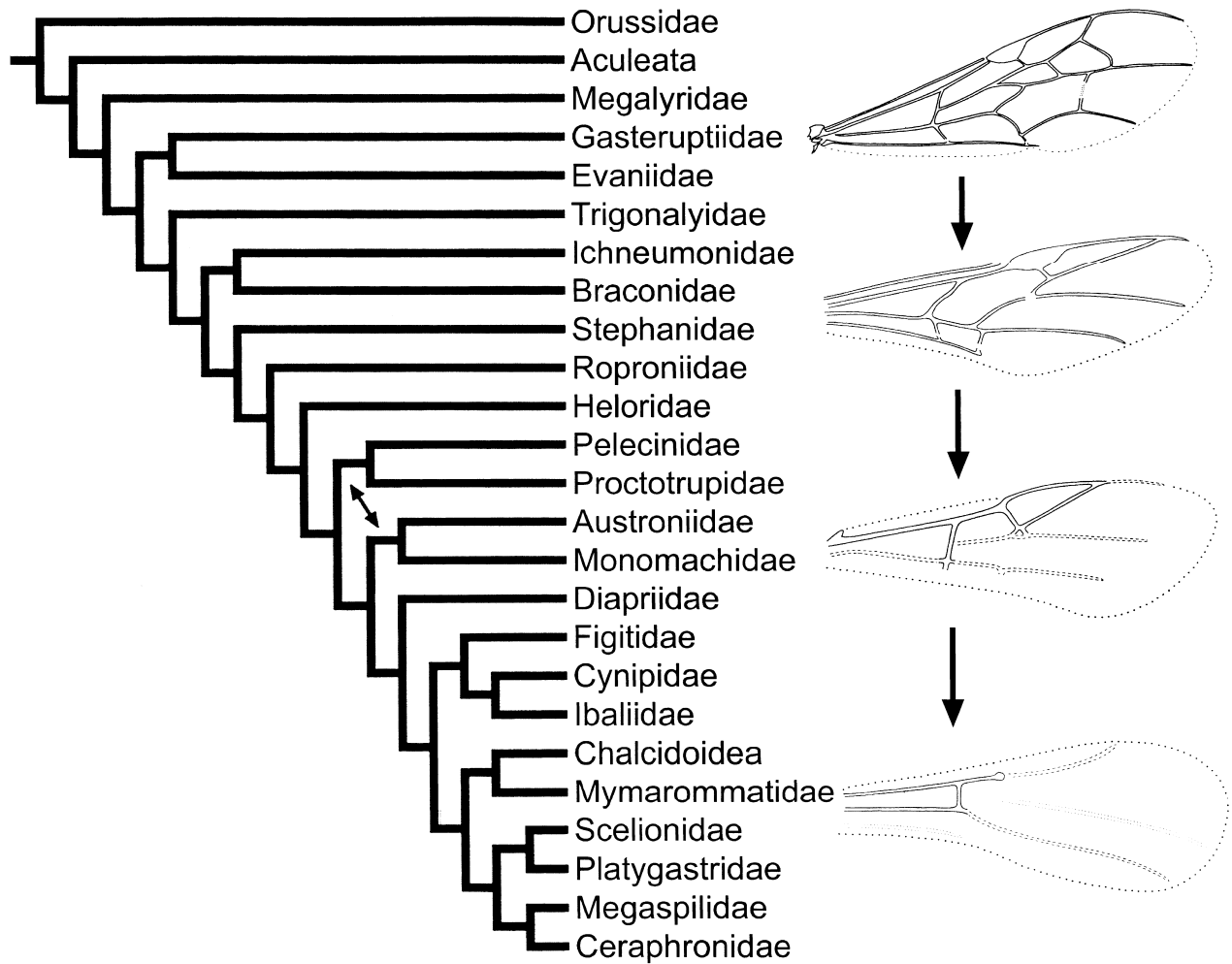


Fig. 2 Strict consensus tree for parasitic Hymenoptera based on the matrix of Ronquist *et al.* (1999). The double-headed arrow indicates a correction of the tree reported by Ronquist *et al.* The wings illustrate the progressive loss of wing venation implied by the tree.

22.5% of their matrix and these include a few characters that are not venational but that appear to be associated with size reduction, e.g. character 97, jugal lobe presence or absence. If the topology of the cladogram remains similar, with wing characters deleted, one can assume that the topology is not solely a product of wing characters. However, if there is a drastic collapse in resolution or if major topographical changes occur, a fundamental dependence on wing characters is demonstrated.

Terminology for wing characters follows Huber & Sharkey (1993).

