BIONOMICS OF THE BRACONIDAE

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INTRODUCTION

The family Braconidae is one of the largest in the Hymenoptera, containing more than 15,000 valid species (87). Together with the Ichneumonidae, it forms a distinctive superfamily among the assemblage of hymenopterans known as the parasitic wasps (39). Adult braconids oviposit almost exclusively in, on, or near other insects, with the immature stages completing their development at the host’s expense. The terms parasitoid and protelean parasite are frequently applied to the various wasps, flies, and beetles that develop in this fashion. Many parasitoids are closely attuned to their hosts and have thus been of primary importance in the biological control of insect pests. Braconids are among the foremost of these beneficial insects. In classical biological-control programs, their success rate is exceeded only by that of aphelinids (43, 60). Braconids are also widely used as models for the study of host-parasitoid interactions, and in this regard, an impressive number of recent contributions have encompassed the broad disciplines of physiology, behavior, and evolutionary biology.

Clausen’s book (19) includes a detailed review of the older literature on braconid biology, and this classic text still serves as an excellent source for general information on parasitic Hymenoptera. More recent volumes (39, 45, 136) provide additional insights into braconid biology and illustrate the diversity of research now being conducted on parasitoids. Several works (9, 87, 121) summarize braconid host relationships by subfamily, and a handbook on braconid classification and biology is now available (94). The exhaustive treatment of braconid biology contained in this handbook is an excellent review of the subject and will undoubtedly become the standard introductory reference for this family.

The term bionomics is ideally suited for this review, which focuses on the
two major modes of development in braconids and on how these are correlated with other biological features and with braconid classification. The work by Shaw & Huddleston (94) obviates a detailed literature review.

CLASSIFICATION

The entire family was cataloged over the past 24 years (33, 69, 101). Nevertheless, major contributions in braconid systematics during this same period, as exemplified by the subfamily treatments of Agathidinae, Alysiinae, Blacinae, Braconinae, Doryctinae, Euphorinae, Homolobinae, Microgastrinae, and Opiinae (9, 18, 86; references in 94), have already made some of these catalogs outdated. The increasing amount of taxonomic activity has led to substantial changes in braconid classification in recent years (87, 94), and such changes are likely to continue for some time.

The number of subfamilies recognized by some workers (87, 121; but see 118) has doubled to about 40 since the review of Matthews (77). Several new and unusual taxa have been described (e.g. *Ecnomios, Khoikhoia, Mesostoa, Vaepellis*), and there has been a noticeable trend to accord subfamily rank to these and to older, formerly subordinate, taxa (e.g. *Gnamptodon, Orgilus, Dirrhope*) that do not readily fit the increasingly refined definitions being proposed for traditional subfamilies. Despite the advances that have been made, the observations of Matthews (77) regarding the stability of braconid subfamilies still apply. For example, meteorines are treated as a subfamily (71) or a tribe of Euphorinae (87). Exothecinae and Rhyssalinae are treated as subfamilies (87), as tribes of Rogadinae (145), or as members of the Doryctinae (9). Blacines are usually treated as a subfamily (72, 87), but probably should be considered as a tribe of Helconinae (16, 118). Many of the recent changes in braconid classification result from the increasing recognition of parallel or convergent evolution in the morphological features used to define major groups and the discovery of several important character systems associated with abdominal glands and reproductive tracts (12, 30, 70, 87). These findings, in turn, have led to very different hypotheses of phylogenetic relationships among the various subfamilies, which can be most readily appreciated by comparing the works of Capek (15) and van Achterberg (121) with those of Tobias (118) and Quicke & van Achterberg (87).

