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Phylogeny and Classification of Hymenoptera*

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Abstract

An overview of recent advances in our understanding of the higher phylogeny and classification is presented. Molecular and morphological cladistic and pre-cladistic studies are summarized. A superfamily-level classification of the Hymenoptera is offered to reflect recent advances in our understanding of the phylogenetic relationships of the Hymenoptera. It differs from most recent classifications in the recognition of the Diaprioidea, to include Diapriidae, Monomachidae, and Maamingidae.

Key words: Diaprioidea, taxonomy, cladistics, life history, Insecta

Introduction

Much progress has been made in our understanding of the phylogeny of Hymenoptera since the advent of cladistic methods. Here I summarize recent influential studies and pre-cladistic studies are also treated, at least cursorily. While writing this short essay it occurred to me that, since this is a celebration of the Linnaeus ter-

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centenary, it may have been more appropriate to concentrate on the history of the higher classification of the Hymenoptera rather than phylogenetic studies. However, modern classification is preceded by, and dependent on, phylogeny so I suppose that the present work concerns classification, at least in an obtuse way. Cladistic analyses of morphological and molecular characters have all pointed to the fact that classical classifications of the Hymenoptera are wrought with para- and polyphyletic taxa. It is the progress in discovering and correcting these errors that is the focus of this paper. In order to present a broad scope I concentrate on superfamily-level analyses, but the most important family and subfamily level cladistic studies are included in Table I.

Recently there have been several reviews of hymenopteran cladistic relationships (Whitfield 1992a, 1998; Ronquist 1999; Nieves-Aldrey y Fontal-Cazalla 1999; Nieves-Aldrey et al. 2006; Hanson and Gauld 2006). The most comprehensive of these is Whitfield (1998). Vilhelmsen (2006) presents a thorough account of symphytan taxonomic and phylogenetic research. There are three recent books covering all aspects of hymenopteran taxonomy and general biology (Goulet and Huber 1993; Hanson and Gauld 2006; Fernández and Sharkey 2006). The latter two books are in Spanish and concentrate on Neotropical fauna but are they are applicable to the world fauna in most aspects. LaSalle and Gauld (1993) edited an important contribution to our understanding of hymenopteran diversity and Clausen's "Entomophagous Insects" (Clausen 1940) remains the seminal text on the biology of parasitoid and predaceous Hymenoptera.

Hymenopteran Diversity

There are approximately 115,000 described species of Hymenoptera. This places them behind the Coleoptera and Lepidoptera but some hymenopterists argue that if undescribed species were included, the Hymenoptera would be more species-rich than all other orders (e.g., Grissell 1999). There are few areas in the world where there is hard evidence for comparative species numbers between orders, however, two studies, one for a temperate area (Gaston 1991) and one for a tropical area (Stork 1991), indicate that Hymenoptera is the most species rich of all orders. Some coleopterists might suggest that beetles are the most diverse order so the question should not be considered as being conclusively answered. Any way the numbers are extrapolated, Hymenoptera probably constitute nearly 10 percent of the species of life. Gaston et al. (1996) estimated that there are between 300,000 and 3,000,000 species of Hymenoptera and my guess is about 1,000,000. Within Hymenoptera, Apocrita are far more diverse than Symphyta. However, contrary to most published reports, Symphyta are probably much more species-rich in the tropics and sub-tropics than they are in temperate regions. In terms of described species, the stinging Hymenoptera and parasitoid wasps have roughly equal numbers. However there are many more undescribed species of parasitoid wasps than stinging Hymenoptera. Among parasitoid wasps Ichneumonoidea and Chalcidoidea are especially species-rich.

Parasitoid Hymenoptera are unique bioindicators because they are representative of the diversity of the hosts that they attack, and these constitute a great part of the diversity of all arthropods. Thus, when sampling parasitoid Hymenoptera, the diversity of arthropods from a wide spectrum of niches may be inferred from the results. Parasitoid Hymenoptera have been shown in numerous studies to be sensitive to ecological perturbations especially pesticides, so that investigators should see fluctuations in parasitoid populations well before they can be observed in their host populations (LaSalle 1993). This sensitivity makes them ideal candidates for conservation studies.

Parasitoid Hymenoptera have often been used in biological control, and these programs demonstrate the great impact that they can have on host populations. A species of parasitoid that occurs in small numbers in its native habitat may be the key force in maintaining a host population at low levels. There have been many successful applications of biological control against host species that were accidentally introduced to a new geographic area (reviewed by Clausen 1978). The new areas lack parasitoids and the population density of the host becomes very high, often causing serious economic injury to crops or forest products. The regulatory effect of parasitoids is well illustrated by an example presented by DeBach and Rosen (1991); lemon trees in their study were sprayed with DDT killing parasitoids of the pest scale insect, *Aonidiella aurantii*, more effectively than they did the scale. As a result unsprayed lemon trees remained healthy and sprayed trees almost died. The typical phytophagus holometabolous insect is host to about five species of parasitoid Hymenoptera and the host range of most parasitoids may be in the same range (Hawkins 1993). Destroying one parasitoid species therefore may have unpredictable and immeasurable effects on the abundance of a number of phytophagus insects with possible cascade effects on an entire ecosystem (LaSalle 1993). These studies not only demonstrate the effectiveness of biocontrol but also suggest how important parasitoids are in their natural habitats.

Aculeate Hymenoptera, especially bees, are known for their essential role in the pollination of flowering plants and the associated agricultural importance (Michener 2000), for their medical importance due to stings (more people are killed from Hymenoptera stings than from all other venomous animals combined), and for the agricultural importance of honey production. Less known is the tremendous biomass of ants (Formicidae) in tropical systems and their ecological importance as decomposers, herbivores (e.g. fungus ants) and predators (Hölldobler & Wilson, 1990). There are a few instances of pests amongst the Hymenoptera; noteworthy examples are some wood wasps (Siricidae), some leaf feeders (Tenthredinoidea), some seed-feeding chalcids (Torymidae), and of course pestilent ants, and some stinging wasps (Vespidae) and bees (Apoidea).

Phylogenetic position within the Holometabola

Hymenoptera is a member of the endopterygote (holometabolous) clade of insects and phylogenetic among of the constituent orders have been much debated. Morphological studies have usually placed Hymenoptera as sister to the remaining endopterygotes (Ross 1965, Rohdendorf and Rasnitsyn 1980b) or as sister to the Mecopteridea = (Mecoptera, Diptera, Siphonaptera, Trichoptera and Lepidoptera, and perhaps Strepsiptera) (Knigsmann 1976; Hennig 1981; Kristensen 1991, 1999). Reviews of morphological hypotheses can be found in Kristensen (1999), and Whiting (2003). The first molecular studies are reviewed by Whiting et al. (1997), and analyses in the same paper employing 28S and 18S sequence data combined with morphological data are inconclusive. Similar to previous studies based on morphological data, most of their results place Hymenoptera as sister to the remaining Holometabola or sister to Mecopteridea. Castro and Dowton (2005), using whole mitochondrial genomes, had equivocal results but stated that the Hymenoptera + Mecopteridea relationship had the best support.

Savard et al. (2006) published a convincing analysis of the holometabolous insects based on 185 nuclear genes assembled from genome projects that placed Hymenoptera as the sister to the remaining Holometabola. Unfortunately, the only other holometabolous orders with available data were Diptera, Lepidoptera, and Coleoptera. A more complete analysis (Trautwein et al. 2006, Wiegmann et al., in prep.), in terms of taxon sampling across the orders, based on six nuclear protein-encoding genes corroborates the results of Savard et al. (2006). Kukalová-Peck and Lawrence (2004) came to the same conclusion based on hind wing morphology, in particular wing folding and articulation. That the Hymenoptera is sister to all other Holometabola appears to be the best-supported hypothesis.

Monophyly of the Hymenoptera

Hymenoptera have long been recognized as a taxonomic group and recent advances have not modified membership. Vilhelmsen (1997b, 2001) presented long lists of putative autapomorphies, reproduced below; text in italics indicates my annotations, and references cited in the list are taken from Vilhelmsen's publications. A less inclusive list may be found in Königsmann (1976) and others may be gleaned from Rasnitsyn's (1988) cladogram.

Autapomorphies of the Hymenoptera

1. Inflected part of the clypeus sclerotized (Vilhelmsen 1996).
2. Labiomaxillar complex unique.
3. Laterocerviciale fused with pro-preepisternum (Kristensen 1991)
4. Posterior notocoxal muscles absent and meron not demarcated on coxa (Kristensen 1991).
5. Apical foretibial spur modified as a calcar, antennal cleaner.
6. Prefemur (trochantellus) present.
7. Anal veins of forewing not reaching wing margin. *Knigsmann (1976) lists a number of other wing vein autapomorphies.*
7. Distal hamuli on anterior margin of hind wing used as a wing coupling mechanism.
8. Presence of anterior mesofurcal arms (Heraty et al. 1994).
9. Presence of two mesofurcal-laterophragmal muscles (Heraty et al. 1994).
10. First abdominal tergite fused (closely associated) with the metapostnotum.
11. Abdominal terga overlap sterna. *Abdominal terga and sterna interleaved with lateral portion of each sternum partly overlying tergum of the following segment* (Kristensen 1991).
12 Abdominal spiracles surrounded by sclerotized cuticle (Kristensen 1991).
13. Basal ring and volsellae present in male genitalia.
14. Presence of basal articulation and associated muscles in the ovipositor.
15. Larval eye with single cornea overlying several ommatidia (Paulus 1979)
16. Haplodiploid; males are usually haploid, the product of unfertilized eggs, whereas females are diploid, the product of fertilized eggs.
17. Presence of chordate apodemes on abdominal tergum 9 of females.
18. The presence of cenchri *(pads on the metanotum to which the hind wings attach when at rest).*

Review of Classical Hymenopteran Classification and Phylogeny

> "I shall also attempt to show how the phytophagous species, under the great law of evolution, gave place to the parasitic and predaceous species;" Ashmead (1896, p. 323)

Hymenoptera has been divided into many formal and informal groups to facilitate discussion of their biology and ecology. The major traditional divisions are Symphyta, and Apocrita. Members of Symphyta have comparatively complete venation, are phytophagous as larvae, and adults do not have a wasp-waist. Apocritan Hymenoptera are those with a wasp-waist formed by the firm attachment of the first abdominal segment to the thorax and a sharp constriction between the first and second abdominal segments leading to the necessity of the terms mesosoma and metasoma to refer to the parts of the body immediately pre- and post-waist. Symphyta has been further subdivided into the sawflies, the woodwasps, and the Orussidae. As the name suggests, the sawflies usually have a laterally compressed ovipositor with serrations along the ventral surface (Fig 1a) that are meant to saw into vegetation in order to deposit eggs. The woodwasp ovipositor is used to penetrate wood and members of Orussidae are external parasitoids of wood-boring Coleoptera. Orussidae represents the unique family of Symphyta with the parasitoid habit. Symphyta and Apocrita have long been considered as suborders of Hymenoptera but since recognition of the paraphyletic nature of the Symphyta (Köningsmann 1977, Rasnitsyn 1988) and the advent of cladistic methods the subordinal classification should be avoided. Likewise the woodwasps are thought to be non-monophyletic, forming a grade that is ancestral relative to Apocrita and Orussidae. The traditional hymenopteran classification is faulty, by cladistic criteria, in the same way as pre-cladistic vertebrate classifications in which groups sharing plesiomorphic characters were recognized as natural, e.g., fishes were once grouped together as "Pisces," which excluded tetrapods.