Results

The analysis of the Ronquist *et al.* matrix without wing characters resulted in 324 minimum length cladograms, with the following statistics: consistency index (CI), excluding uninformative characters = 0.41, retention index (RI) = 0.79,

rescaled consistency index (RC) = 0.32. The strict consensus tree is presented in Fig. 3. The topology of the Symphyta section of the cladogram is isomorphic with that generated by the original matrix (Figs 1, 2), but that of the parasitic Hymenoptera (including Orussidae) is mostly unresolved. Eleven of the 23 nodes disappear, and of the 12 that remain most are obvious relationships within superfamilies that have been recognized for a considerable time, i.e. Braconidae + Ichneumonidae, Figitidae + Cynipidae + Ibalidae, Chalcidoidea + Mymarommatidae, Scelionidae + Platygasteridae, and Megaspilidae + Ceraphronidae. Effectively, all that is interesting about the resolution of the Apocrita is dependent on wing characters, most of which are reductional or loss characters. It seems appropriate therefore to investigate the wing characters to judge their quality. Before this, the nature and difficulties associated with wing characters are outlined in the following section.

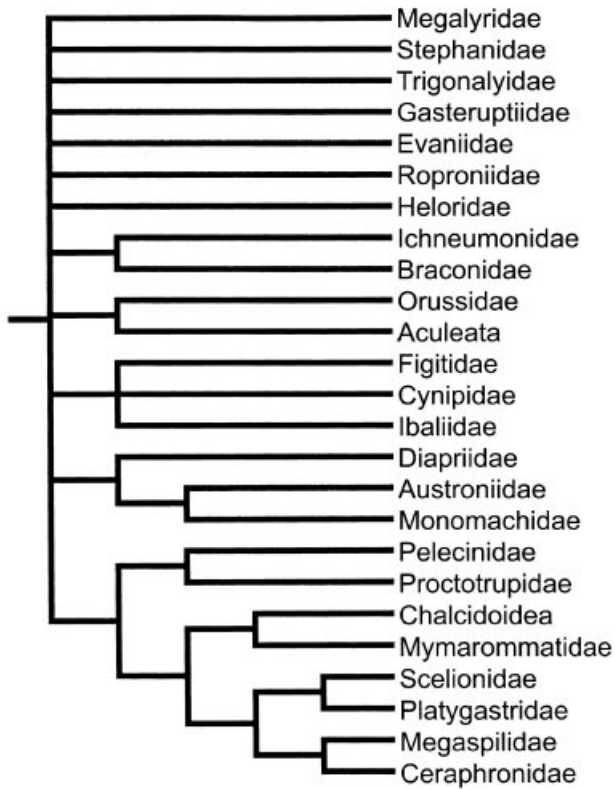


Fig. 3 Strict consensus tree from the matrix of Ronquist *et al.* (1999) with wing characters deleted.

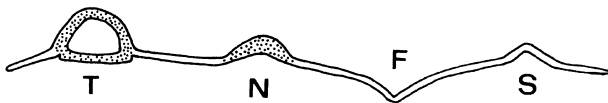


Fig. 4 Cross-section of a hypothetical wing illustrating vein nomenclature. T, tubular vein; N, nebulous vein; F, wing fold; S, spectral vein. Redrawn from Mason (1986).

The trouble with wing characters

Most of the apocritan venational characters that are readily observable are reduction or loss characters. These have two major deficiencies: they are difficult to code subjectively and they are prone to much homoplasy.

According to the standards proposed by Mason (1986) wing veins are manifested in three forms, i.e. tubular, nebulous, and spectral (Fig. 4). To paraphrase Mason: 'Tubular veins are hollow and therefore appear darker along their edges than they do medially. Nebulous veins are not tubular and are usually pigmented and darkest medially where they are thickest. Their edges are not clearly defined, thus the name nebulous. Spectral veins are not swollen nor pigmented and are indicated only by a flexion of the wing surface. Thus, when the wing is flattened by a slide cover, spectral veins are no longer observable.'

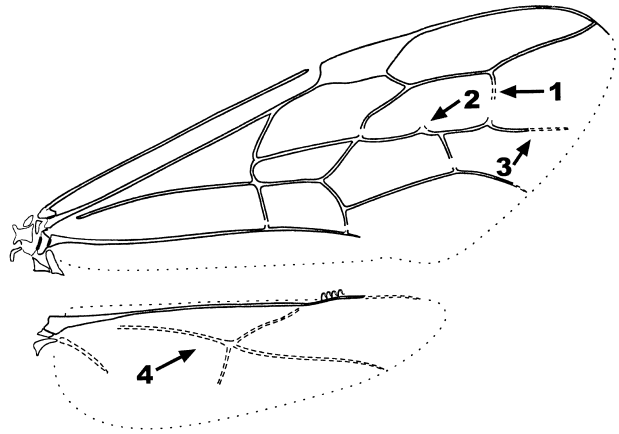


Fig. 5 Hypothetical ground plan venation of the Trigonalidae showing variability in states of wing veins. 1, cross-vein 3r-m; 2, cross-vein 2r-m; 3, vein M; 4, hind wing veins. Redrawn from Roy (1995).

