

# PHYLOGENY AND EVOLUTION OF HOST-PARASITOID INTERACTIONS IN HYMENOPTERA

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## ABSTRACT

Recent studies of hymenopteran phylogeny using both comparative morphology and DNA sequence data have greatly enhanced our understanding of the evolution of that order. Resulting phylogenetic hypotheses make possible more rigorous investigations of the evolution of various biological life-styles, among them the parasitoid habit. This paper reviews the current findings from higher-taxon phylogenetic analyses of the order. A “consensus” phylogeny derived from these findings is used to trace the most likely evolutionary pathways leading to the current diversity of parasitoid habits. Taxa and biological phenomena for which our current understanding is fragmentary are highlighted. Based on current evidence, it appears that parasitism arose, from mycophagous ancestors, a single time within the order. Many subsequent elaborations of the parasitic mode of life (e.g. endoparasitism, secondary phytophagy, etc) apparently evolved independently more than once.

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## OVERVIEW

The Hymenoptera are one of the four mega-diverse orders of holometabolous insects, along with the Coleoptera, Diptera, and Lepidoptera, that dominate the faunas of terrestrial areas throughout the world. Although the order is a distant second to Coleoptera in numbers of described species, it is actually the most species-rich in the most surveyed temperate regions (e.g. the United

Kingdom) (39). In many tropical arthropod samples the Hymenoptera appear to rival the diversity of the beetles (54, 88, 118), especially among the less studied parasitoid groups.

The abundance of species in the order is matched by a rich spectrum of ways of life. Hymenopterans live in virtually all terrestrial and freshwater habitats and play numerous ecological roles. Many Hymenoptera are critical pollinators or seed dispersers of flowering plants (52, 53); others help keep populations of insects and other arthropods in check through predation or parasitism (52); and still others feed on plant or fungal tissue directly (52, 53, 77). It has been suggested that no other order of insects contains so many species beneficial to humans (52).

Several recent major reviews provide excellent insights into the general ecological and evolutionary implications of the parasitoid life-style (50, 55, 56, 95). Here, efforts are instead devoted to relating the known taxonomic distributions of biological life-styles among Hymenoptera to what we know of their phylogeny, in order to reveal the patterns of evolution leading to their biological diversity.

New data on both taxonomic and biological diversity within Hymenoptera are accumulating rapidly, and recent efforts to reconstruct the evolutionary history of the order have begun to present a fairly consistent, if fuzzy, picture. Excellent reviews of the biology of Hymenoptera, especially parasitoids, are available (2, 7, 16, 32, 44, 53, 62, 95, 127); most of them, however, have not taken an explicitly phylogenetic approach to reviewing the diversification of biological life-styles (exceptions are 32, 33, 46, 95, 127).

It has only recently been possible to complement the large number of comparative morphological studies of both extant and fossil Hymenoptera with phylogenetic studies that employ molecular data. I provide a brief comparative summary of views of the origin and phylogeny of Hymenoptera, with emphasis on recent work. I then present the conservative “consensus” phylogeny that I believe is best supported by the current evidence. Finally, I use this phylogeny as a framework to discuss the most likely evolution and diversification of many aspects of hymenopteran parasitoid biology.

## ORIGIN OF THE HYMENOPTERA

The identity of the sister-group of the Hymenoptera is still uncertain. Most modern treatments using comparative morphology (including fossils) focus on one of two principal alternatives: the Mecopteroidea (Mecoptera, Trichoptera, Lepidoptera, Diptera, and Siphonaptera) or a clade containing all other extant holometabolous orders. Kristensen (69–71) and Königsman (65) supported the former view, based largely on comparative morphology of extant taxa, whereas Rasnitsyn (101) incorporated comparative information from the fossil

order Miomoptera to infer the latter hypothesis. Recent comparative morphological studies on pleural structures by Gibson (49) and on the preoral cavity by Vilhelmsen (123) have not supported either hypothesis definitively.

A few workers have attempted to resolve the relationships of the Holometabola using molecular data (13, 14, 92). Most of them have utilized sequences from the 18S rRNA gene and, interestingly, have had the same degree of difficulty in resolving holometabolite relationships as comparative morphologists. This uncertainty as to the position of the Hymenoptera among the Holometabola applies even to the most recent analysis by Whiting et al (130a), who employed 18S and 28S rDNA sequences along with morphology.