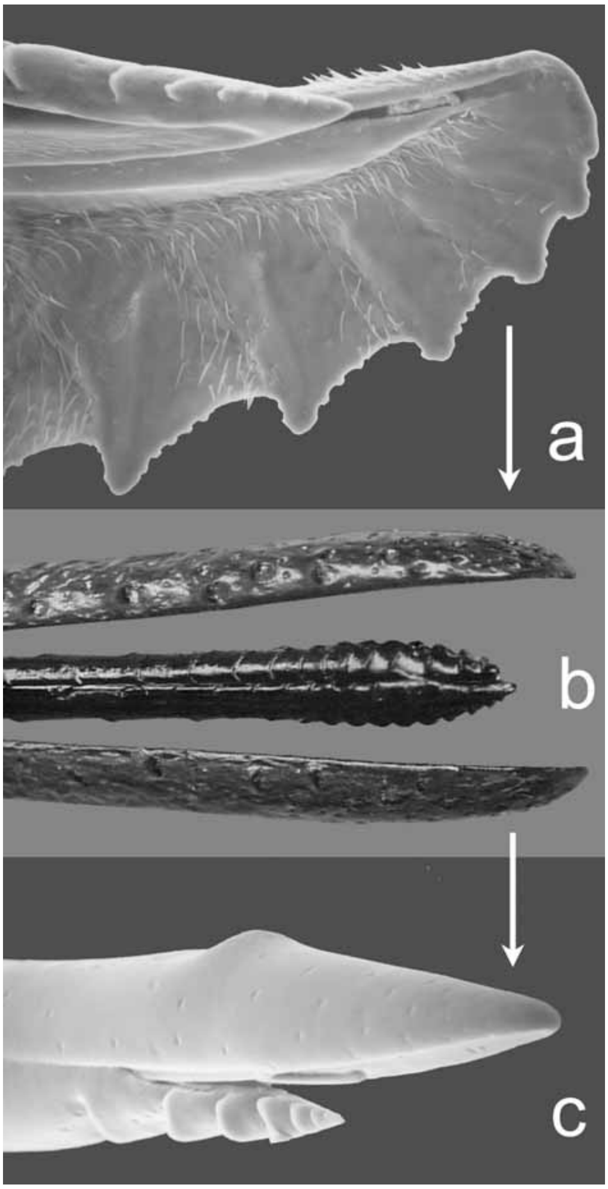


FIGURE 1. Ovipositors. 1a, Sawfly, Tenthredinidae. 1b, woodwasp, Siricidae. 1c, parasitoid, Braconidae. Arrows indicate character state transformation series.

Apocritan larvae are maggot-like with reduced segmentation and sclerotization and they lack thoracic appendages (Fig. 2c). Apocrita is monophyletic and it is often informally divided into two groups, Aculeata (also a monophyletic group) and the parasitoid wasps. The latter group is also known as the Parasitica, Terebrantia, or the parasitoid Hymenoptera. The stinging wasps include the taxa that most laypeople are familiar with, i.e., bees, social wasps, and ants. No convincing evidence has been brought forward indicating that Aculeata is the sister of the Parasitica, and most recent analyses place it as derived within the Parasitica. Despite the non-phylogenetic nature of the names, Symphyta, sawflies, woodwasps and Parasitica still have utility and are commonly found in the literature.

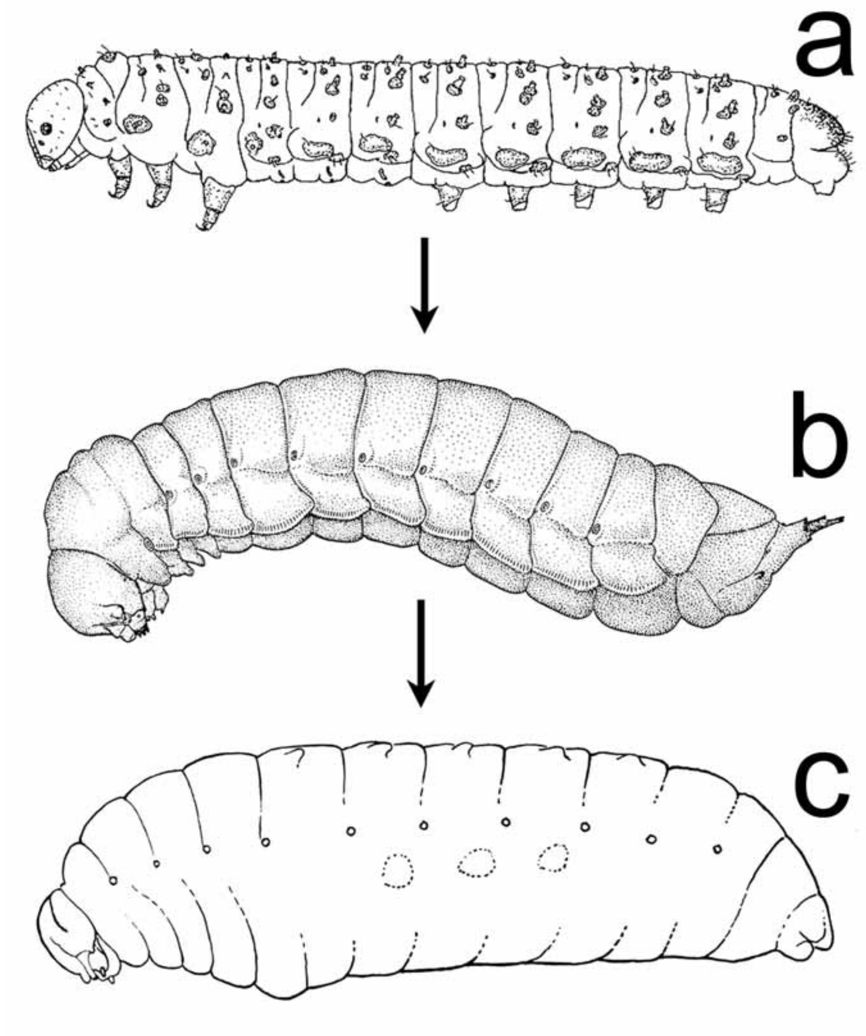


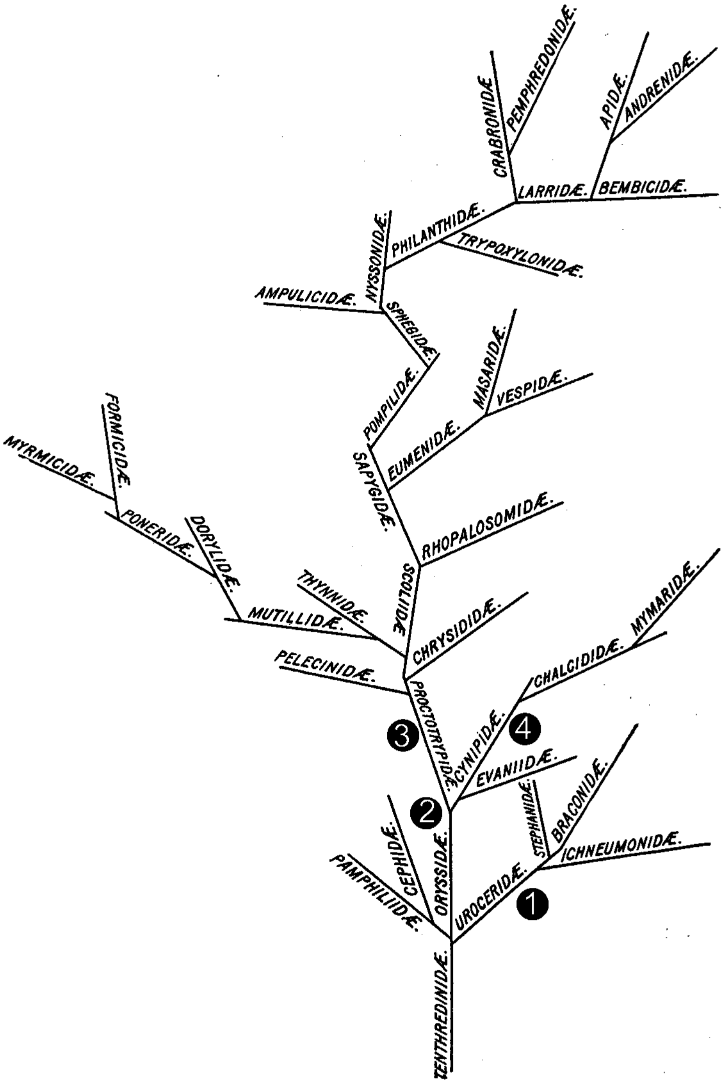
FIGURE 2. Hymenoptera larvae. 2a. Sawfly, *Atomacera debilis* Argidae (modified from Evans 1987). 2b. Woodwasp, *Syntexis libocedrii* Anaxyelidae (modified from Evans 1987). 2c. Apocrita, *Vespa* sp. Vespidae (modified form Peterson 1948). Arrows indicate character state transformation series.

The Parasitica is not subdivided into less inclusive informal divisions but Aculeata is broken into four, i.e., the bees (Apiformes or Anthophila), predatory wasps, parasitoid aculeates, and ants. The bees have returned to the phytophagus lifestyle and feed primarily on pollen and nectar. They are primarily known for their role as pollinators, though some, such as members of the stingless bees (Apidae: Melponini), are also important scavengers and carrion feeders in the tropics. There is overwhelming evidence that bees have their origin within the Spheciformes; the sistergroup to bees apparently being Crabronidae, the largest of the sphecid families (Melo 1999; Prentice 1998). Ants comprise the family Formicidae (Vespoidea). Predatory wasps are a polyphyletic assemblage comprised of members of the Spheciformes and Vespoidea. Unlike parasitoid wasps, predatory wasps usually carry prey to their nests and may provision their progeny with more than one individual prey item (host). The remainder of Aculeata, the parasitoid aculeates, comprising Chrysidoidea and the remaining Vespoidea, is polyphyletic and includes the most families, e.g., Dryinidae, Bethylidae, Scoliidae, Mutillidae.

The following list summarizes the commonly encountered vernacular names for higher-level hymenopteran taxa and grades. Those names in parentheses are mostly classical synonyms. Names in italics are thought to be monophyletic.