Braconids have traditionally been divided into cyclostomes (dominated by the Braconinae, Doryctinae, and Rogadinae) and noncyclostomes, based on the morphology of the lower face. Alysiinae, Gnamptodontinae, and Opiinae may be treated as presumptive cyclostomes because of their close relationship to some rogadines (87, 140, 143). Unfortunately, placement of many of the smaller taxa that have sometimes been classified as cyclostomes (Apozyginae,
Betylobraconinae, Mesostoinae, Telengainae, Vaepellinae, Ypsistocerinae) is hampered by their rarity and the complete lack of host data. Most of the noncyclostomes, for the purposes of this review, may be divided into a microgastroid complex (Adeliinae, Cardiochilinae, Cheloninae, Dirrhopinae, Khoikhoiinae, Microgastrinae, and Miracinae) and a helconoid complex (Amicrocentrinae, Agathidinae, Blacinae, Cenocoeliinae, Euphorinae, Helconinae, Homolobinae, Macrocentrinae, Meteorideinae, Meteorinae, Orgilinae, Sigalphinae, Trachypetinae, and Xiphozelinae). The placement of three other subfamilies discussed below (Aphidiinae, Ichneutinae, and Neoneurinae) is uncertain.

EVOLUTION OF ENDOPARASITISM

Idiobionts and Koinobionts
Parasitoids may be classified as either ectoparasitic or endoparasitic, with endoparasitism usually treated as the derived condition in braconids (14, 116) because of the need to overcome the host’s internal defenses. In an effort to define host relationships more precisely, the concepts of koinobiont (= koinophytic) and idiobiont (= idiophytic) were proposed, respectively, for those parasitoids that allow their hosts to continue functioning after being parasitized (paralysis is temporary or nonexistent) and those that do not (paralysis is permanent or host is killed) (2, 46). These functional definitions have been particularly useful for describing the evolution of endoparasitism in Rogadinae (93). Because nearly all braconids are either koinobiont endoparasitoids or idiobiont ectoparasitoids (38, 94), however, the terms can often be used interchangeably for members of this family. In addition to the exceptions documented by Shaw (93) for the Exothecinae, a few of the Braconinae appear to be idiobiont endoparasitoids of lepidopteran pupae and a few Doryctinae may be koinobiont ectoparasitoids (38, 94).

Cyclostomes and Noncyclostomes
Most cyclostomes are ectoparasitoids; noncyclostomes, comprising the majority of the braconid subfamilies, are endoparasitoids. Improvements in our understanding of the biology of the Rogadinae, a group of endoparasitic cyclostomes, have provided an explicit hypothesis for the evolution of endoparasitism from ectoparasitism in this lineage and affirmed the concept of a cyclostome grouping (93). This landmark work, based on such characteristics as egg placement, effect of venom, and oviposition behavior relative to host exposure and host pupation site, has facilitated comparison of other endoparasitoids with cyclostomes for elucidation of their relationships (87, 121, 140, 143). One such group is the Gnamptodontinae. For gnamp-todontines, which are well known as parasitoids of Nepticulidae (Lepidoptera)
the precise host relationship is still unknown (93, 94). The tentative placement of gnamptodontines in the Opiinae on the basis of morphology (34) was recently rejected (120, 140), largely on the basis of host relationships. Opines are hypothesized to develop exclusively as koinobiont endoparasitoids of cyclorrhaphous Diptera (140). Yet if gnamptodontines are eventually confirmed as koinobiont endoparasitoids (15, 93, 120), at least a sister-group relationship between Gnamptodontinae and (Alysiinae + Opiinae) could be supported both morphologically and biologically.

Although endoparasitic groups such as rogadines and opiines can now be more readily derived from presumptive ectoparasitic ancestors among the cyclostomes (15, 93, 118, 121, 140, 143), the majority of the endoparasitoids cannot. For example, the origin of the Aphidiinae, widely used in applied entomology (102), is highly controversial (15, 69, 87, 118, 121). In aphidiines, the method of pupation, formation of teratocytes, and morphology of both venom gland and germarium varies. Variation in these features is not well correlated among the different genera, further increasing the difficulty of associating aphidiines with other braconid subfamilies. Similarly, the placement of the microgastroid complex (75, 87), one of the largest and most extensively studied groups of subfamilies within the Braconidae, is completely unresolved. In addition to the multiple hypotheses discussed by Quicke & van Achterberg (87), Tobias (118) alluded to a derivation of the microgastroids from Helconinae through the Cardiochilinae, but with little supporting evidence.