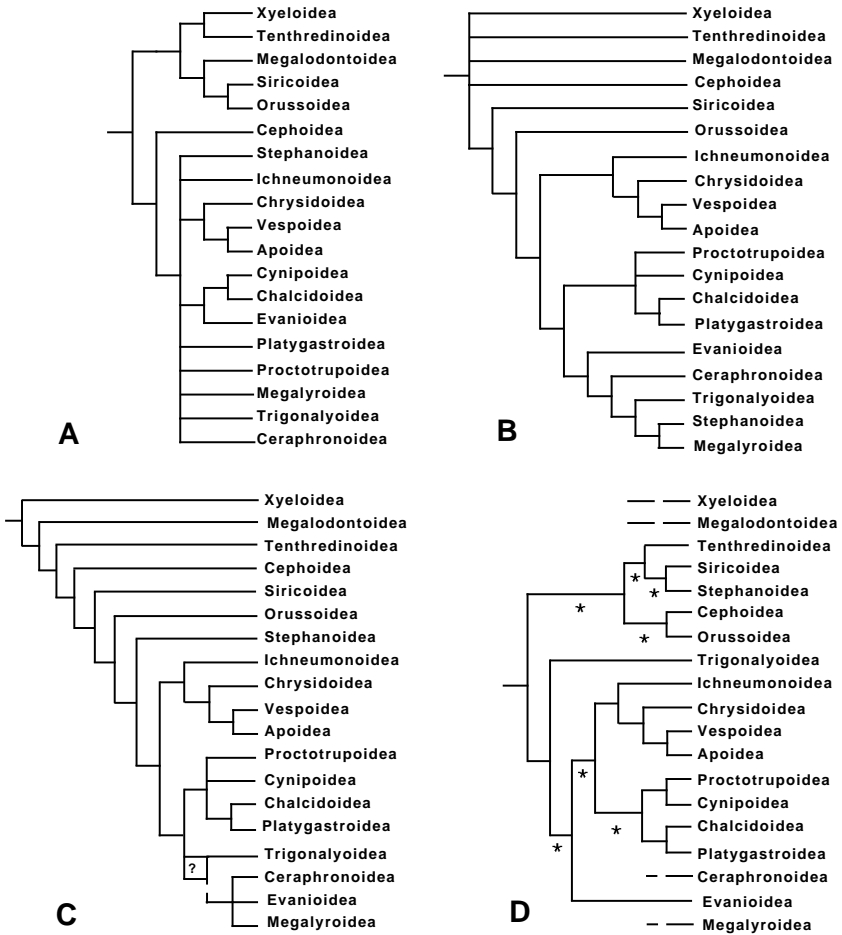
The order is known from fossils from at least 220 million years ago (MYA) (46, 72, 75, 99, 103), and there is recent indirect evidence from fossil plant damage that the actual origin may have been as early as 300 MYA (74). The diversification of the order probably was enhanced by the concurrent diversification of flowering plants and their other associated insect faunas, but critical events in this interaction would be difficult to pinpoint using currently available data. Several of the parasitoid groups had appeared by 160 MYA, and all superfamilies of Hymenoptera apparently were present by the late Cretaceous (65–70 MYA) (44, 46, 99–102).

## RECENT PHYLOGENETIC STUDIES OF HYMENOPTERAN GROUPS

Most modern treatments of the phylogeny of Hymenoptera as a whole stem from the work of Königsman (65–68) and Rasnitsyn (98–102). These two authors presented the first phylogenetic hypotheses based on large sets of data and using (at least in part) modern phylogenetic argumentation.

Königsman's phylogenetic scheme (redrawn in Figure 1A) was based primarily on a literature review of the comparative morphological and fossil evidence available at the time. He used Hennigian principles. Unfortunately, despite the rigor of his approach, the evidence he compiled was incomplete even for that time; only a few relationships within the order were resolved, and some of those were not well supported. However, his efforts to compile comparative data made subsequent work considerably easier and stimulated research to resolve many of the phylogenetic uncertainties revealed by his analysis.

Rasnitsyn (98–102) incorporated knowledge of many fossil taxa that were at that time poorly known outside the former Soviet Union. His thorough treatment of fossil morphology and paleoecology was combined with a comprehensive analysis of comparative morphology of extant taxa to produce the first well-resolved phylogeny for the order (101, 102), which is summarized in Figure 1B. In 1988, Rasnitsyn presented his slightly modified conclusions in a phylogenetic tree labeled with proposed synapomorphies (102).



*Figure 1* Four of the more recently proposed phylogenies for the Hymenoptera. The trees have been simplified somewhat from the originals, in order to standardize the terminal taxa for direct comparison. (A) Hypothesis of Königsmann (65–68), based on a literature review of morphological evidence—this phylogeny was also used in Hennig (57). (B) Hypothesis of Rasnitsyn (102), based on comparative morphology, biological habits, and fossil evidence; fossil groups have been deleted from the tree and the basal relationships have been simplified from Rasnitsyn’s proposed diphyletic origin of Xyeloidea. (C) Composite phylogeny of Whitfield (127), based on Rasnitsyn’s hypothesis modified by newer data from comparative morphology (22, 47, 48); basal relationships have been added from Gibson (49) and Heraty et al (59). (D) Phylogeny obtained from 16S mtDNA sequences by Dowton & Austin (27); *asterisks* denote branches supported by bootstrap values lower than 50%, and *dashed lines* indicate taxa not examined by Dowton & Austin.

In many ways Rasnitsyn's conclusions formed the framework for all subsequent investigations, many of which found large areas of agreement with his scheme. His methods of phylogenetic and classificatory procedure were not entirely cladistic, however, which led to some logical inconsistencies in his scheme.

Meanwhile, new data on comparative morphology accumulated to test Rasnitsyn's phylogeny. WRM Mason conducted an exhaustive series of dissections of the mesosomal-metasomal articulation in the 1980s that shed new light on higher-taxon relationships among Hymenoptera. Some of Mason's unpublished but influential results are included in the discussions of comparative morphological data below.

Gibson (47–49) carried out a series of comparative morphological studies on thoracic skeletomusculature centered on Chalcidoidea and Symphyta but extending throughout the Hymenoptera. Johnson (63) and Whitfield et al (130) conducted comparative studies of midcoxal articulations and metapostnotal structure and musculature, respectively. Darling (22) focused on labial structure, and Heraty et al (59) studied the mesofurca and mesopostnotum within the order. In 1992, Whitfield (127) summarized the evidence up to that time and produced a "current consensus" phylogeny—basically Rasnitsyn's interpretation modified by more recent work (Figure 1C). More recently, Vilhelmsen (123) reported results of an exhaustive study of the preoral cavity in Hymenoptera (especially featuring the basal lineages), and Donald Quicke's research group produced surveys of ovipositor structure (96, 97) and the antenna cleaner (5). The results of all of these morphological studies are incorporated into the discussions of relationships below.

In 1994, Downton & Austin (27) produced the first fairly comprehensive molecular phylogeny of Hymenoptera (Figure 1D), using sequence data from the 16S rRNA mitochondrial gene. Further tests of the basal lineage relationships were later provided by data from the cytochrome oxidase I mitochondrial gene (28).