Symphyta (Chalastogastra, Sessiliventres, Phytophaga)
    Sawflies (Phyllophaga)
    Woodwasps (Xylophaga)
    Orussidae
Apocrita (Clistogastra, Petioliventres, Heterophaga)
    Aculeata = Vespomorpha (Stinging Hymenoptera)
        Parasitic/Parasitoid Aculeata
        Predatory wasps
        Bees (Anthophila)
        Ants = Formicidae
    Parasitica (Parasitic/Parasitoid Hymenoptera, Terebrantia, Terebrantes, non-aculeate apocritans)

Before 1970 it was not common for classifications to directly reflect phylogeny but hymenopteran phylogeny was much discussed in the literature previous to this date. Ashmead (1896) appears to be the first to have published a phylogenetic tree of Hymenoptera. His tree is reproduced in Figure 3 and it is a good example of the pre-cladistic phylogenetic paradigm. In Ashmead's tree taxa are not only depicted at the terminals but also included in the stem regions to indicate paraphyly. Apparently, the idea of paraphyly was understood and considered acceptable. This is corroborated in Ashmead's text; for example he states, "From the Cynipidae came the Chalcididae, a recent type; while from the Proctotrypidae, which I believe represent some of the most ancient types of hymenopters, we have a distinct line of descent into the Scoliidae, Mutillidae, and the higher Aculeata." (Ashmead 1896, p. 333). In Ashmead's tree (Fig. 3) a paraphyletic Cynipidae is indicated at node 4, and a paraphyletic Proctotrypidae at node 3. Ashmead's Cynipidae corresponds to our current concept of Cynipoidea and his Proctotrypidae roughly corresponds to Proctotrupoidea, which may indeed be a paraphyletic or polyphyletic assemblage. Ashmead (1896) thought Apocrita to be biphyletic with Ichneumonoidea and Stephanidae originating from Siricoidea (his Uroceridae, node 1 Fig. 3), and the remaining apocritan taxa emanating from Orussidae (his Oryssidae, node 2 Fig. 3). Ashmead (1896) had a "great chain of life" view of evolution, believing that evolution proceeded from generalized (lower) to specialized (higher) types. Evidence is given in the following quote, "there is ever an upward tendency to a higher or more specialized type; since man is the highest type of animal life, so a bee or an ant is the highest type of insect life" (Ashmead 1896, p. 323). Although most readers will disagree with his premise regarding humans, many hymenopterists will undoubtedly concur with his conclusion vis-à-vis ants and bees. Few other trees were published before the late 1960s though that of Telenga (1952, 1969 English translation) also indicated a biphyletic origin of Apocrita. The phylogenetic tree of Ross (1965) suggested a paraphyletic Symphyta with a monophyletic Apocrita originating from Siricoidea. Though he did not publish a tree, Tillyard (1927) appears to be the first to suggest that Apocrita was derived from Orussidae. In modern terminology he would likely have suggested a sister-group relationship between Orussidae and Apocrita which is in accord with our current understanding (see below).



Phylogeny of the Hymenoptera.

FIGURE 3. First published phylogenetic tree of the Hymenoptera from Ashmead (1896, p. 328).

Phylogenetic (Cladistic) Studies of Hymenoptera

The godfather of cladistics, Willi Hennig, who was primarily a dipterist, presented the first cladogram of Hymenoptera based on explicit cladistic argumentation (Hennig 1969, Fig. 132). However detailed phylogenetic research on the order as a whole began with a series of papers by Rasnitsyn (1969, 1980, 1988) and Königsmann (1976, 1977, 1978a, 1978b). Königsmann's research was mostly composed of morphological characters taken from the literature, and though ostensibly cladistic, the data were analyzed intuitively with little resolution obtained at the superfamily level. His major contribution was assembling the vast amount of literature relating to hymenopteran character state distributions and these have facilitated subsequent phylogenetic studies. He suggested that Symphyta is paraphyletic, however his thesis of a sister-group relationship between Cephidae and Apocrita, based primarily on the convergent constriction between the first and second abdominal segments, was often cited in the literature in non-cladistic terms and was not supported by the totality of his own data. This is not surprising since numerical cladistic methods were not yet commonly employed. Königsmann's (1977) suggestion that the remaining Symphyta (i.e., Symphyta minus Cephidae) comprise a monophyletic group based on the presence of cenchri was unique but it is almost certainly incorrect.

The monumental efforts of Rasnitsyn (1980, 1988) were truly groundbreaking, if methodically flawed. Rasnitsyn's (1988) analysis is not a standard cladistic work; for example he did not include a matrix or a list of characters and states and he deliberately recognized paraphyletic taxa. Despite the lack of a matrix, each node of his cladogram is numbered and these are annotated in the text with putative apomorphies. The apomorphies are usually straightforward and objective but convergent occurrences and losses are difficult or impossible to track. There are a number of inclusions of non-cladistic characters, e.g. "larva parasitizing on hosts other than xylophilous larva", and "hind wing lacking all tubular veins but R." From a cladistic perspective, the fault with such characters is that the synapomorphies are not defined. In the first example all states that do not represent the groundplan state are presumed to be homologous. Similarly, in the second example the veins that are lost (the synapomorphy or synapomorphies) are not listed. There is no explicit criterion used to analyze or optimize the characters. It is likely that Rasnitsyn weighted the characters intuitively based on presumed consistency across both extant and extinct taxa and time of origin in the fossil record also played a role. This latter criterion is clearly implied in Rasnitsyn (2000) in which he shows, using "the ghost range test", that a modified version of his 1988 cladogram is the most consistent with the fossil record. Despite any shortcomings, Rasnitsyn (1988) represents the starting point of modern hymenopteran phylogenetic analysis and many of his clades have been corroborated by recent conventional analyses. It is difficult to represent Rasnitsyn's phylogenetic trees in a standard format because he recognizes paraphyletic groups; nonetheless a simplified interpretation of Rasnitsyn's (1988) evolutionary argument is presented in Figure 4.

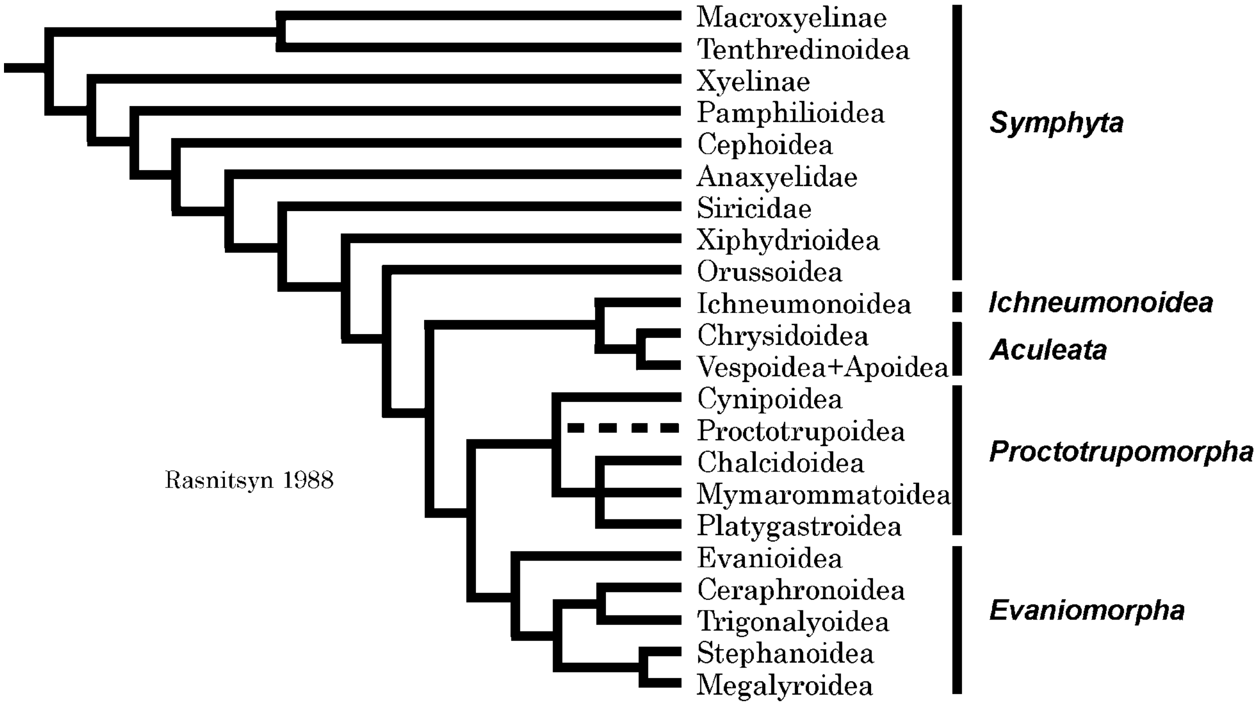


FIGURE 4. Simplified interpretation of the phylogenetic tree from Rasnitsyn (1988). Dashed branch indicates Proctotrupoidea as a paraphyletic grade.

Rasnitsyn (1988) introduced a new nomenclature for clades above the family group level, based on the same rules as family-group names. His ordinal name Vespida for Hymenoptera, and subordinal names Siricina for the woodwasps + sawflies, a paraphyletic group, have not been much followed. However there has been reference to Vespina, a monophyletic group, which he coined for the clade Orussidae + Apocrita. The most noteworthy aspects of Rasnitsyn's 1988 essay follow; those that are in bold font are currently accepted; those that are in italics are currently doubted, and regular font indicate statements with equivocal evidence.

1. Xyelidae is polyphyletic, Macroxyelinae being the sister to Tenthredinoidea, Xyelinae the sister to the remaining Hymenoptera.

2. The remaining Symphyta form a grade and are paraphyletic with respect to Apoctita.

3. Orussoidea is sister to the Apocrita implying a single origin of parasitoidism in Hymenoptera.

4. Numerous infraorders are introduced into hymenopteran classification.

5. Apocrita comprises four infraorders, i.e., Ichneumonomorpha (=Ichneumonoidea), Vespomorpha (= Aculeata), **Proctotrupomorpha**, and Evaniomorpha.

6. Aculeata is sister to the Ichneumonoidea.

7. The Proctotrupoidea is paraphyletic, forming a grade within the Proctotrupomorpha.

8. Two suborders are recognized, Siricinia (sawflies + woodwasps) and Vespina (Orussidae + Apocrita).

9. Polyphyletic taxa, e.g., Xyelidae, and paraphyletic taxa, e.g., Siricinia and Proctotrupoidea, are recognized.

Rasnitsyn (2002) published a revised version of his 1988 analysis using the same methods and again incorporating much fossil evidence. Rasnitsyn et al. (2004) proposed a new family, Khutelchalcididae, based on a fossil dated as lower Cretaceous or upper Jurassic and proposed new relationships within the Proctotrupomorpha. A simplified interpretation of Rasnitsyn's hypothesis as modified by these publications is presented in Figure 5. Though all four infraorders and a sister-group relationship between Aculeata and Ichneumonoidea remain, the following details differ; Ceraphronoidea is sister to (Trigonalyoidea (Stephanoidea + Megalyroidea)); Mymarommatoidea is sister to Chalcidoidea, and this clade is sister to Platygastroidea; Diapriidae is sister to Cynipoidea; Proctortupoidea (minus Diapriidae) is a paraphyletic grade basal to the remaining Proctotrupomorpha; and extant Xyelidae are monophyletic and sister to the remaining Hymenoptera.