There appears to be a logical order to these character states: tubular — nebulous — spectral — absent. It must be decided whether to include these variations of presence or simply to code veins or abscissae as present or absent. There are many possibilities. For example, venational characters can be coded as 'tubular or not tubular', or any indication of a vein could be considered as presence. Veins and/or abscissae could be divided into two-state characters in other ways such as tubular or nebulous vs. spectral or absent.

Decisions have to be made regarding veins and vein abscissae that are partially absent or that are composed of sections that appear in different states. For example, is a vein considered tubular if it is tubular for more than half its length? In Fig. 5, cross-vein 2r-m (indicated with the numeral 2 in the figure) could be considered present or absent as there is only a trace of it left. Cross-vein 3r-m and the apical abscissa of vein M, indicated with the numerals 1 and 3, respectively (Fig. 5), could be coded as present, absent, tubular, nebulous, or polymorphic as all states are present. Most of the hind wing venation is not tubular and could be coded as absent if tubular(ness) is the sole criterion.

Another problem with wing veins is the extent of convergent evolution in the character system. When apocritan Hymenoptera evolve into smaller forms, wing venation disappears and tends to concentrate anterobasally. This is exemplified in most superfamilies and even within many families. For example, Fig. 6 illustrates three taxa: Bethyliidae, Pelecinidae (note: fossil pelecinids are very tiny, much smaller than extant taxa), and Diapriidae, that have undoubtedly lost most of their wing venation convergently as each has closely related taxa with far more complete venation. Notice that it is the same veins that survive the reduction process. This intra-taxon variation casts doubt on many reductional vein characters.

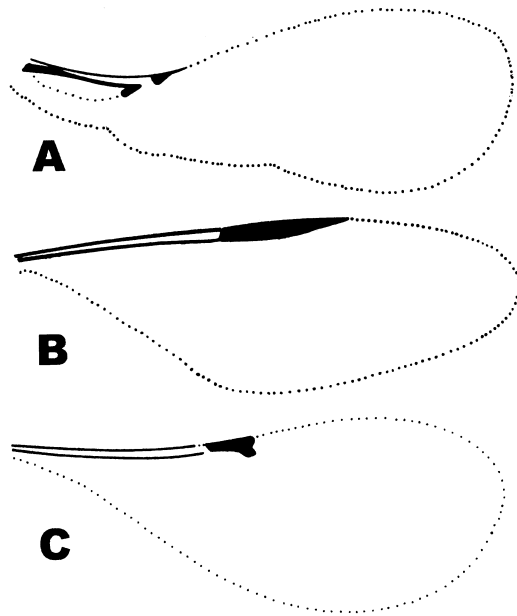


Fig. 6 A–C. Fore wings of three families of Hymenoptera illustrating convergent evolution of reduced venation. —A. Bethyliidae. —B. Pelecinidae. —C. Diapriidae. Redrawn from Goulet & Huber (1993).

The next section of this paper deals with the manner in which Ronquist *et al.* dealt with these and other problems associated with the coding of wing vein characters.

One of the most outstanding difficulties with their coding is that of continuous characters. Eight wing characters (72, 76, 77, 84, 90, 91, 98, 106) refer to continuous traits; in all of these cases there is no objective definition of the character states. For example, character 72 poses three states for the size of the pterostigma: '(0) large, distinct; (1) small; (2) absent'. How does one distinguish between large and small? As another example consider character 76. 'Costal cell of fore wing: (0) wide; (1) moderately narrow; (2) very narrow; (3) missing.' The reader has not the means to differentiate among the first three character states.

Character 82 is a rare example of a continuous character with an objective definition, but the definition appears to be *ad hoc*. 'Cross-vein 1r of fore wing: (0) short, equal to or shorter than 2r; (1) long, longer than 2r; (2) incomplete or absent.' The authors do not provide a justification for dividing this continuously varying character into three states. Furthermore, the character seems to be a composite of two independent characters. These are, the length of the vein and the presence or completeness of the vein. Because the authors define this character as ordered (012) they (inadvertently?) increase the cost of a loss or reduction of the vein from the short state (state 0 to state 2). If there is some justification for this assumption it is not presented in their discussion.

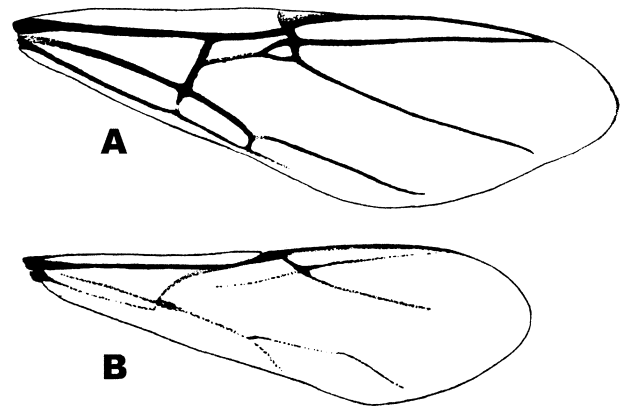


Fig. 7 A, B. Fore wings showing the similarity of venation when all vein qualities (tubular, nebulous, and spectral) are considered. —A. Ibaliidae. —B. Leucospidae. Redrawn from Bradley (1955).