## PHYLOGENY OF THE HYMENOPTERA: A CURRENT SUMMARY

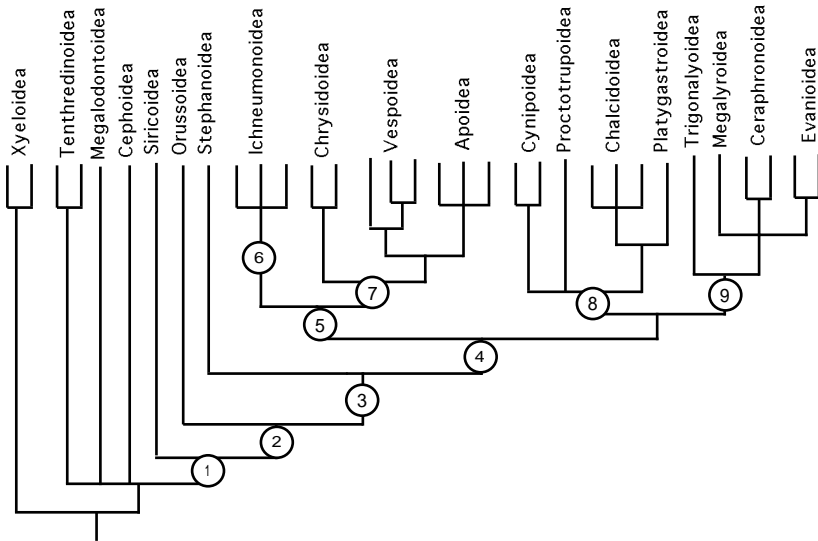
The reader should refer to Figures 1A–D, the recently proposed phylogenies. The analyses summarized in this section were used to generate the new consensus phylogeny (Figure 2), and that was then used to show the evaluation of larval feeding (Figure 3). The hypothesized new phylogeny is a modification of those presented in Figures 1C and D based on new evidence. Thus, unresolved or conflicting branching sequences are resolved to be consistent with more recent data. A completely new synthesis based on all available data is not currently feasible because many of the data sets do not agree in taxonomic representation.

*“Symphyta” (Sawflies, Horntails, and Woodwasps)*

Rasnitsyn’s concept of a diphyletic Xyeloidea, one lineage related to the Tenthredinoidea and the other related to all other Hymenoptera, has not been supported by further studies. However, the basal position of Xyeloidea and to a lesser extent Tenthredinoidea within the Hymenoptera is sustained (49, 123). The monophyly of Hymenoptera other than Xyeloidea and Tenthredinoidea is upheld by the position and musculature of the labrum (123), the presence of a hypostomal bridge (102), and the absence of larval pro-legs (65, 66), although the position of the Megalodontoidea is still somewhat uncertain. The traditional concept of the suborder “Symphyta,” constituting the sawflies, horntails, and woodwasps (Xyeloidea + Tenthredinoidea + Megalodontoidea + Cephoidea + Siricoidea + Orussoidea), thus corresponds to a paraphyletic group, as it phylogenetically should include the Apocrita (all other superfamilies).

*The Phylogenetic Position of Apocrita (True Wasps, Parasitic Wasps, Ants, Bees)*

Königsmann (67), as well as some earlier authors, proposed that Cephoidea (the stem sawflies) constituted the sister group to the Apocrita, whereas most recent authors, including Rasnitsyn (98, 101, 102), have suggested that some member of the Siricoidea (horntails) or Orussoidea (parasitic wood wasps) is actually the nearest extant relative. The exact relative phylogenetic positions of

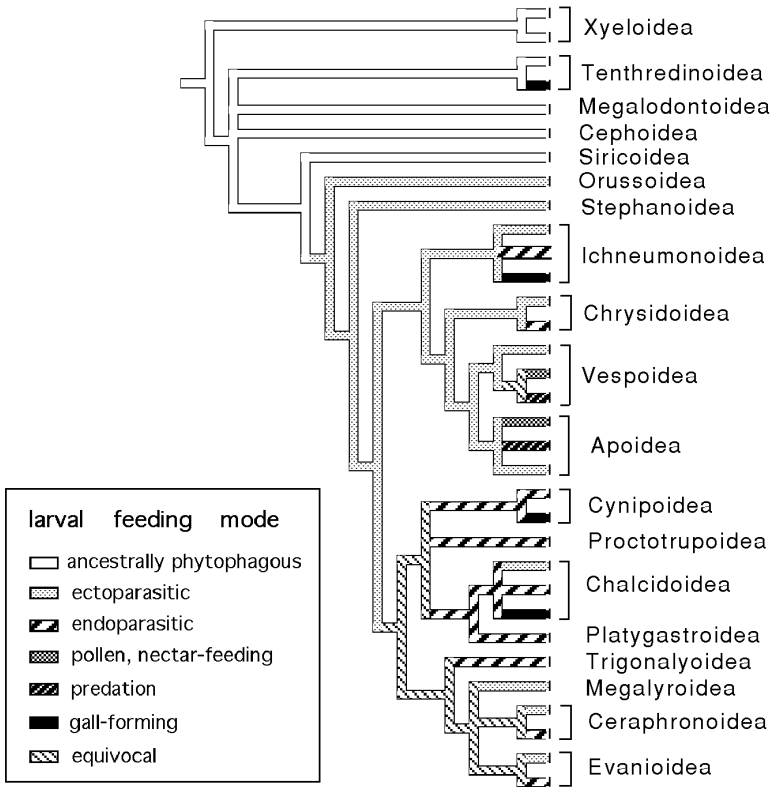


the various siricoids and Cephoidea still remain uncertain, but morphological evidence (see Figure 2) is mounting in favor of at least the following set of relationships: [Siricoidea + (Orussoidea + Apocrita)]. Molecular data thus far have not supported this exact relationship, but it is among these most ancient (basal) divergences that one would expect the 16S mitochondrial DNA (mtDNA) data to have the highest noise-to-signal ratio (see bootstrap values in Figure 1D).