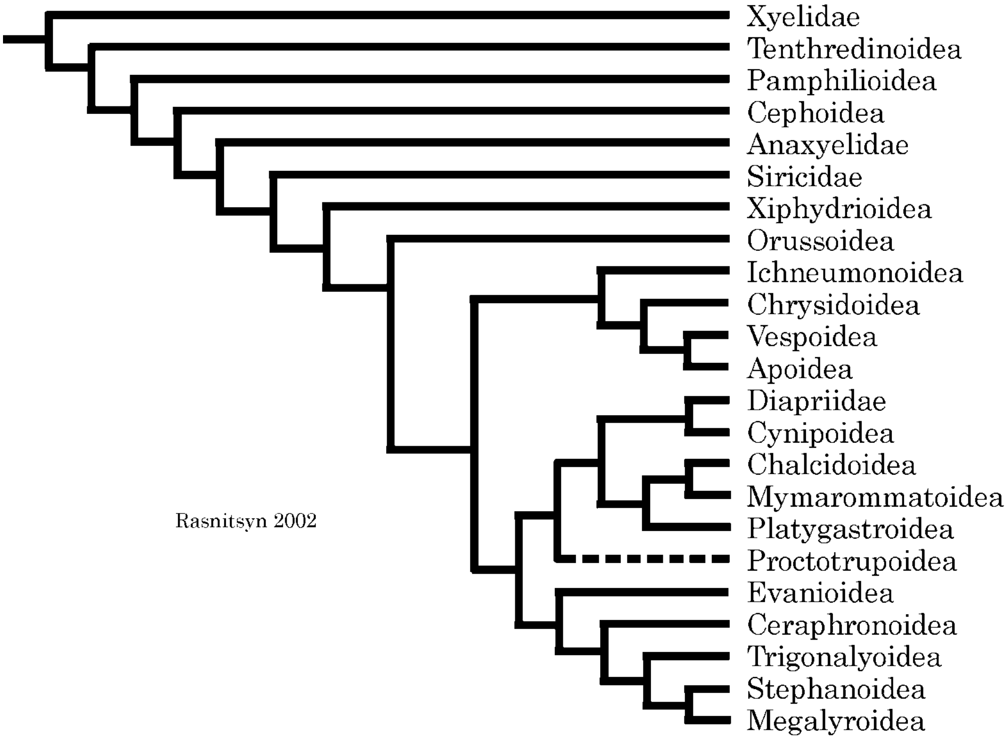


FIGURE 5. Simplified interpretation of Rasnitsyn's most recent hypothesis inferred from Rasnitsyn (2002) and Rasnitsyn et al. (2004).

Dowton and Austin (1994) presented the first comprehensive molecular phylogenetic analysis of Hymenoptera. Their strict consensus tree (Dowton and Austin 1994: Fig. 2, p. 9913) is simplified and reproduced in Figure 6. As expected from a parsimony analysis of one gene, 16S rRNA, their strict consensus tree is not fully resolved and some relationships conflict with convincing morphological evidence. Nonetheless there are two particularly interesting results; Rasnitsyn's (1988) concepts of Proctotrupomorpha and the clade Ichneumonoidea + Aculeata were both corroborated.

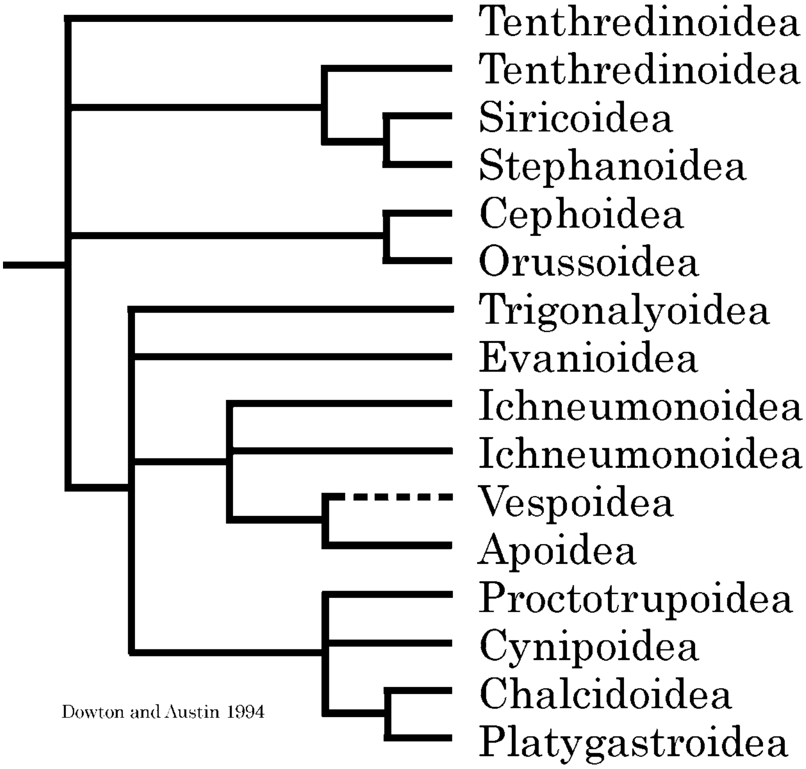


FIGURE 6. Strict consensus tree of hymenopteran relationships based on unweighted parsimony analysis of 16S data, simplified from Dowton and Austin (1994).

Ronquist et al. (1999), revisited Rasnitsyn's 1988 data and constructed a list of characters and states, coded the characters it into a numerical cladistic matrix, corrected a number of taxon scorings and conducted a parsimony analysis using hypothetical ground-plan ancestors. The goal was to reproduce Rasnitsyn's (1988) characters and analyze them using the parsimony criterion; the goal was not to correct or re-interpret the characters. The resulting strict consensus tree (not reproduced here) was resolved for symphytan taxa and similar to Rasnitsyn's (1988) tree for these taxa. Although the apocritan taxa were also resolved the relationships among the superfamilies were very unlike those proposed by Rasnitsyn (1988). The infraorders Evaniomorpha and Proctotrupomorpha were not recovered nor was the sister-group relationship between Aculeata and Ichneumonoidea.

Sharkey and Roy (2002) looked critically at the characters of the matrix that pertain to wings (37 of the169 characters). They showed that most of the resolution in the apocritan clade was the result of wing vein characters. Since these are mostly reduction characters, i.e., the loss of wing veins, they edited these in an attempt to rid the analysis of potential redundancy and reintroduced some of them into the data set. The resulting strict consensus tree was mostly unresolved for apocritan taxa. Sharkey and Roy (2002) noted that many of the non-wing characters were also flawed, e.g. character 111: "Length and shape of the female metasoma: (0) short, laterally compressed; (1) moderately elongate; (2) distinctly elongate and slender; (3) moderately elongate in normal repose but strongly extendable in length during oviposition. Ordered 0123."

(Ronquist et al. 1999, p. 46). Although there is valuable information in the morphological data set it should not be used without careful editing as it has been in several cladistic analyses, e.g., Carpenter and Wheeler (1999); Dowton and Austin (2001). The results of Ronquist et al. (1999), though they are supported by unweighted parsimony analysis, are not supported by Rasnitsyn (pers. comm.). As mentioned above, Rasnitsyn's (1988) cladogram is intuitively weighted and his more recent results (Fig. 5) remain similar to his 1988 tree.

Symphytan studies

Vilhelmsen (1997b) conducted a comprehensive cladistic analysis of symphytan relationships based on 98 morphological characters and ground-plan reconstructions of 21 hymenopteran families including six apocritans. His strict consensus tree is reproduced in Figure 7 (simplified to only include superfamilies) and it agrees in almost all aspects with Rasnitsyn's (1988) hypothesis. The only difference at the superfamilial level is that Xyelidae is no longer necessarily biphyletic but is placed at the base of the tree in a trichotomy with the remaining Hymenoptera. Vilhelmsen (2001), citing deficiencies in his previous analysis, compiled a far more comprehensive dataset employing 44 exemplars (38 Hymenoptera) and 236 morphological characters from all life stages. Consistent with methodological advances, he used an exemplar approach instead of hypothesizing ground-plans. His strict consensus tree based on an unweighted parsimony analysis of unordered characters (Fig. 8) is similar to his previous result (Vilhelmsen 1997b) except that Xyelidae is monophyletic; there is a basal hymenopteran trichotomy, and a tricotomy at the base of Anaxyelidae + Siricoidea + (Xyphidrioidea + Apocrita). Vilhelmsen also chose to treat 29 of the characters as ordered (additive) and the result of this analysis differs from his previous result (Vilhelmsen 1997b) (Fig. 7) at the superfamily level only in monophyly of Xyelidae.

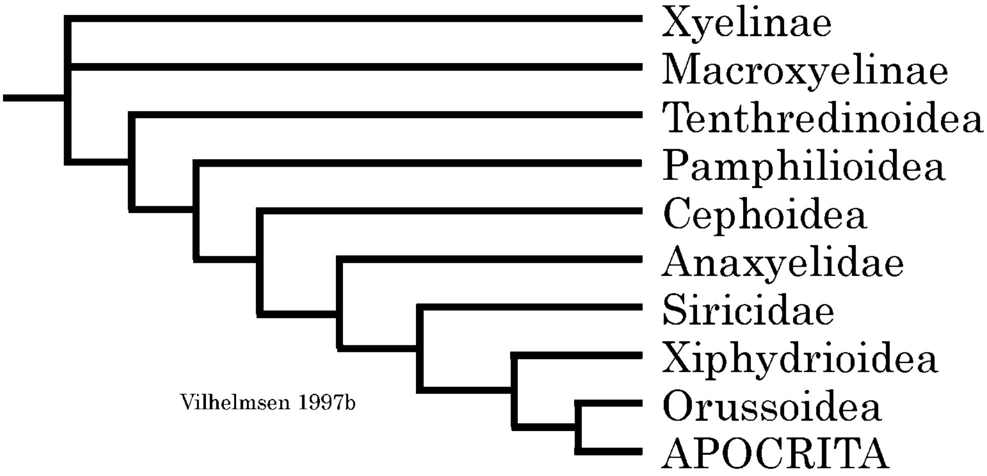


FIGURE 7. Strict consensus tree of basal hymenopteran taxa based on unweighted parsimony analysis of unordered morphological data, simplified from Vilhelmsen (1997b).