The 20 characters (73, 75, 79, 80, 83, 85, 86, 87, 89, 92, 93, 95, 99, 100, 101, 102, 104, 105, 108, 110) that concern the presence, absence, and condition of veins as tubular, nebulous, and spectral are treated inconsistently. They are coded in at least five different ways: 1. '(0) present; (1) absent'; 2. '(0) tubular; (1) not tubular (including absent)'; 3. '(0) tubular to nebulous; (1) spectral to absent'; 4. '(0) tubular; (1) nebulous; (2) absent'; and 5. '(0) at least partly tubular; (1) not at all tubular'. Sometimes a nebulous vein is considered present sometimes not. Sometimes nebulous is considered synonymous with tubular. Other times nebulous is considered synonymous with absent, etc. Why there is variation in these codings is not clear, but it probably has a great influence on tree topology.

Replacement set of wing characters

It is the aim of the remainder of this paper to introduce a set of wing characters that improves on that discussed above.

Roy (1995) produced a matrix of 55 wing characters. Of these, the senior author (MJS) selected and modified 37 (see Appendix). These were chosen because they are potentially informative and can be objectively defined. All presence-absence venational characters are simply coded as such, i.e. present or absent. No attempt was made to code them into multistate characters to include their condition as tubular, nebulous, or spectral due to the difficulties discussed previously. This coding greatly decreases the weight of reductional wing characters, but it also makes them potentially more informative. Consider Fig. 7 which is redrawn from Bradley (1955). When all chalcidoid and cynipoid veins are considered, regardless of their state, there is a great similarity between the ground plans of Chalcidoidea and Cynipoidea. If the veins are coded as tubular vs. not tubular these similarities (potential synapomorphies) are lost.

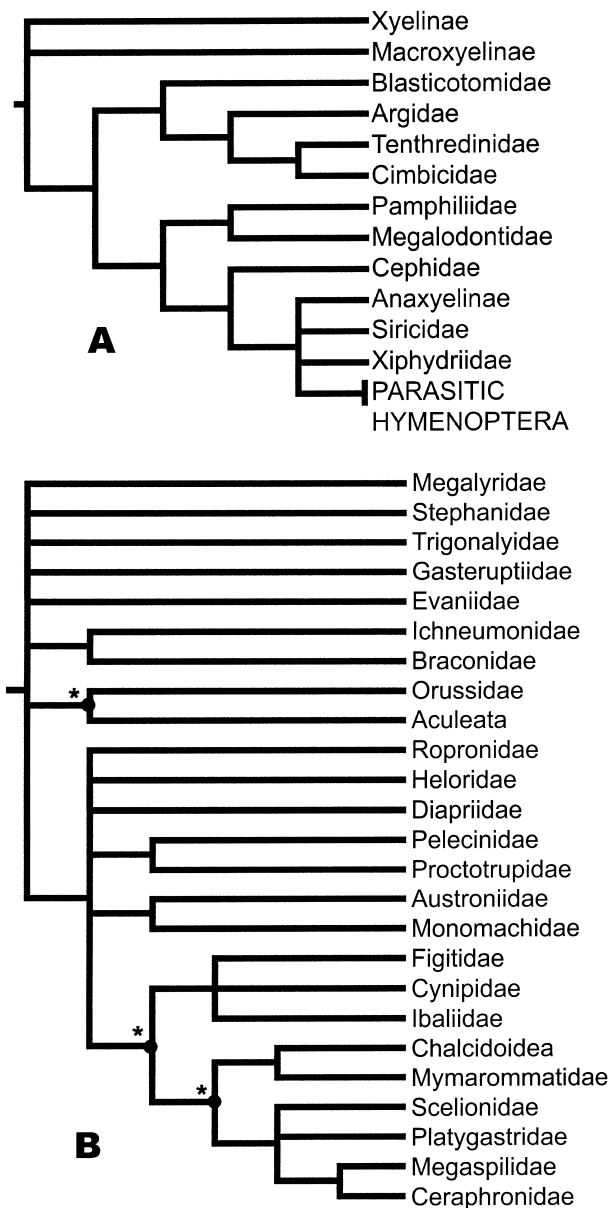


Fig. 8 A, B. Strict consensus tree derived from a hybrid matrix employing the wing characters from the Appendix (see also Table 1) and the nonwing characters of Ronquist *et al.* (1999). Branches with an asterisk collapse when a 30% ambiguity filter is applied (see text). —A. Symphyta except Orussidae. —B. Parasitic Hymenoptera.

The matrix of wing characters is presented in Table 1 and is also available at <http://www.uky.edu/~mjshar0>. Each taxon was scored using a hypothetical ground plan for each taxon. Usually, if a vein was present in any member of a taxon it was included in the ground plan. The few exceptions to this rule are carefully detailed in the Appendix. Continuous characters are few but these are defined with

exact comparisons to other structures and some discussion is included in the Appendix to enable the reader to repeat the observations.