Monophyly of the relationship Orussoidea + Apocrita is now supported by a host of synapomorphies; interestingly, it is this morphologically well-supported sister-group relationship that is most strongly contradicted by the mtDNA data of Downton & Austin (27, 28). The molecular data do, however, suggest a



*Figure 2* Intuitive phylogenetic hypothesis for the Hymenoptera, based on current evidence. Proposed morphological synapomorphies supporting each of the numbered nodes, accompanied by their references, follow: *Node 1*—shape of the labrum, reduction of the number of labial palpal segments, and absence of larval eyes (123); long, subcylindrical, and heavily sclerotized ovipositor with elongated rhachis (WRM Mason, unpublished data). *Node 2*—presence of pronotal lobe, absence of postspiracular sclerite, and fully developed parapsidal lines (47, 49), presence of midcoxal articulations and absence of furco-sternal muscles (63); first abdominal tergite undivided and fused with metapostnotum (130); upper ovipositor valves fused at apex (97), presence of fore basitarsal notch and fully developed basitarsal comb (5); distal portion of paraglossae reduced, usually combined with a longitudinally folded glossa (123). *Node 3*—presence of hypopharyngeal lobe (123), absence of furcal-basalar and metafurcal-spinal muscles (59), anterior corners of abdominal sternite 2 with a field of proprioceptor hairs (WRM Mason, unpublished data), and articulation between abdominal segments 1 (propodeum) and 2 being tergum-to-tergum (WRM Mason, unpublished data). *Node 4*—note that these are apparent plesiomorphies shared with Orussidae but absent in other Apocrita and are *not* true synapomorphies; large labral apodemes (123); shape of the labrum, tormae, and epipharynx (123); vertex with a ring of cuticular teeth around the median ocellus (102); enlarged mesothoracic basalare (47, 49). *Node 5*—presence of ovipositor valvilli (96); sternites 2–3 and 3–4 separated and not forming articulations or fusions along with their tergites (WRM Mason, unpublished data). *Node 6*—adult mandible with two teeth (85); prepectus fused to posterolateral margin of pronotum, combined with mesothoracic spiracle position above prepectus and location of external pit marking location of spiracular occlusor muscle near posterior pronotal margin (47); sternum of first metasomal segment divided into heavily sclerotized anterior section and weakly sclerotized posterior section (84, 85); metasomal segments 1 and 2 articulated by a pair of dorsolateral condyles (85); costa and radius of fore wing adjacent, appressed, or fused (WRM Mason, unpublished data); vein 2r-m of fore wing absent (convergently lost in some small-bodied taxa in other groups) (109); larval head with hypostomal spur (109). *Node 7*—modification of the ovipositor apparatus such that the egg is no longer laid through the ovipositor canal, but instead through a separate opening, and the ovipositor is specialized for stinging (89); loss of cerci in the females (8). *Node 8*—loss of the medial scutal sulcus, the head with lower tentorial bridge intervening between postgenae to reach occipital foramen and to replace postgenal bridge, and the prepectus extending behind and above above the first spiracle (101). *Node 9*—shape of the mesal lobes and their articulation with the midcoxae (63, 101).



*Figure 3* The most parsimonious evolution of larval feeding modes of Hymenoptera using the phylogeny (same as Figure 2) of Whitfield (127), partly modified basally with reference to more recent evidence as well as to the views of Gauld & Hanson (46). The distribution of the larval habits given in the box were optimized onto the phylogeny using MacClade version 3.06 (80). Data on larval habits were compiled from References 16, 32, 44, 53, 95, and 127. Inquilinism was not treated separately as a habit—it tends to occur sporadically among those groups containing both parasitic and secondarily phytophagous (including gall-forming) lineages.

close relationship between members of Siricoidea *sensu lato* (Xiphidriidae, Orussidae, Siricidae) and Apocrita, so morphological and molecular data are at this stage in conflict only in the details of branching order. At this stage, the Orussidae + Apocrita relationship is slightly favored on the strength of the strong morphological support and also because it requires only a single origin of parasitism within the Hymenoptera.

Monophyly of Apocrita, a long-recognized group, is supported by a series of synapomorphies summarized in Figure 2.

### *Relationships Within Apocrita*

Recent studies suggest that the Stephanoidea (consisting only of the Stephanidae) represents the most basal extant lineage of Apocrita, in contrast to Rasnitsyn's (102) inclusion of the Stephanidae in his "Evaniomorpha." That basal position also is supported by molecular data from Dowton & Austin (27); in fact, in their study the Stephanidae are positioned even more basally among the symphytan lineages.

The remaining superfamilies of the Apocrita fall out into four main lineages that correspond in general outline with the phylogeny of Rasnitsyn (102 but not 101). The placement of Stephanoidea mentioned above is the exception. Two of these lineages are commonly recognized groups that have only recently been considered as sister groups to one another based on morphology: Ichneumonoidea and Aculeata. That relationship is supported by the molecular analyses of Dowton & Austin (27), as well as by earlier, much less comprehensive studies using the same gene by Derr et al (23, 24).

Monophyly of the Ichneumonoidea, including only Ichneumonidae and Braconidae among extant groups, is supported by a strong array of synapomorphies listed by Sharkey & Wahl (109), some of which have been modified within each of the two families. All published molecular studies support this relationship.