Schulmeister et al. (2002) sequenced between 2000 and 2700 base pairs for 39 taxa (35 Symphyta and six Apocrita) from the nuclear rRNA genes 18S and 28S and mitochondrial genes 16S rRNA and CO1. They analyzed the data using direct optimization (Wheeler 1996) under a number of different parameter settings (indel to transversion, transversion to transition, and indel to transversion to transition ratios constituted the variable parameters). The cladogram in Figure 9 is a simplified representation of their majority rule tree from these analyses. This includes those branches found in more than 50% of the individual analyses. To differentiate it from the usual majority rule tree they refer to it as a stability tree. There is little resolution and some of the resolved clades are strongly contradicted by morphological data, e.g., Amphiesmenoptera nested within Hymenoptera. Perhaps most interesting, in the way of positive results, is the corroboration of a monophyletic Xyelidae as sister to the remaining Hymenoptera (ignoring the placement of Amphiesmenoptera). Schulmeister et al. (2002) also included Vilhelmsen's (2001) data in a series of combined morphological and molecular analyses. To decide which set of parameters to include with the morphological data they selected that tree that resulted "from the most congruent simultaneous analysis". That is the tree resulting from the parameter setting that was most similar to the morphological tree and that which resulted in the least extra homoplasy when the data sets were combined. This had a 4:1:1 indel to transversion to transition ratio. The result of this combined analysis (Schulmeister et al. 2002, p. 469, Fig. 7) differs from Vilhelmsen's (2001) result (Fig. 8) in a sister-group relationship between Tenthredinoidea and Pamphilioidea, and a sister-group relationship between Siricidae and Anaxyelidae. Schulmeister (2003c) revisited symphytan morphological data and added new characters and obtained the same topology as Rasnitsyn's 2002 study (Fig.5) except for the sister-group relationship of Anaxyelidae and Siricidae. Schulmeister (2003b) in a combined morphological and molecular analysis came to similar conclusions.

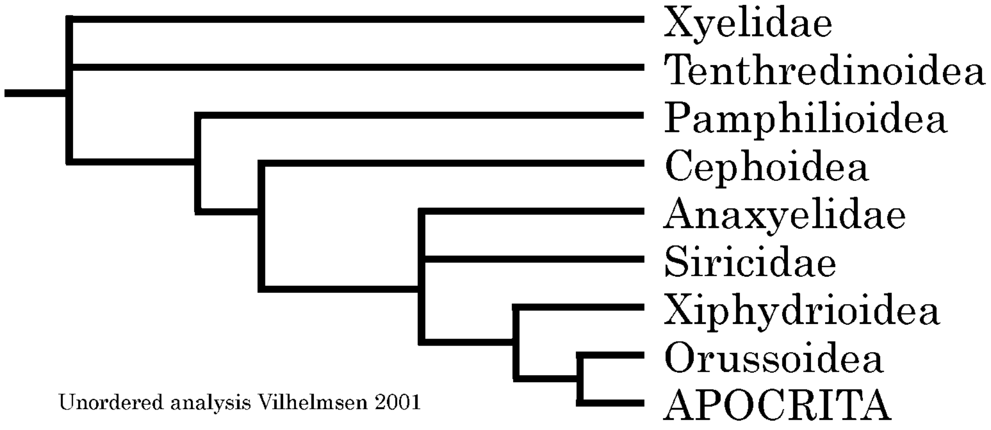


FIGURE 8. Strict consensus tree of basal hymenopteran taxa based on unweighted parsimony analysis of unordered morphological data, simplified from Vilhelmsen (2001).

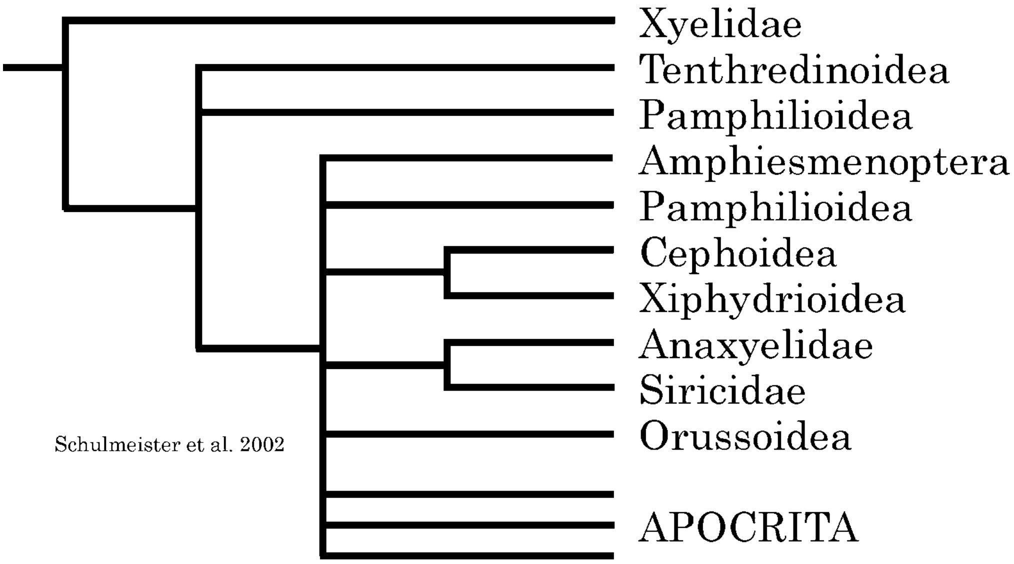


FIGURE 9. Summary tree of basal hymenopteran taxa based on nuclear rDNA genes 18S and 28S and mitochondrial genes 16S rDNA and CO1, simplified from Schulmeister et al. (2002).

Apocritan analyses

Most of the major dichotomies of the symphytan Hymenoptera have been largely resolved since Rasnitsyn's (1988) and Vilhelmsen's (1997b) first studies, however resolution of apocritan relationships remains problematic. Dowton and co-authors published three influential papers centered on the phylogeny of Apocrita. The first of these studies (Dowton et al. 1997) employed only one marker, 16S, and 35 ingroup taxa representing all superfamilies except Stephanoidea, which was excluded due to aberrancies in the 16S gene. They conducted two analyses using parsimony. The first employed the regions of 16S that could be aligned using secondary structure and excluded three length-variable regions. The strict consensus tree illustrated in their paper is quite unresolved. They then used an interesting technique to incorporate the three variable-length regions. They identified taxonomic units that were well corroborated in their preliminary analysis and generally accepted by the scientific community, e.g., Chalcidoidea, and conducted separate alignments for the variable regions for each taxonomic unit using CLUSTAL W. These were then "aligned to each other using the profile align subroutine of CLUSTAL W". A problem with this technique, and with CLUSTAL alignments in general, is that the order of the exemplar taxa has an influence on the resulting alignment. To circumvent this problem, Dowton et al. (1997) conducted three separate alignments with taxa entered in different orders and chose the alignment that produced the shortest tree when combined with the data sequenced using secondary structure. Their strict consensus tree is reproduced in a simplified form in Figure 10. All of Rasnitsyn's (1998) infraorders are monophyletic with the exception of Proctotrupomorpha, but this is only because Cynipoidea is placed as sister to all other Apocrita; 16S data are clearly misleading in this unique result. Also agreeing with Rasnitsyn is the sister-group relationship between the infraorders Ichneumonomorpha (Ichneumonoidea) and Vespomorpha (Aculeata). The superfamily relationships within the infraorders Proctotrupomorpha and Evaniomorpha are quite different than those proposed by Rasnitsyn (1988) (Fig. 4).

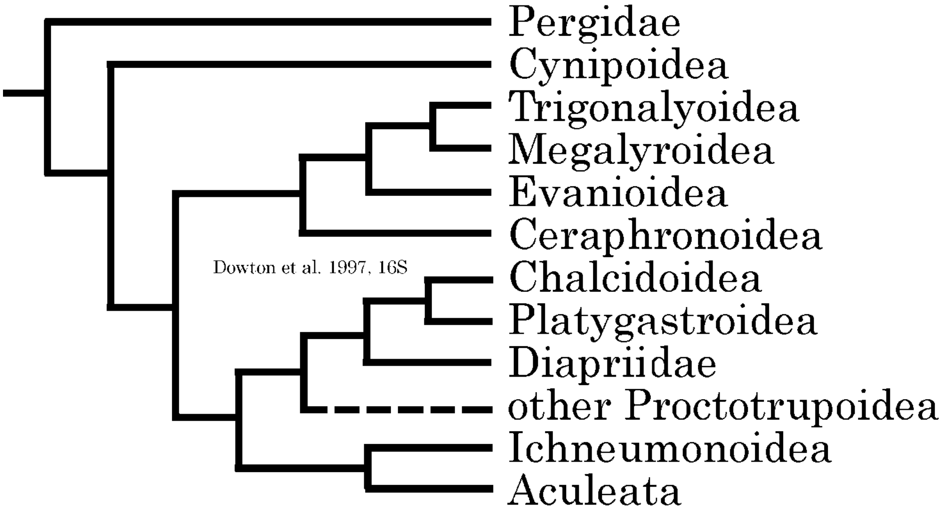


FIGURE 10. Strict consensus tree of apocritan taxa based on mitochondrial gene 16S rDNA, simplified from Dowton et al. (1997). Dashed line indicates a paraphyletic Proctotrupoidea.

Dowton and Austin (2001) were the first to analyze Apocrita with a dataset comprised of multiple genes; i.e., 16S rDNA, 28S rDNA, and CO1 mitochondrial DNA. A simplified version of their results, at the superfamily level, is presented in Figure 11. This is the strict consensus tree of 10 minimum length trees from their unweighted parsimony analysis. They also illustrated a number of trees generated with different weighting options using different models of evolution. These are not presented here but results varied. Dowton and Austin (2001) also conducted a combined analysis of their molecular data with the morphological data of Ronquist et al. (1999). Despite the fact that they emphasized this result, the morphological data set is too flawed to add value to their molecular results. The results of the expanded molecular analyses were very different from those recovered with 16S alone (Dowton et al. 1997). Positive results include Proctotrupomorpha, including Cynipoidea, as monophyletic; and Monomachidae (Diapriidae + Maamigidae) as the sistergroup to Chalcidoidea. On the doubtful side is the placement of Roproniidae + Pelecinidae as sister to the Cynipoidea. Almost certainly misplaced (not shown in Fig. 11) is Orussidae as a derived ichneumonoid, Heloridae as sister to Evaniidae, and Gasteruptiidae as sister to Aculeata. Other areas of disagreement between this and their 16S analysis, as well as Rasnitsyn's (1988) analysis, are that Evaniomorpha is polyphyletic and the Aculeate + Ichneumonoidea sister-group relationship is not recovered.