Reanalysis

The senior author (MJS) deleted Ronquist *et al.*'s 39 wing characters and replaced them with 37 characters. This revised data set can be found at: <http://www.uky.edu/~mjshar0>. MJS then ran the data with the same software and settings as those reported for Ronquist *et al.*'s original parsimony analysis (see above). Two taxa, Pterygophoridae and Bradynobaenidae, were removed from the data set because specimens were not available for study. The analysis resulted in 88 minimum length trees, each with a length of 690 steps. The statistics for the trees are: CI, excluding uninformative characters = 0.38; RI = 0.77; RC = 0.29. The strict consensus tree is reproduced in Fig. 8. The results for the Symphyta (minus Orussidae) are isomorphic with those obtained from the Ronquist *et al.* matrix except that two nodes collapse. Contrastingly, relationships among the parasitic Hymenoptera are largely unresolved, much as in the results obtained with the wing characters deleted (Fig. 3). Once again, what resolution there is occurs mostly for family groupings within superfamilies whose monophyly has been strongly supported for many years. An exception to this is the unlikely sister-group relationship suggested for Aculeata + Orussidae, which is also present in the matrix lacking wing characters. The data set was then analysed with a 30% ambiguity filter using the Ratchet option of Winclada/Nona (Goloboff 1994; Nixon 1999). This has the effect of inactivating all characters for which character states are unknown for 30% or more of the taxa. Platnick *et al.* (1991) showed that spurious cladograms can be generated from matrices with missing entries. Running the matrix with an ambiguity filter is a confidence test of sorts to see if clades might be the product of characters that are poorly known across all taxa. The branches marked with an asterisk in Fig. 8 are those that collapse with the 30% ambiguity filter. These include, not only the Orussidae + Aculeata clade, but also two basal clades within the microhymenoptera.

Discussion

The strict consensus tree (Fig. 8), obtained from the modified set of wing characters, does not offer much resolution, but this is not a negative reflection of the wing characters and codings. The tree represents most of what wing veins have to offer for the reconstruction of hymenopteran phylogeny. This may be considered to be a starting point for further research into the phylogeny of the Hymenoptera, a matrix that is not biased by an overabundance of potentially nonindependent wing characters. Ronquist *et al.* did an excellent, numerical cladistic interpretation of Rasnitsyn's (1988) intuitive analysis.

The problem lies with the character coding and the non-cladistic nature of many of Rasnitsyn's original characters. It was not the intention of Ronquist *et al.* to create a solid base for incorporation with newly discovered data. They went so far as to state 'nor does it [their reanalysis] represent the optimal coding of the included data' (Ronquist *et al.* 1999: 36). Their intention was to put Rasnitsyn's (1988) characters, regardless of their quality, into a cladistic framework so that it could be properly evaluated (Ronquist personal communication).

The obvious next step is to glean the cladistic characters from the rest of the Ronquist *et al.* matrix. To this matrix the many other characters in the literature may then be added (for example, the Basibuyuk *et al.* matrix at <http://www.bio.ic.ac.uk/research/dLq/matrix.pau>). Fortunately, the nonwing characters of Ronquist *et al.* are generally more objectively defined than the wing characters, although some clearly need reworking, e.g. their character 111: 'Length and shape of female metasoma: (0) short, laterally compressed; (1) moderately elongate, slightly depressed; (2) distinctly elongate and slender; (3) moderately elongate in normal repose but strongly extendable in length during oviposition. Ordered 0123'. This character and others are rather confused and ill-defined. However, a remedy is beyond the scope of this paper.

Acknowledgements

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Appendix

Wing characters

Fore wing

- Costal vein (C): present (0); absent (1). The presence/absence of C is a relatively consistent character within families. In Megalyridae, however, it is variable.
- Median vein (M), abscissa distad Rs + M: present (0); absent (1). In Evaniidae, this abscissa of M becomes much narrower shortly after it separates from Rs + M (about half the thickness of the preceding abscissa); a similar condition is present in Gasteruptiinae (Gasteruptiidae), although the constriction occurs slightly more distally. This vein is tubular in the Symphyta (except Orussidae), most Aculeata, Ichneumonidae and Trigonalyidae. It is nebulous in Orussidae, Megalyridae, Evaniidae, Vanhorniidae, Peradeniidae, Pelecinidae, Diapriidae, Scelionidae, Chalcidoidea, and most Cynipoidea, Chrysidoidea, Bradynobaenidae, Sierolomorphidae, and Heterogynidae. It is spectral in Platygastriidae. It is absent in the ground plan only in Ceraphronoidea, but it has been lost independently in other Hymenoptera with reduced wing venation (some Platygastroidea, Chalcidoidea, Cynipoidea, and Diapriidae).
- Vein Rs + M: present (0); absent (1). Rs + M is tubular in all Symphyta and macrohymenoptera (except Ichneumonidae and a few derived or specialized braconid subfamilies and aculeate families), in Ibaliidae, and in some Proctotrupoidea (Renyxidae, Heloridae and Roproniidae). It is nebulous in Orussidae, Bethyloidea, Pelecinidae, Vanhorniidae, Chalcidoidea, and most Cynipoidea. This vein (or the first abscissa of this vein) is absent in all other taxa, even in groups where the venation is

relatively complete and tubular (Monomachidae and Austroniidae). In basal genera of Ichneumonidae, e.g. *Megarhyssa*, *Pimpla*, a stump of this vein is present joining 1m-cu.