The Aculeata also are a long-recognized group, which is most notably supported by the modification of the ovipositor apparatus so that the egg is laid through an opening independent of the ovipositor. Its family composition has remained essentially unchanged for many years, but the consolidation of a larger number of superfamilies into only the current three (Chrysoidea, Vespoidea, Apoidea) dates from the 1975 study of Brothers (8). The proposed family-level relationships within each of these three superfamilies continue to be investigated; current views are summarized by Brothers & Carpenter (10) and by Alexander (1).

The remaining two major clades, the Evaniomorpha (minus Stephanidae) and Proctotrupomorpha sensu Rasnitsyn (102), are less familiar groupings. The relationship between them and the Ichneumonoidea/Aculeata clade is not well understood, although the available molecular results from Dowton & Austin (27) shown in Figure 1D support conclusions based on morphology that were summarized earlier by Whitfield (127) (Figure 1C).

The monophyly of the Evaniomorpha [including Evanidae (ensign wasps), Aulacidae, Gasteruptiidae, Trigonalidae, Megaliridae, Stephanidae, Megaspilidae, and Ceraphronidae] was one of the most surprising proposals of Rasnitsyn (102). As outlined above, most recent work has removed the Stephanidae from this lineage, as indeed Rasnitsyn did in earlier work (101).

This grouping in general has been weakly supported morphologically (Figure 2). The first molecular analysis by Dowton & Austin (27) suggested that the Evaniomorpha would not be monophyletic if Trigonalysidae were included; more recent work by the same group, with increased taxonomic representation, established that Evaniomorpha minus Stephanidae is monophyletic (29). Rasnitsyn's concept of Evaniomorpha has held up to further testing remarkably well.

The Proctotrupomorpha of Rasnitsyn (102) included the families traditionally assigned to the Proctotrupeoidea (except the Megaspilidae and Ceraphronidae, which are now treated as the Ceraphronoidea), the Cynipoidea, and the Chalcidoidea. A number of the morphological characters used by Rasnitsyn to support this clade are too variable among the groups to be very strong indicators. Some of his proposed synapomorphies show promise but require further comparative morphological study to confirm their generality. Quicke et al (97) suggested that ventrally overlapping ovipositor valves generally characterize this group, but these are missing in Cynipoidea and some Proctotrupeoidea and are convergently present in Ceraphronidae. Thus the morphological evidence supporting this clade is not very convincing, but neither has much contradictory evidence accumulated. Dowton & Austin's original molecular work (27) weakly supported the Proctotrupomorpha as monophyletic, but a later more taxonomically complete survey (29) indicated that the Cynipoidea possibly might not belong to this group.

The family-level relationships within the Proctotrupeoidea (82, 87) and Chalcidoidea (51, 131) remain notoriously unstable, despite progress in resolving some of them (e.g. 48, 76). However, essentially all recent studies, both morphological and molecular, support the removal of Ceraphronidae and Megaspilidae from the Proctotrupeoidea, as originally proposed by Masner & Dessart (83), and the recognition of Platygastroidea (Scelionidae and Platygastriidae) as a lineage distinct from the Proctotrupeoidea and probably forming the sister group to Chalcidoidea (27, 29, 102). The Platygastroidea have recently been further studied phylogenetically using the ovipositor system (4). The skeletomuscular studies of Gibson (48) convincingly established the Mymarommatidae as the sister group to the remaining Chalcidoidea; however, disagreement remains as to whether this family should be recognized as a separate superfamily (97) or be included within Chalcidoidea (51).

To summarize this discussion of hymenopteran relationships, the phylogenetic hypothesis of Rasnitsyn (102) (Figure 1B) has been largely corroborated but partly contradicted by further evidence from both comparative morphology and DNA sequence data. A complete, comprehensive, and rigorous analysis of all of the available data remains to be performed and will require extensive reexamination of the character data across all taxa. A representation of the phylogenetic relationships suggested by current evidence is attempted in Figure 2. This

consensus phylogeny (not to be confused with an actual consensus tree of the individual competing phylogenetic hypotheses) is used in the following section and in Figure 3 to determine the probable evolution of parasitism and some associated traits. Continuing comparative morphological and molecular research into the higher level phylogenetic relationships within the Hymenoptera is likely to further clarify the evolutionary history of the forms of parasitism.

## EVOLUTION OF THE PARASITOID LIFE-STYLE

### *The Origin of Parasitism*

As outlined in Figure 3, the current phylogeny suggests that parasitism arose once, in the common ancestor of the Orussoidea and Apocrita. The alternative hypothesis that Siricoidea (especially Siricidae) is the sister group of Apocrita would imply two origins of parasitism within the order, but these two groups are phylogenetically close. Either case entails an origin of parasitism from a precursor that specialized in larval feeding within tunnels in wood and at least partly upon fungi. These fungi were introduced and/or promoted by secretions coming from the adult female wasp at the time of oviposition (44, 46, 53). The ability to target oviposition toward hosts in concealed situations such as galleries in wood was then already present in siricoids or orussoids with their aciculate form of ovipositor (98).

The ancestral form of parasitism almost certainly was external, and in many still extant basal taxa the parasitoid egg is laid near rather than on or in the host. The extent to which adult females of many of the basal lineages within Apocrita are able to use venom to incapacitate or paralyze the host has not been completely surveyed. From what we do know, the ability to paralyze the host, permanently or temporarily, is relatively widespread within Apocrita (Table 1) and probably developed very early (44, 98, 122, 127). In the few cases that have been studied thoroughly, the induction of permanent paralysis or even death by venoms appears to be the ancestral state, and more subtle effects such as temporary paralysis or the redirection of the venom function toward more diverse physiological impacts appear later (40, 111, 128). Virtually all of these early parasitic lineages of Apocrita still primarily attack hosts within concealed situations such as galleries in wood or plant galls. That behavior may result either simply from retention of the ancestral host search pattern or by selection against having more exposed hosts that, when paralyzed, would be exceptionally vulnerable to general predators and scavengers (53, 98, 122).