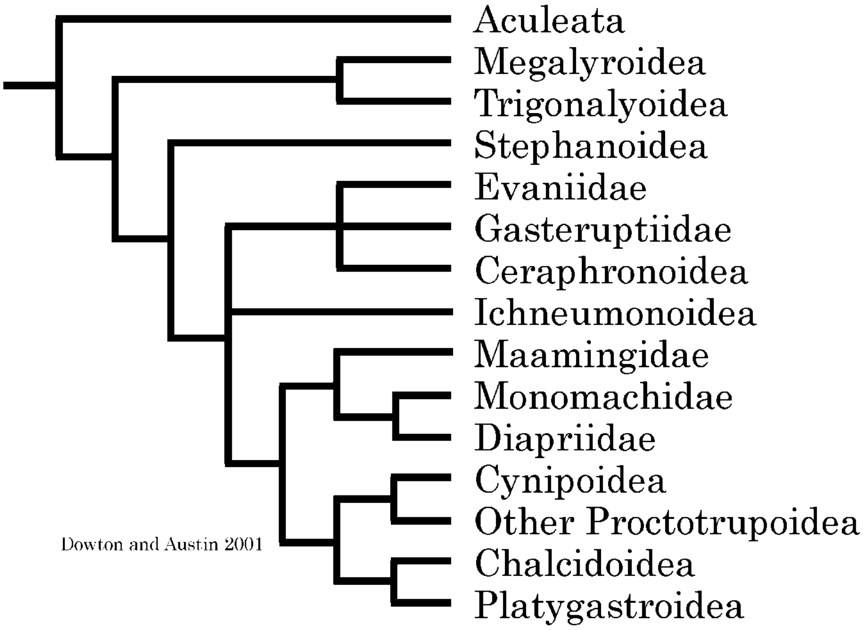


FIGURE 11. Strict consensus tree of apocritan taxa based on mitochondrial genes 16S rDNA and CO1, and nuclear gene 28S rDNA, simplified from Dowton and Austin (2001).

The most recent molecular phylogenetic analysis of Apocrita (Castro and Dowton 2006) added partial sequences of the 18S gene to the Dowton and Austin (2001) dataset and included Bayesian analyses. A simplified representation of their Bayesian tree, generated with a partitioned analysis and employing Mr. Modeltest is presented in Figure 12. Much focus in their paper was given to the monophyly of the clade (((Monomachidae + Maamingidae) (Diapriidae)) (Chalcidoidea)) which was recovered in most Bayesian and parsimony analyses. It is noteworthy that Diapriidae was also recovered as sister to Chalcidoidea in the Dowton et al. (1997)16S analysis that did not include ambiguous gene regions (Dowton et al. 1997, Figure 1, pg. 248), (Maamingidae was not included in the matrix). In Castro and Dowton (2006) Proctotrupomorpha is recovered and strongly supported but Evaniomorpha is not recovered nor is the sister-group relationship between Ichneumonoidea and Aculeata. Evanioidea is paraphyletic with respect to Ceraphronoidea. Two other problems include Heloridae being misplaced and the remaining Proctotrupoidea forming a paraphyletic grade. Interestingly Ichneumonoidea is sister to the remaining Apocrita, but support for the non-ichneumonoid clade is weak.

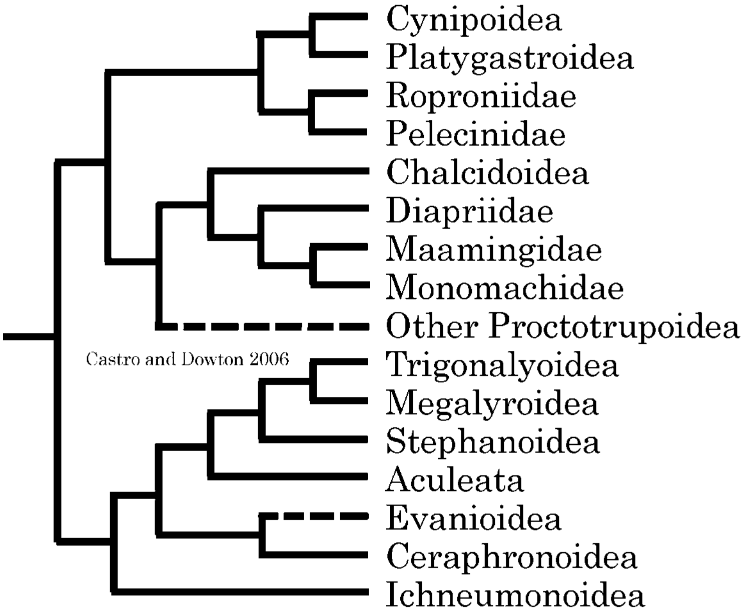


FIGURE 12. Strict consensus tree of apocritan taxa based on mitochondrial genes 16S rDNA and CO1, and nuclear genes 28S rDNA and 18S rDNA, simplified from Castro and Dowton (2006). Dashed lines indicate taxa that may be paraphyletic.

Morphologcial character systems

We are fortunate in that there have been many investigations into morphological systems across Hymenoptera or at least across Symphyta or Apocrita. These efforts have not, however, been incorporated into a comprehensive, cladistic, matrix for all Hymenoptera. These studies, presented below, constitute an invaluable resource for present and future studies.

Head Characters. General: Beutel and Vilhelmsen (2007). Labrum: Darling (1988). Antennae: Basibuyuk and Quicke (1999b). Preoral cavity: Vilhelmsen (1996). Antennal bases: Vilhelmsen (1997a). Occipital region: Vilhelmsen (1999).

Thoracic and mesosomal characters. General thorax, including musculature: Gibson (1985), Vilhelmsen (2000b). Pleuron: Gibson (1993). Midcoxal articulations: Johnson (1988). Metapostnotum: Whitfield et al. (1989). Mesofurca and metapostnotum: Heraty et al. (1994). Antennal cleaners and grooming behavior: Basibuyuk and Quicke (1995, 1999a). Wing characters: Basibuyuk and Quicke (1997), Sharkey and Roy (2002). Orbiculae: Basibuyuk et al. (2000). Plantulae: Schulmeister (2003d).

Abdominal characters. Thoraco-abdominal boundary: Vilhelmsen (2000a). Ovipositor: Oeser (1961), Rasnitsyn (1968), Quicke et al. (1992a, 1994, 1999b), Rahman et al. (1998), Vilhelmsen (2000c). Male genitalia: Schulmeister (2003a). Spermatozoa: Quicke et al. (1992b).

What We Think We Know

The cladogram in Figure 13 represents the relationships among the hymenopteran superfamilies that are reasonably well corroborated. It is a compilation derived from the analyses discussed above, especially those of Rasnitsyn 1988, Vilhelmsen 2001, and Dowton and colleagues. The dashed branches in Figure 13 represent clades with doubtful or unconfirmed monophyly. Rasnitsyn's (1988) analysis suggested a biphyletic Xyelidae, and although recent analyses have recovered Xyelidae as monophyletic, the concept is weakly supported. The most recent evidence (Beutel and Vilhelmsen 2007), investigating adult head characters, provides new evidence both for and against a polyphyletic Xyelidae. Diapriidae may be monophyletic but it is questioned here due to the somewhat doubtful placement of *Ismarus* (Ismarinae). Unlike the monophyly of Chrysidoidea and Apoidea, the monophyly of Vespoidea has never been convincingly demonstrated. A recent molecular analysis of Vespoidea by Pilgrim et al. (in prep.) places more doubt on the validity of the taxon but the question remains open.

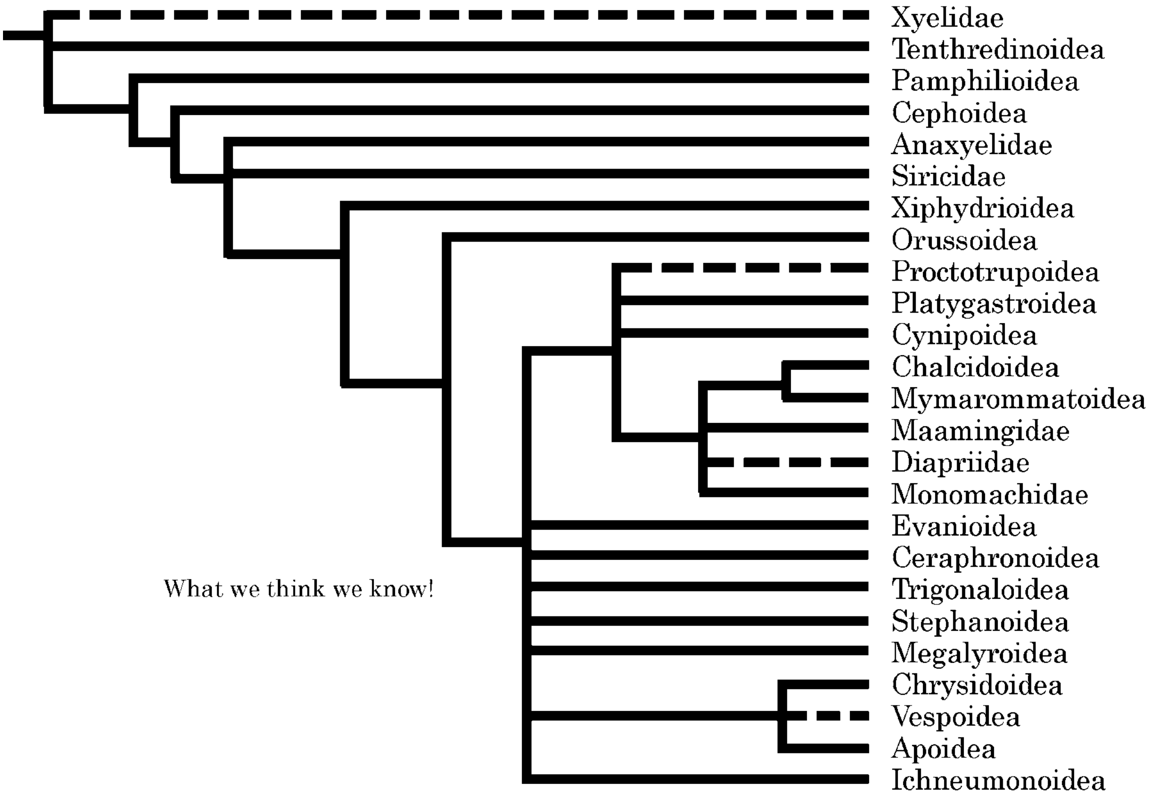


FIGURE 13. Phylogenetic tree summarizing relationships that are reasonably well corroborated by published analyses. Dashed lines indicate taxa of questionable monophyly.

Table I lists the hymenopteran superfamilies with references to papers on phylogenetic relationships within the superfamilies as well as some references to a few hymenopteran analyses that were not discussed in the text. References are not given for symphytan families since most of these are included in the symphytan analyses discussed previously. In the list I recognize 22 superfamilies and 89 families and this differs from recent classifications due to the inclusion of Diaprioidea, and a monotypic Platygastroidea. Diaprioidea, as here defined to include Diapriidae, Maamingidae and Monomachidae, is strongly supported in Castro and Dowton (2006). The decision to synonymize Scelionidae with Platygastridae is based on the phylogenetic analysis of Murphy et al. (2007) demonstrating the long-suspected paraphyly of Scelionidae (Austin and Field 1997; Dowton and Austin 2001) and the inadvisability of subdividing a morphologically homogeneous taxon like the Platygastridae *s.l.* into multiple families. Of the two included family-group names Platygastridae is the older.