4 Second anal vein (2A), abscissa basad a: independent from 1A (0); partially fused to 1A (1); completely fused to 1A (2). Some Symphyta have character state 0. In Argidae, it is partially fused (close to the anal cross-vein), and in Pergidae and Orussidae, it is completely fused to 1A. In all Apocritans, cross-vein a is completely absent (fused to 1A) as the ground plan and its presence in a few Braconidae is assumed to be secondary. This character is unordered.

5 Subcostal vein (Sc), distal (free) section: present (0); absent (1). This abscissa of Sc bends at a right angle, relative to the basal abscissa of Sc, towards the radius. When Sc is fused with R (resulting in Sc + R) only the free section of Sc between C and R remains visible and it appears to be a cross-vein. In Tenthredinoidea and Xiphydriidae only this section of Sc remains. In other taxa the distal abscissa of Sc is lost.

6 2rs-m: present (0); absent (1). For the terminology of rs-m cross-veins, this paper agrees with Rasnitsyn (1980, 1988) and Sharkey (1988) in that 1rs-m is absent in all Hymenoptera and that only 2rs-m and 3rs-m are present. In Apocrita, 2rs-m is present as a stump in many Aculeata, Trigonalidae, and Aulacinae (Gasteruptiidae).

7 3rs-m: present (0); absent (1). 3rs-m is tubular in Ichneumonoidea, Aulacinae (Gasteruptiidae), most Aculeata, and even in a few Cynipoidea. It is generally reduced to a spectral state in Evaniidae and Megalyridae, and lost in other groups with strong venation (Proctotrupoidea, Stephanidae and Gasteruptiidae).

8 1r: present (0); absent (1). This vein is characteristic of all Symphyta except Orussidae, although it is reduced in a few Cephidae.

9 Combined length of vein 2-Rs + M and 2-Rs: less than or equal to the abscissa of Cu (1-Cu) between 1-M and 2cu-a (0); at least 1.25 the length of 1-Cu (1); at least 1.5 the length of 1-Cu (2). In most Hymenoptera, these two abscissae are shorter than 1-Cu, but in most Proctotrupoidea 1-Rs + M is angled posteriorly causing it to intersect 2-Rs + M basally, thereby increasing the combined length of 2-Rs + M and 2-Rs. A similar condition is found only in Gasteruptiinae (Gasteruptiidae), but in this family, 1-Rs + M is not angled (it is continuous with and on the same plane as M + Cu) and 1-Cu is very short. Therefore, character state 1 is a potential synapomorphy for Proctotrupoidea whereas character state 2 is an autapomorphy for Gasteruptiinae (Gasteruptiidae). The character is unordered.

10 1m-cu: present (0); absent (1). This cross-vein is tubular in macrohymenoptera (except Bethyidae, Dryinidae, Sclerogybidae, Scolebythidae and Megalyridae) and Proctotrupoidea (except Pelecinidae). It becomes nebulous

in Bethyidae, Dryinidae, Scolebythidae, Megalyridae and Pelecinidae.

11 2m-cu: present (0); absent (1).

12 2cu-a: present (0); absent (1). This cross-vein is tubular in macrohymenoptera and Proctotrupoidea (except Megalyridae, Stephanidae, a few derived Aculeata, and Pelecinidae); it is nebulous in most other Apocrita.

13 Junction of 1cu-a with Cu vein: 1cu-a closer to the middle of cell 1M than to vein 1-M (0); 1cu-a closer to vein 1-M (1); 1cu-a displaced basally, reaching the basal half of the anal vein (2). Some taxa of Symphyta possess state 0: Xyelidae, Megalodontoidea, Tenthredinoidea, Anaxyelidae, and Siricidae. In these groups, 1cu-a is situated at the middle of the cell, except in Anaxyelidae where it meets Cu closer to the first third of cell 1M. 1cu-a has migrated closer to 1-M in Cephidae, where it is still not continuous with this abscissa, and Xiphydriidae, Orussidae, and Apocrita, where it is usually continuous with 1-M. In the Apocrita, variations occur: 1cu-a may be proximal or distal to 1-M in Ichneumonoidea and Aculeata, but if distal, it is usually closer to the first abscissa of M. The Formicidae are peculiar in having 1cu-a displaced to the middle of M + Cu and A. The Vespidae is the only other family with the 1cu-a cross-vein displaced to the basal half of 1A, although it is not basad the elongated 1-M.