Many of the basal clades within the Orussoidea, Stephanoidea, Ichneumonoidea, and Aculeata (Figure 3) are ectoparasitoids of concealed hosts, often within galleries in wood. This is also true for Megalyroidea and some members of the Evanioidea, and some members of the Chalcidoidea and Ceraphronoidea

are ectoparasitoids. However, some basal Cynipoidea attack hosts within galleries in wood but are endoparasitic. In the Chalcidoidea, Evanioidea, Ceraphronoidea, and Cynipoidea, optimization (determination of the most parsimonious patterns of evolution) of the taxonomic distributions of ectoparasitism and endoparasitism onto the higher-level phylogeny of Figure 2 obscures the ancestral form of parasitism (Figure 3). This is due to the absence of known members of the Proctotrupeoidea, Platygastridae, or Trigonalioidea that are ectoparasitic. From a strictly natural-history point of view, it seems more likely that the common ancestors of the “proctotrupomorph” (Proctotrupeoidea, Platygastridae, Chalcidoidea, and Cynipoidea) and “evaniomorph” (Evanioidea, Trigonalioidea, Megalyroidea, and Ceraphronoidea) lineages would have been ectoparasitic, but at this stage that conclusion cannot be reached solely on the basis of the phylogenetic distribution of the traits.

Some of the more specific aspects of parasitism and its derivative life-styles are outlined in Table 1, where they are organized by superfamily (with references). Some aspects are discussed below, also by superfamily, in an attempt to reconstruct evolutionary transitions in parasitism that are evident from the phylogeny. This provides a rather coarse view of the evolutionary pathways, which is partly due to uncertainties about phylogeny, but results even more from our uneven knowledge of the biology. Expansion of comparative surveys of the female genitalia and ovipositor system (19, 79, 89, 91, 96, 97), including venom glands (30, 105) and ovipositional secretions (17, 64, 78, 116, 117), might quickly enhance our understanding of the taxonomic distribution of many habits. The presence of venom components and glandular structures is likely to be a good predictor of host/parasitoid biology. Other details can only be filled in through careful comparative studies of host-parasitoid relationships in the field and laboratory.

### *Orussoidea*

The Orussoidea have retained a relatively ancestral form of ectoparasitism of buprestid beetles and siricid woodwasps (11, 44, 94). Little is known of the mode of action of the venom, if any, but late-instar larvae appear to feed on or in the host after it is dead (44).

### *Stephanoidea*

The Stephanidae are a small group of ectoparasitoids of wood-boring beetles and woodwasps. Although little is known of the details of their relationships with host insects, they appear to have diverged relatively little from orussids in basic biology.

### *Ichneumonoidea*

Although it consists of only two recognized extant families, Braconidae and Ichneumonidae, this may be one of the two or three largest superfamilies of

living things in number of described species (at least 100,000). This species richness is accompanied by a high level of diversification in biological habits. The basal lineages of both families appear to be composed of ectoparasitoids of wood-boring beetles, woodwasps, gall-formers, and other endophytic insects (40). They generally tend to paralyze, otherwise incapacitate, or even kill their hosts at oviposition, and the developing parasitoid larva has a relatively short-lived interaction with the host [idiobiosis *sensu* Askew & Shaw (3)]. A constellation of different relationships with host insects and other arthropods (most commonly larvae of Diptera, Coleoptera, and Lepidoptera) has arisen from this grand plan (40). There apparently have been several independent origins of endoparasitism in each family (40, 111, 112, 114, 128), usually accompanied by the development of complex long-term relationships with the living host [koinobiosis *sensu* Askew & Shaw (3)]. Such complex interactions have been facilitated by the development of complex venoms that produce specific physiological changes in the host (17, 64, 78, 93, 110, 115, 127) and sometimes also by fragmentation of the egg serosa or trophamnion into "giant cells" or teratocytes with nutritive and secretory functions (20, 21). Perhaps the most remarkable development has been the independent origin in campoplegine ichneumonids, opiine braconids, and microgastroid-complex braconids of associations with hereditary viruses and virus-like particles that, among other effects, compromise host immune responses (31, 38, 104, 107, 108, 117, 121, 124, 126, 129). The taxonomic extent of various venom properties, teratocytes, and associated viruses and virus-like particles has not yet been fully investigated.

The eggs of some endoparasitic ichneumonoids have been adapted for absorption of host nutrients and, lacking yolk, have developed holoblastic cleavage. In some of these groups with tiny eggs and holoblastic cleavage, polyembryony has arisen, in which many embryos develop from a single egg (120). Polyembryony has also evolved, apparently independently, in the Platygastroidea (see below).

### *Aculeata*

Basal lineages of the aculeates (Chrysoidea, some lineages of Vespoidea, and Apoidea) have also retained the ectoparasitoid habit. The occurrence of true endoparasitism in the Aculeata is relatively rare (e.g. chrysidid parasitoids of walkingstick eggs), but in many chrysidoids (especially Dryinidae and Embolemidae) various forms of idiobiont ectoparasitism verging on endoparasitism (the parasitoid larva lives in a sac partially embedded in the active host) have developed (9). The details of the effects of the parasitoid on its host are not well understood in many aculeates, with the exception of some of the more conspicuous spider, cricket, and caterpillar hunters. Some elaborate stinging behaviors are known that appear to be targeted towards specific host or prey ganglia (115). A common evolutionary trend among aculeates (principally in