TABLE I. Classification of extant Hymenoptera. Citations refer to publications containing phylogenetic analyses not mentioned or stressed in the main text.

Xyeloidea
Xyelidae
Pamphilioidea
Megalodontesidae
Pamphiliidae
Tenthredinoidea
Argidae
Blasticotomidae
Cimbicidae
Diprionidae
Pergidae
Tenthredinidae
Cephoidea
Cephidae
Siricoidea
Anaxyelidae
Siricidae
Xiphydrioidea
Xiphydriidae
Orussoidea
Orussidae
Stephanoidea
Stephanidae
Trigonalyoidea
  Carmean and Kimsey (1998)
Trigonalidae
Megalyroidea
Megalyridae
Evanioidea
  Deans and Jennings (2005)
  Jennings and Austin (2000)
  Jennings and Austin (2004)
  Deans et al. (2006)
Aulacidae
Evaniidae
Gasteruptiidae
Ceraphronoidea
Ceraphronidae
Megaspilidae
Proctotrupoidea
  Naumann and Masner (1985)
Austroniidae
Heloridae
Pelecinidae
Peradeniidae
Proctotrupidae
Proctorenyxidae
Roproniidae
Vanhorniidae
Diaprioidea
Diapriidae
Monomachidae
Maamingidae
Platygastroidea
  Austin et al. (2005)
  Murphy et al. (2007)
Platygastridae
Cynipoidea
  Ronquist (1995, 1999)
  Liljeblad and Ronquist (1998)
  Nylander et al. (2004)
  Liu et al. (2007)
Austrocynipidae
Cynipidae
Figitidae
Ibaliidae
Liopteridae
Chalcidoidea
  Gibson (1986a, 1999)
  Gibson et al. (1999)
  Campbell et al. (2000)
Agaonidae
Aphelinidae
Chalcididae
Encyrtidae
Eucharitidae
Eulophidae
Eupelmidae
Eurytomidae
Leucospidae
Mymaridae
Ormyridae
Perilampidae
Pteromalidae
Rotoitidae
Signiphoridae
Tanaostigmatidae
Tetracampidae
Torymidae
Trichogrammatidae
Mymarommatoidea
Mymarommatidae
Ichneumonoidea
  Quicke and Achterberg (1990)
  Wharton et al. (1992)
  Sharkey and Wahl (1992)
  Wahl and Gauld (1998)
  Belshaw et al. (1998)
  Dowton et al. (1998)
  Dowton and Austin (1998)
  Dowton (1999)
  Quicke et al. (1999a, c)
  Quicke and Belshaw (1999)
  Dowton et al (2002)
  Shi et al. (2005)
  Pitz et al. (2006)
  Laurenne et al. (2006)
Braconidae
Ichneumonidae
ACULEATA/VESPOMORPHA
  Königsmann (1978b)
  Brothers (1975, 1999)
  Brothers and Carpenter (1993)
  Carpenter (1990)
Chrysidoidea
  Carpenter (1986, 1999)
Bethylidae
Chrysididae
Dryinidae
Embolemidae
Plumariidae
Sclerogibbidae
Scolebythidae
Apoidea
  Alexander (1992)
  Melo (1999)
  Prentice (1998)
  Ohl and Bleidorn (2006)
  Danforth et al. (2006)
Ampulicidae
Andrenidae
Apidae
Colletidae
Crabronidae
Halictidae
Heterogynaidae
Megachilidae
Melittidae
Sphecidae
Stenotritidae
Vespoidea
  Pilgrim et al. (in prep.)
Bradynobaenidae
Formicidae
Mutillidae
Pompilidae
Rhopalosomatidae
Sapygidae
Scoliidae
Sierolomorphidae
Tiphiidae
Vespidae

Best Guess

My "best guess" tree in Figure 14 incorporates less convincing evidence form a multiple of sources. Most of this comes from the molecular analyses of Dowton and co-authors but a substantial part of the speculation is based on morphological data. In the course of putting the "best guess" together I changed by mind often. The infraorders of Rasnitsyn (1988) are all in place, as is the sister-group relationship between Aculeata and Ichneumonoidea. These have also been recovered in some molecular analyses. The relationships of all of the Evaniomorpha superfamilies are problematical as is their monophyly, and there is much molecular evidence to suggest that Aculeata is not sister to Ichneumonoidea. It is quite likely that the non-Proctotrupomorpha apocritan superfamilies form a grade between Symphyta and Proctotrupomorpha. If this turns out to be the case the superfamilies Stephanoidea and Megalyroidea are likely to fall near the base of the grade. As an apology for the subjective and intuitive nature of this hypothesis I quote Ashmead. "it is just as permissible for naturalists, as it is for philosophers, to draw sometimes upon their imagination in order to interpret nature" (Ashmead 1896, p. 329).

Current and future research

The traditional molecular markers used in insect phylogenetic studies are not providing the information necessary to resolve hymenopteran relationships. Adding new markers, especially nuclear protein-coding genes, seems to be a logical next step and adding more taxa is another possible solution. A large project, HymATOL (Hymenoptera: Assembling the Tree Of Life. www.hymatol.org), funded by the U.S. National Science Foundation, is nearing completion of a five year project that has incorporated these ideas.

To date comprehensive phylogenetic analyses of Hymenoptera have been conducted without a quality morphological data set and without protein coding nuclear genes. These lacunae are being addressed, to a limited extent, by the HymATOL group. It is hoped that the combination of new data will result in some progress. Undoubtedly there will remain numerous problematic areas and a genomic approach, such as that conducted by Savard et al. (2006), is another promising avenue of investigation.

Key Innovations and the Evolution of life history traits, a phylogenetic approach

Though we know little about apocritan relationships there are generalizations that can be made concerning the evolution of life history traits across Hymenoptera. One of the interesting autapomorphies of Hymenoptera is that they are haplo diploid, meaning that females have the full complement, 2N, number of chromosomes, and functional males have only half of the full complement; i.e., haploid. After copulation sperm are stored in the female spermatheca; as eggs pass down the oviduct the female may or may not release sperm to fertilize the egg. If no sperm are released a male is produced and if sperm fertilize the egg a female is usually produced although diploids that are homozygotes at the sex locus (loci) result in sterile or inviable diploid males. One obvious result is that this allows the female to control the sex ratio of her offspring, and this control is used effectively by most social Hymenoptera in which sex ratios are highly skewed with a female bias.

Another effect of haplodiploid sex determination is that males, because they are haploid and express all genes, are not very successful at carrying deleterious genes and very good at carrying the compliment, good genes. A low load of deleterious genes seems like a good idea. One of the positive qualities of haplodiploidy was thought to be that it allows for increased inbreeding (Hedrick and Parker 1997). However Zayed and Packer (2005) showed that single locus sex determination, which is prevalent throughout Hymenoptera, imposes a significant genetic load because of an increase in homozygosity at the sex locus. Contrary to previous beliefs, most members of hymenopterans may be especially sensitive to extinction at low population levels.

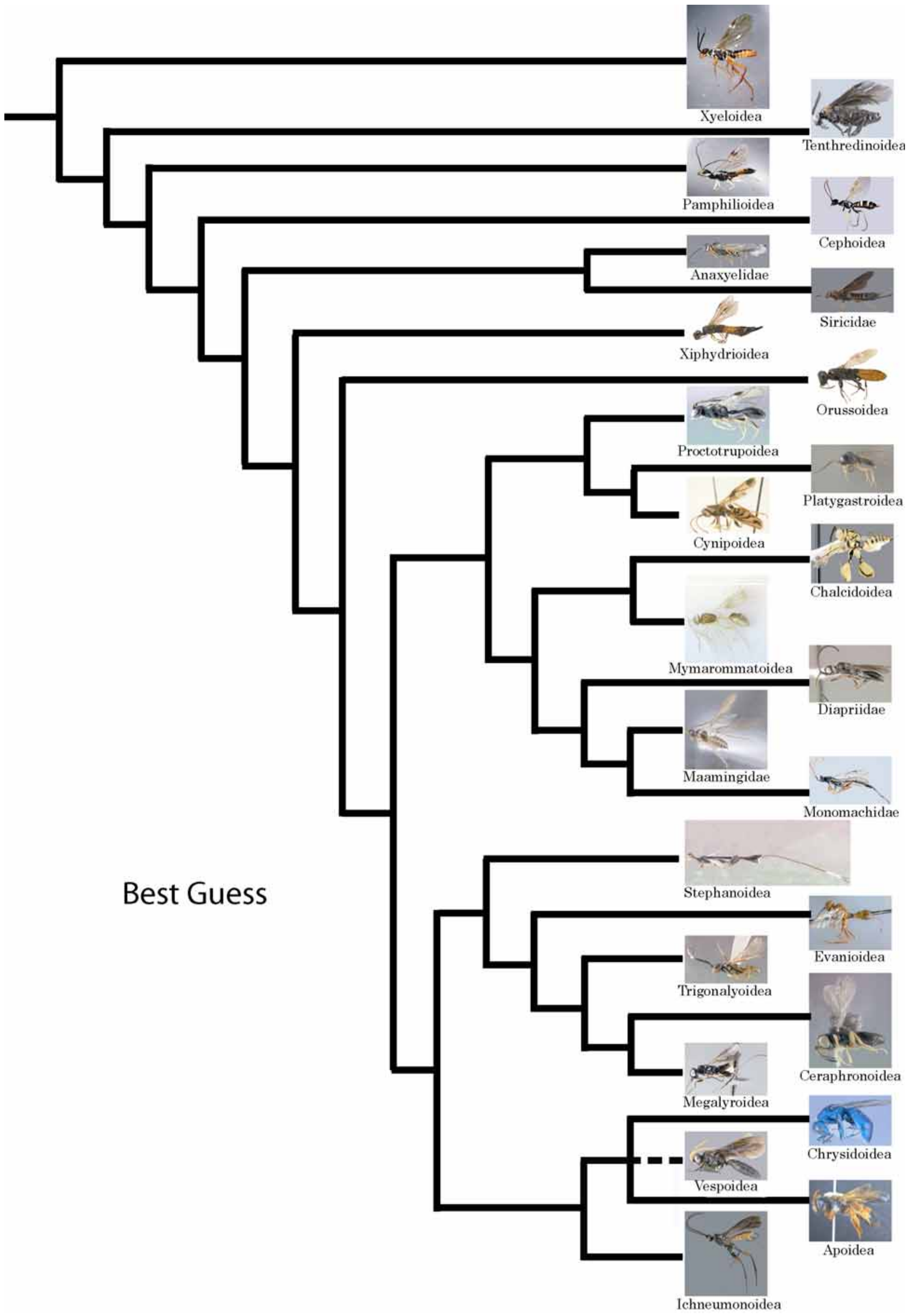


FIGURE 14. Intuitive phylogenetic tree based on relationships that have some support in published analyses. Click on thumbnail images to link to larger images.