14 Costal cell: at least 0.75× the width of the first radial cell (0); less than 0.75× the width of the first radial cell but wider than vein Sc + R (1); narrower than vein Sc + R or absent (2). The costal cell is usually wide in the Symphyta and basal Apocrita (when the costal vein is absent the width is measured from the radial vein to the fore margin of the wing), but it is reduced or absent in Ichneumonoidea and unknown in the Ceraphronoidea where vein R is absent.

15 Stigma: present (0); absent (1). The stigma is present in most hymenopteran taxa but has been reduced in a number of families. It is reduced or absent in some Diapriidae. It is absent in Cynipoidea (except Austrocynipidae), Chalcidoidea, and Platygastroidea, all taxa that have lost the costal vein.

16 Position of the cubital vein (Cu), abscissa distad 2cu-a: at the same level or anterior to the section between the two cu-a cross-veins (2cu-a is usually longer than 1cu-a) (0); posterior to the abscissa between the two cu-a cross-veins (part of Cu runs on the same axis as 2cu-a, and 2cu-a is usually shorter than 1cu-a) (1). In almost all Hymenoptera, Cu follows a course in which the abscissa between 1m-cu and 2cu-a bends twice, once posteriorly and once distally. 2cu-a is usually shorter than 1cu-a, except in Gasteruptiinae (Gasteruptiidae) because vein A, distal to 1cu-a, is also bent towards the hind wing. But even here, the distal abscissa of Cu is posterior to the more proximal sections. State 0 can be found in all microhymenoptera, although Cu is absent in Ceraphronidae.

17 2-Rs vein: present (0); absent (1). This abscissa of Rs is tubular in Symphyta and most parasitic Hymenoptera, nebulous

in Scelionidae, Chalcidoidea and Diapriidae, and absent only in groups with very reduced venation (Ceraphronoidea and Platygasteridae). When present, its length varies from about half that of r (Cynipoidea and Ichneumonoidea), to much more than half.

18 Rs2 vein: present (0); absent (1). This vein is found only in Xyelidae, some Chrysoidea (Plumariidae and some Chrysoidea), Pelecinidae and some Chalcidoidea (Chalcididae and Leucospidae). In agreement with most authors (Burks 1938; Bradley 1955; Rasnitsyn 1988), the extra vein found in Chalcidoidea and Pelecinidae is homologized with 3rs-m instead of Rs2.

19 Basal abscissa of the Sc vein: present (0); absent (1). A separate first abscissa of the subcosta is found only in a few Symphyta: Xyelidae, Megalodontoidea, and Siricidae (as a nebulous vein).

20 1-Rs: present (0); absent (1). This abscissa of Rs is absent in most Tenthredinoidea (Blasticotomidae excepted) and Pamphiliidae, as well as in some apocritans with highly derived venation (Ceraphronidae and Mymarommatidae). In the Symphyta the absence of 1-Rs is due to the fact that Rs + M is displaced anteriorly, connecting directly with R. In Apocrita, the absence of 1-Rs is due to a reduction in wing venation.

21 Position of 1-Rs: distant from the pterostigma (distance is equal to 0.75× of the pterostigma or greater) (0); close to the pterostigma (distance is about half the length of the pterostigma or less) (1). 1-Rs is tubular in Xyelidae, Cephidae, Anaxyelidae, and most microhymenoptera. It is nebulous in most Aculeata, Ichneumonoidea, Trigonalidae, Megaspilidae (1-Rs is absent in Ceraphronidae), Evaniidae, Megalyridae, and Gasteruptiidae (exceptions occur in these latter two families). Some aculeate families have a few representatives with the tubular condition (Tiphidae, Sphecidae), but this is due to reduction of the pterostigma and may be a secondary feature. In Chalcidoidea, Platygastroidea, and most Cynipoidea the absence of a stigma makes it difficult to evaluate the condition, but the position of Rs is just as basal on the wing as in the Proctotrupoidea and therefore these taxa are also coded with state 0.

Hind wing

22 Rs vein: present (0); absent (1). This vein is tubular in all Symphyta (except Orussidae) and in most Aculeata, as well as in Ichneumonoidea, Megalyridae and Trigonalidae. It is nebulous in Orussidae, Stephanidae, Plumariidae, Scleroglybidae, Heterogynidae, Sierolomorphidae, Scoliidae, and Chalcidoidea; and spectral in Bradynobaenidae and Ceraphronoidea.

23 M vein: present (0); absent (1). This vein is tubular in Symphyta (except Orussidae), Ichneumonoidea, Aculeata, Trigonalidae, Monomachidae and Austroniidae. It is

nebulous in Stephanidae, Gasteruptiinae (Gasteruptiidae), Plumariidae, Chrysoidea, Embolemidae, Rhopalosomatidae, Sierolomorphidae and Roproniidae, and spectral in Scoliidae, Heloridae, Proctotrupidae, Vanhorniidae, Peradeniidae, and Ceraphronoidea.