**Table 1** Comparative aspects of parasitoid biology among the superfamilies of Hymenoptera

Superfamily	Larval Development	Venom Modifications	Viruses Known	Teratocytes	References
Orussoidea	Ectoparasitoids	Possibly paralyzing venoms; venom properties not known	None described	None described	11, 16, 46, 53, 94, 102, 122
Stephanoidea	Ectoparasitoids	Very little known; possibly paralyzing	None described	None described	43, 44, 53
Ichneumonoindea	Both ectoparasitoid and endoparasitoid lineages in both families; holoblastic cleavage and miniaturized eggs in some groups; polyembryony in some Braconidae	Basal lineages with paralyzing venoms; derived ones with a variety of developmental and immunological effects on host as well as modification of nutritive value of host	Polydnaviruses in derived lineages of braconids and ichneumonids	Known from a wide range of braconid subfamilies; not described from ichneumonids	16, 17, 38, 40, 44, 53, 62, 64, 78, 110, 111, 112, 114–117, 122, 126–129
Chrysoidea	All are ectoparasitoids except some chrysidid egg parasitoids; a few ectoparasitoid chrysidines, sclerogibbids, embolomids, and dryinids are koinobionts	Paralyzing venoms in most families; a few of the endoparasitoids may have more complex venom properties	None described	None described	10, 45, 53, 115
Vespoidea	All parasitoid taxa are ectoparasitoids; some provide “nest” protection for larva and host	Paralyzing venoms; may also use venoms to defend nest	None described	None described	9, 34, 44, 53, 62, 78, 81, 86, 93, 100, 115, 122
Apoidea	Some lineages include true parasitoids; some provide “nest” protection for larva and host	Paralyzing venoms; may also use venoms to defend nest	None described	None described	34, 44, 53, 62, 81, 90, 93, 100, 115, 122
Cynipoidea	All parasitoid taxa are endoparasitoid; many have unusually modified first-instar larvae	Not really known; only a few taxa with any detailed information on parasitoid/host interaction	Virus-like particles found at least in <i>Leptopilina</i> (Eucollini)	None described	16, 35–37, 44, 53, 93, 101, 104, 106, 115

Proctotrupoidea	All endoparasitoids, many koinobionts; some have unusual first-instar larvae (e.g. Heloridae)	Not known, some may have temporary paralytic effect; probably some complex physiological effects	None described	None described	16, 44, 53, 82, 87
Chalcidoidea	Both endoparasitoids and ectoparasitoids, and a few have become secondarily parasitoids or gall-inducers; some groups have plandial first-instar larvae	Some have paralytic effects; some venoms clearly with more complex effects on host physiology, but poorly surveyed	None described	None described	6, 16, 17, 20, 46, 51, 53, 58, 64, 78, 79, 119, 120, 124, 127
Platygastroidea	All endoparasitoids; scelionids are idibionts; platygastriids split between idibiont egg parasitoids and koinobiont parasitoids of insect larvae or nymphs; polyembryony in some Platygastriidae; some first-instar larvae of Platygastriidae cycloptiform	Scelionid venoms halt development of host egg; probably koinobiont platygastriid venoms have more complex effects	None described	Known from both Platygastriidae and Scelionidae	16, 17, 20, 21, 53, 82, 95, 115, 119, 120, 124, 127
Trigonalyoidea	All endoparasitoids; hyperparasitism typical except for one Australian genus	Oviposition on plants, not directly on host; venom properties not known	None described	Not known	12, 16, 44, 53, 62, 125
Megalynoidea	Ectoparasitoids (but see main text)	Probably paralyzing venom, but poorly known	None described	Not known	16, 44, 53, 113
Ceraphronoidea	Both Ceraphronidae and Megaspilidae appear to contain both ectoparasitoids and endoparasitoids; a few may be koinobionts	Basically nothing known about venom effects; possibly some of koinobionts have complex venoms	None described	Not known	16, 25, 26, 44, 53, 83
Evanioidea	Aulacidae are endoparasitoids of wood-boring beetles; gasteruptionids are cleptoparasites in aculeate nests; evaninids parasitize roach eggs	Very little known of venom properties; none appear to be very complex koinobionts	None described	Not known	16, 41, 42, 44, 53, 61

Vespoidea and Apoidea) has been the adoption of food sources smaller than themselves, so that the distinction between parasitism (one or more individuals developing per host) and predation (more than one "host" or prey individual eaten by each developing larva) is more a matter of degree than of a radical change in biology (34, 44, 53).

In the aculeates, the ovipositor has lost its function as an egg-laying mechanism (89) and has been completely specialized as a sting for envenomating hosts, prey, or enemies. It is secondarily reduced or lost in the stingless bees. The capacity for paralyzing or incapacitating hosts or prey probably was already present in the common ancestor of aculeates and ichneumonoids. Some aculeates have specialized their venoms to produce pain and allergic responses in vertebrates, in order to defend themselves and their resources (93). Many of the Vespoidea and Apoidea excavate burrows or construct nests of various materials in which to deposit hosts or prey items as well as to protect their offspring (9, 34). The development of progressive provisioning of these nests, along with defense of the nests by using the sting, has led in some groups to eusociality (18, 73) and to the use of larval food items such as seeds, pollen, and nectar instead of insect hosts or prey (53, 60, 90).

### *Cynipoidea*

The basal lineages of Cynipoidea (Austrocynipidae, Liopteridae, Ibalidae) are all parasitoids of wood- or stem-boring holometabolous larvae (106). They appear to initiate their larval lives as endoparasitoids and only later become ectoparasitic. The more derived lineages have diverged strongly. The Figitidae are endoparasitoids of Hymenoptera (sometimes as hyperparasitoids of hymenopterous parasitoids in Homoptera), Diptera, and Neuroptera, whereas the Cynipidae have become gall-formers on plants (106). Some of the eucoiline Figitidae have bizarrely modified first-instar larvae, the significance of which is not understood (16). The Figitidae include at least some species known to use viruses to suppress the immune responses of their dipteran hosts (104); it is not known how widespread this characteristic is within Cynipoidea. In the Cynipidae, salivary secretions of the developing larva within the plant appear to induce the gall, in contrast to the parasitic forms in which secretions from the adult female modify the host environment for offspring (44).