Current optimizations of feeding strategy states on the phylogenetic relationships generally accepted for the group (Fig. 13) indicate that Hymenoptera began with larvae that feed externally on plant tissue. From this habit feeding inside woody tissue developed and this biology gave rise to carnivory as ectoparasitoids of xylophagous Hymenoptera and Coleoptera. This is the ground-plan condition of Apocrita but within Apocrita there have been many convergent reversals (s.l.) to the phytophagous condition. Amongst Aculeata, bees provision their larvae with pollen and nectar, social vespids commonly provision with plant products such as nectar and rotting fruit, and ants may feed on seeds (harvester ants) or on other plant products such as plant bodies, food corpuscles or extrafloral nectaries (Hölldobler and Wison 1990). The Parasitica also have many phytophagus members. One outstanding group is Agaonidae (Chalcidoidea), fig wasps, members of which feed exclusively within the fruits of *Ficus* (Moraceae) species. Both female and male fig wasps live within the fig fruit and are almost solely responsible for pollinating this large group of plants. Their association with figs is mutualistic. In exchange for food (fruit) the fig wasps act as pollinators. Another chalcidoid family with numerous phytophagous members is Eurytomidae, also known as seed chacids. Although many eurytomids have insect hosts, others utilize seeds or are gall formers. These represent the two most common forms of phytophagy within the Parasitica. Other families that include seed feeders are Torymidae, Pteromalidae and Tanaostigmatidae (Chalcidoidea), Braconidae (Ichneumonoidea), and families that include gall formers are Eulophidae, Pteromalidae, Tanaostigmatidae, Torymidae (all Chalcidoidea), Cynipidae (Cynipoidea), and Braconidae (Ichneumonoidea). Seed feeding in non-aculeate Apocrita might better be referred to as parasitoidism because it usually fulfills two criteria of the definition, i.e., only one host is attacked and the host is killed.

The ground-plan for hymenopteran larvae is possessed by most sawflies. It is eruciform (caterpillar-like) (Fig. 2a), with well developed thoracic legs as well as abdominal prolegs, and feeding is usually in the form of external foraging on exposed vegetation. Superficially these larvae look much like those of Lepidoptera, but unlike most Lepidoptera, the prolegs of primitive hymenopteran larvae do not have crochets, specialized hooks to grab the substrate, and the larvae of primitive Hymenoptera usually have more than 5 prolegs whereas lepidopteran caterpillars almost never have more than five. Lepidopteran larvae have more than one pair of stemmata (simple eyes or ommatidia) unlike larval Symphyta, which have only one pair, an autapomorphy of the order. The next biological stage in the phylogenetic grade leading to the apocritan Hymenoptera is represented by the Cephoidea, Siricoidea and Xiphydrioidea. The larvae of these taxa are xylophagous, feeding internally on woody tissue. Larvae of members of Siricoidea and Xiphydrioidea feed on wood that is infected by a symbiotic fungus inoculated into the wood during oviposition. These taxa and those of all Orussidae and Apocrita share the synapomorphies of a loss of abdominal prolegs (Fig. 2b).

The next major step was perhaps the most drastic and important in the evolution of the hymenopteran larvae. A xiphydriid-like ancestor gave rise to Orussidae, the first hymenopteran parasitoid, or at least, the first parasitoid with extant representatives. Their larvae, like those of Apocrita (Fig. 2c) are maggot-like with a further reduction of thoracic appendages, segmentation, and sclerotization. The members of Orussidae are external, idiobiont parasitoids of larval *Sirex* (Hymenoptera: Siricidae) and Buprestidae (Coleoptera) (Burke 1917, Gourlay 1951, Rawlings 1957, Powell and Turner 1975, Nuttall 1980). Idiobiosis (Askew and Shaw 1986) is a type of parasitism in which the parasitoid begins to consume its host immediately after coming in contact with it. This biology is typically associated with ectoparasitoids. Idiobiosis contrasts with koinobiosis in which a parasitoid lives, usually as a first instar larva, for a prolonged period before beginning to consume its host. Orussidae are sister to all extant Apocrita, and their biology as idiobiont, ectoparasitoids of xylophagous holometabolous insect larvae is prevalent throughout Apocrita. The following superfamilies, or higher taxa, exhibit this suite of traits: Megalyroidea, Ichneumonoidea, Aculeata, Chalcidoidea, and Stephanoidea. That this is the apocritan ground-plan suite of biological characters is likely for all of these taxa except Chalcidoidea. Most morphological and molecular analyses place Chalcidoidea as derived Proctotrupomorpha, all members of which are endoparasitoids. If one is to contrive that the groundplan of Chalcidoidea includes ectoparasitism, at least three independent origins of endoparasitism are inferred in Proctotrupomorpha (e.g., Fig. 12). Contrary to this evidence, it is hard to imagine a switch from endoparasitism to the most primitive suite of ectoparasitic habits as exhibited some Eupelmidae and Pteromalidae. Including hymenopteran taxa like Proctotrupoidea, Aulacidae, and Cynipoidea that are exclusively endoparasitic (except for derived phytophagus lineages) parasitism of xylophagus insects is the most widespread (but not the most common) biology amongst apocritan superfamilies and it is from this biology that much of the current biological and species diversity appears to have emanated.

There are undisputed switches from ectoparsistism to endoparasitism within Apocrita. This transition occurred multiple times within Ichneumonoidea, and at least once in each of the Proctotrupomorpha, Ceraphronoidea, Chrysidoidea, Trigonalyoidea, Evanioidea, and possibly multiple times within Chalcidoidea. Amongst parasitoid apocritans, endoparasitism is the most common biology, i.e., most species are endoparasitoids. In general endoparasitoids appear to be more species-specific than ectoparasitoids and host specialization, which is associated with endoparasitism, may have facilitated an increased rate of speciation.

All examined apocritan larvae have blind digestive systems, an apparent autapomorphy for the clade, therefore they do not defecate until the end of the last larval instar. At this time the midgut and hind gut unite and all built-up wastes are ejected at once. This waste package is termed a meconium, as it is with placental newborns, and it is a practical adaptation for an organism that must live in or on its food source. All known members of Apocrita have retained this character, even the many aculeate Hymenoptera that have lost the parasitoid habit. The condition in Orussidae has been unknown until recent research by Lars Vilhelmsen (2003) showed that the mid- and hind guts are apparently continuous in the larva and that no meconium is produced. There are, however, a series of transverse cuticular folds in the hindgut which might serve as a seal when the musculature of the hindgut is contracted. The presence of a meconium is unknown for members of Stephanidae and Megalyridae and since both of these taxa may be basal apocritans this information is essential to definitively state that a meconium is an autapomorphy of Apocrita. A striking synapomorphy of members of Apocrita is the "wasp waist", a constriction between the first and second abdominal segments, and an even stronger fusion of the first abdominal segment with the thorax than is found in Symphyta. The resulting flexibility and maneuverability must certainly have had an influence on the success of apocritans.

Aculeata is also known as the stinging Hymenoptera because the ovipositor is modified such that it no longer functions to lay eggs. Rather, eggs are exuded from the base of the ovipositor, and the ovipositor, or sting as it can be described, is used exclusively to deliver venom to prey and/or potential predators. This modification has occurred convergently in at least one species of parasitoid wasp in the family Ichneumonidae (Eberhard 2000). Aculeata is well known for members like ants, social wasps and bees that exhibit eusocial behavior, a characteristic that has evolved independently in several lineages within Vespoidea and Apoidea. The ground plan of Aculeata includes the parasitoid habit and many of the diverse habits displayed by this interesting clade are derived from parasitoidism.

The primitive condition in Hymenoptera is for the last larval instar to spin a cocoon, using silk spun from labial spinnerets. This habit is found in Xyeloidea, Tenthredinoidea (except perhaps for Blasticotomidae) and Cephidae. A cocoon is apparently not present in members of Pamphilioidea but they do use silk produced from labial glands to roll leaves and form webs in which to feed. The remaining symphytans (Siricidae, Anaxyelidae, Xiphydriidae, and Orussidae) do not spin a cocoon. Among Apocrita, larval production of labial silk is part of the ground plan of the Ichneumonoidea, Aculeata, Trigonalidae, Gasteruptiidae and Aulacidae (Sharkey 1994), and may prove to be a re-expression of a primitive trait in these groups. Cocoons are also found in some chalcidoids and platygastroids, however these cocoons are not constructed with labial silk. Rather, secretions produced in the malphigian tubules and excreted through the anus and/or mouth cover the final instar larvae and then harden into a cocoon-like structure (Flanders 1938, Colazza and Bin 1992, Ceresa-Gastaldo and Chiappini 1994). There has been some controversy over the origin, labial or malphigian, of trigonalid silk. David Carmean (pers comm.) has informed me that in the pre-pupal cell of *Bareogonalos* *canadensis* (Trigonalidae) the only place the silk is found is on the top of the cell just under the very thin yellowjacket cap. This corresponds to the oral end of the larvae and the cell appears to be too narrow for the trigonalid larvae to flip end-to-end. This suggests that the silk is excreted from the anterior end of the larvae and is almost certainly therefore produced by labial glands.

Hymenoptera and Rhaphidioptera are unique among Holometabola in possessing an ovipositor, though pseudo-ovipositors have been developed in some Diptera such as Tephritidae. Other Neuropterida retain ovipositor sheaths, and the ovipositor of raphidiopterans is highly modified. Although they function primarily for defense and egg-laying, the modifications of the ovipositor in Hymenoptera are remarkable.

As the name suggests, the ovipositors of sawflies are serrate (Fig.1a); they are laterally flattened with a serrate surface at least on the ventral side. This is the primitive condition in Hymenoptera and the saw is usually used to cut a slit in plant tissue, often leaves, into which an egg is deposited. This is the condition found in Xyeloidea, Pamphilioidea, and Tenthredinoidea. The Cephoidea, have retained serrated edges throughout most of the length of the ovipositor but the apex is sharp and it is used to drill into wood, secondarily modified to drill into herbaceous stems in derived clades. Members of Siricoidea and Xiphydriidea have ovipositors with reduced serrations (Fig. 1b) that are restricted to the apex and this condition is found throughout Apocrita in species that drill into wood. The ovipositor found in Siricoidea, Orussidae and the vast majority of the Apocrita have a cylindrical shape. Whether this is a synapomorphy for Siricoidea + Xiphydriidae, + Orussoidea + Apocrita with a reversal in Xiphydriidae, or a convergence condition in Siricoidea and in Orussoidea + Apocrita is unknown. There is a grand variety of ovipositor morphologies among apocritans (e.g., Fig. 1c) indicative of their central role in facilitating the diverse life histories possessed by one of the most successful clades of life.

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