24 Cu vein (first abscissa): present (0); absent (1). This vein is present and tubular in Symphyta (except Orussidae), Ichneumonoidea, most Aculeata, Trigonalidae, Megalyridae, Evaniidae, Roproniidae, Peradeniidae, Monomachidae, Heloridae, and Austroniidae. It is nebulous in Stephanidae, Gasteruptiinae (Gasteruptiidae), Plumariidae, Chrysoidea, Heterogynidae, Sierolomorphidae, Proctotrupidae, Vanhorniidae, Diapriidae, Chalcidoidea, Platygastroidea, and most Cynipoidea, and it is spectral in Ceraphronoidea, Pelecinidae, and some Cynipoidea.

25 1A vein: present (0); absent (1). 1A is the only anal vein present in most parasitic macrohymenoptera; it is tubular in Ichneumonoidea, most Aculeata, and Trigonalidae, and nebulous in Aulacinae (Gasteruptiidae) and Stephanidae.

26 1rs-m cross-vein: present (0); absent (1). 1rs-m is the only cross-vein remaining in the hind wing of most Apocrita. This cross-vein is tubular in Symphyta (except Orussidae), most Aculeata, Ichneumonoidea, and Trigonalidae. It is nebulous in Stephanidae, Gasteruptiidae, and in many Cynipoidea and Chalcidoidea. Its presence in minute taxa (such as Platygasteridae where it is fused with the cubitus to form a composite vein, rs-m&Cu&cu-a), suggests that it is a relatively stable character, i.e. it does not necessarily become reduced due to a reduction in body size.

27 3rs-m cross-vein: present (0); absent (1). The terminology follows Rasnitsyn (1969, 1988) and is referred to as 3rs-m because a third cross-vein is found between 1rs-m and 3rs-m in Macroxyelinae (but not in Xyelinae). Often this vein is referred to as 2rs-m (2r-m), but we agree with Rasnitsyn (1969, 1988) and Sharkey & Wahl (1992) that this vein represents 3rs-m.

28 cu-a cross-vein: present (0); absent (1). This cross-vein is usually short in Apocrita. It is present and separate from Cu in most Aculeata, in Ichneumonoidea, Stephanidae, Trigonalidae, and Monomachidae. In Platygastroidea, it is most probably fused with the first free section of Cu, creating the vein Cu&cu-a.

29 Costal vein: complete (0); partial (1); absent (2). Ordered (012). The costa is usually absent in parasitic Hymenoptera (as well as in Orussidae); a stump can be seen in Cephidae, Anaxyelidae, a few aculeates, Ichneumonoidea, and Trigonalidae, and it is complete in most Aculeata. The costa is never nebulous or spectral, whether on the fore or hind wing.

30 m-cu cross-vein: present (0); absent (1). This cross-vein is present only in some Symphyta.

31 Basal hamuli: present (0); absent (1). The basal group of hamuli is present only in Symphyta and in some basal apocritan

lineages (Ichneumonoidea, Trigonalidae, Plumariidae, Tiphidae, Sapygidae, and Sphecidae). In Anaxyelidae, Orussidae and Braconidae, a single hamulus can be found. The basal hamuli are not functional (lacking a hook) in some Aculeata and all Braconidae. Contra Basibuyuk & Quicke (1997), basal hamuli are here defined as hamuli that are positioned on the basal half of the wing well basad the juncture of R1 and the fore margin of the wing.

32 Intersection of 1rs-m with M vein: with M (0); with M + Cu (1). This character measures the presence or absence of a basal abscissa of vein M. When the 1rs-m cross-vein unites with M, the free section of M develops an extra abscissa. This character is present in Symphyta and most basal Apocrita (Aculeata, Ichneumonoidea, Aulacinae (Gasteruptiidae), some Stephanidae, Ceraphronoidea, Monomachidae, and Austroniidae). When 1rs-m makes contact with M + Cu, the extra abscissa of M is absent.

33 Sc vein: present (0); absent (1). A separate longitudinal subcosta is present in Pamphiliidae, Siricidae, and Xyelidae.

34 Free basal segment of Cu and M veins: present (0); absent (1). The split of these two veins at the base of the hind wing is present only in Xyelidae and some other holometabolous orders.

35 2rs-m cross-vein: present (0); absent (1). Found only in Macroxyelinae.

36 Anal cell (A): closed (0); open (1). This cell is bordered by the veins 1A and a. It is closed in all Symphyta except Orussidae and it is open in all Apocrita.

37 Orientation of the first abscissa of the Median vein (1-M): continuous with M + Cu (0); anterior to M + Cu (1). In all Symphyta and most Aculeata, M is anterior to M + Cu whereas in nonaculeate Apocrita, it is continuous with the latter. In taxa where the M is anterior to M + Cu, the basal abscissa of M (1-M) is angled towards the anterior part of the wing.