### *Proctotrupoidea*

All proctotrupoids for which the life history is known are endoparasitoids of larval Coleoptera (Proctotrupidae, Vanhorniidae, Pelecinidae), Hymenoptera (Roproniidae), Neuroptera (Heloridae), or Diptera (Diapriidae) (44, 53, 82). Thus it will be difficult if not impossible to reconstruct the series of changes involved in the transition from ectoparasitic ancestors. As in the Cynipoidea,

some of the first-instar larvae (especially Heloridae) are highly modified in form (15). Because most species are koinobionts and all are endoparasitic, many interesting aspects of their host relationships can be anticipated, but we know virtually nothing of their physiology, and there are only a few host records for some families. This is especially unfortunate in the case of the Diapriidae, an abundant and highly diverse group, especially in tropical forests (82).

### *Chalcidoidea*

Generalizations about this superfamily are perhaps the most difficult, partly because phylogenetic relationships within it are so poorly known and partly because its range of biological habits is enormous. In many cases it is even difficult to characterize individual families in terms of their biology. Endo- and ectoparasitoids, predators, and phytophagous forms all occur, which attack eggs, larvae, nymphs, pupae, and adults of a huge array of insect taxa as well as other arthropods and which form galls and eat seeds of plants. Development in some cases includes specialized first-instar larvae of several forms, including mobile planidial stages (58) and some of the most extreme cases of polyembryony, in which thousands of embryos develop from a single egg (some Encyrtidae) (120). With the exception of a few egg parasitoids (119, 120), comparative aspects of the host/parasitoid interaction are very poorly known. The interested reader is referred to References 6, 16 and 53 for reviews of chalcidoid biology.

### *Platygastroidea*

Platygastrids are all endoparasitoids that attack the eggs (rarely young larvae) of other insects and a few other arthropods. In the Scelionidae, development is completed in the host egg (which dies relatively quickly after attack), whereas Platygastridae do not appear to emerge until the host is a fully grown larva (44). A few of the platygastrids appear to be polyembryonic (120), and first-instar larvae of both families are often bizarrely modified (16). In some Scelionidae the physiological interactions with the host have been studied (119), whereas in Platygastridae the presumably more koinobiont interaction is not well understood (44, 53).

### *Trigonalynoidea*

Trigonalynids have adopted an unusual life history among the parasitoids, in that they lay tiny hard eggs on plant tissue and then depend on these eggs to be eaten by lepidopteran or sawfly larvae. These eggs typically only develop if the lepidopteran larva is subsequently parasitized or eaten by another hymenopteran (or occasionally tachinid flies), but in some cases they develop directly in sawfly larvae (12, 62, 125). Presumably the success of some aspect of their interaction with hosts depends on them being hymenopteran or dipteran, but the reasons for this limitation are not understood.

### *Megalyroidea*

This superfamily appears to have mostly retained a conservative biology (ectoparasitism of wood-boring beetles), but at least one species is known to attack mud-nesting sphecid wasp larvae and is possibly endoparasitic (86, 113). Little more can be said from the biological evidence, despite a relatively well-resolved phylogeny based on both extant and fossil taxa (113).

### *Ceraphronoidea*

Information on the biology of ceraphronoids is fragmentary and relatively confusing. Most species appear to be endoparasitic, many of them are hyperparasitic, but at least some (possibly all) Megaspilidae are ectoparasitic (25, 26, 44, 53). Both families are reported from a bewildering array of insect hosts. Neither a robust phylogeny nor a clear picture of the host relationships within the group are yet available.

### *Evanioidea*

Of the three included families, Aulacidae has retained the habit of attacking wood-boring Coleoptera but appears to have developed a form of endoparasitic koinobiosis (41, 44). All known Evaniidae are parasitoids in the oothecae of cockroaches, each larva usually consuming more than one egg during its development and thus perhaps qualifying more as a predator than a parasitoid (61). The Gasteruptiidae have been described as ectoparasitoids of larval solitary sphecids, vespids, and apids, but at least some of them actually consume the food store of these "hosts" rather than the larvae themselves and thus act as cleptoparasites (44). Transitions from parasitism of wood-boring insects to attacking nesting Hymenoptera in cavities or twigs has apparently evolved independently in Ichneumonoidea and Megalyroidea (113), so it is possible that the habits of gasteruptiids are derived from those of aulacid-like ancestors. It is difficult to imagine how the parasitism of cockroach oothecae by evaniids developed.

## CONCLUSION

Much progress has been made in the last several decades in elucidating the phylogeny of the Hymenoptera. A number of additions to our knowledge of the life histories and specializations of many groups also have been made. The general outlines of the evolution of parasitism within the order and within some superfamilies are becoming clearer. Nevertheless, we are still a long way from being able to even generalize about the biological habits of many of the component lineages within several superfamilies (Ceraphronoidea, Proctotrupoidea, Chalcidoidea), let alone to hypothesize about their evolutionary trends.

What is most needed now to understand the evolution of the parasitic diversification is an increasing focus on basic research on the natural history and comparative physiology of more poorly known groups. Such a seemingly unglamorous pursuit would ultimately pay large dividends in the predictive capacity of hymenopteran comparative biology.

Hymenoptera encompass a vast array of biological life-styles, including two truly remarkable diversifications within the insects: the largest development of eusocial taxa among the animals and the greatest elaboration of parasitic behavior among the insects. The order will continue to provide the material for rewarding comparative research for many years to come.

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