Helconinae are frequently treated as one of the most primitive subfamilies of the Braconidae because of the retention of many plesiomorphic morphological features and because they attack xylophagous hosts (116, 118, 121). Yet few hypotheses have been advanced for the evolution of endoparasitism in helconines, and the most widely cited of these (116; reviewed in 94) suggests an origin from an unknown common ancestor shared with the cyclostomes, rather than an origin from within the cyclostomes. Thus, two distinctly separate lineages of endoparasitic braconids have been proposed: one associated with helconines and the other with rogadines. Instead of a gradual development of koinobiont, endoparasitic habits concomitant with a switch from concealed to more exposed hosts, as seen in rogadines (93), helconines may have developed endoparasitic habits totally within hosts who are always well concealed (94, 116). Thus, the idiobiont-to-koinobiont evolutionary scenario, which calls for allowing less concealed hosts to complete development and find a more secluded pupation site (38, 93), seems inappropriate for helconines. For helconines, hypotheses that deal with the selective advantage of increased efficiency and speed of oviposition relative to ectoparasitoids (to decrease interspecific encounters that either result in
predation on ovipositing females or otherwise disrupt oviposition) may be more appropriate.

Understanding the origins of endoparasitism in the helconoid lineage is the key to understanding the evolution of this vast group. Unfortunately, we lack basic information on the nature of the endoparasitic interaction for all but a handful of species in subfamilies such as the Helconinae (94) and Blacinae (16), and our nascent phylogenies (87, 121) have left us with a range of poorly known basal taxa from which to choose for comparative research. The selection of Helconinae as the basal-most taxon needs to be critically examined in any case. Much of the support for xylophagous Coleoptera as the putative ancestral host of braconids, for example, is somewhat circular: groups with a primitive morphology have xylophagous hosts and therefore xylophagous hosts are primitive.

**Host Paralysis**

Ectoparasitic braconids generally paralyze their hosts prior to oviposition (93, 94). Endoparasitoids do not, or only do so temporarily at the time of oviposition (13, 83, 93, 139; but see 19, 96). Oviposition in ectoparasitoids is a two-step process; venom injection and oviposition are separate events (93). In most endoparasitoids (see 93 for exceptions), eggs and venom-gland products (paralytic or otherwise) are injected at the same time, and this process can be extremely rapid [1–10 s in a wide range of both solitary and gregarious species (10, 13, 19)].

Unfortunately, we have very few detailed observations on host paralysis by Braconidae (6, 83). One of the best comparative studies to date (93) shows a transition in exothecines, rhyssalines, and rogadines from permanent paralysis caused by *Oncophanes* spp. to temporary paralysis with complete recovery (until killed by the developing larva) known for *Aleiodes* spp. In the seven cyclostome genera examined by Shaw (93), venom injection and oviposition are separate events, even though *Clinocentrus* and *Aleiodes* spp. are endoparasitoids. As Shaw clearly demonstrated, changes in the effect of the venom could have been an integral feature in the evolution of endoparasitism from ectoparasitism in the rogadine lineage. The temporary paralysis recorded for a few noncyclostomes may be either an indication of their relationship to the cyclostome lineage or a by-product of oviposition in a ganglion [known to occur in several subfamilies, but most frequently reported in Agathidinae and Aphidiinae (13, 94)]. The difference between temporary paralysis caused by venoms and behavioral immobility caused by the shock of oviposition is not always easy to distinguish.

The discovery (117) of huge, type-I venom glands in the genus *Megalohelcon*, with the same sclerotized reservoir and other morphological features
typical of the type-1 glands in cyclostomes (6, 30), and the disparate findings regarding venom-gland morphology in the genus Homolobus (30, 87), suggest that paralyzing venoms may have an important function in at least some endoparasitoid braconids outside the cyclostome lineage. Both Megalohelcon (Trachypetinae) and Homolobus (Homolobinae) are members of the helconoid lineage. If paralyzing venoms are used by these or other groups, the question remains whether this is a retention of the primitive cyclostome characteristic or a secondary acquisition for subduing large prey during the oviposition act (the genus Megalohelcon, for example, contains some of the largest known braconids).

HOSTS

Patterns in the Utilization of Host Taxa

Braconid classification has always reflected biology to some extent, especially in regard to host associations (14, 15, 116). Although hosts from more than 120 families are attacked, the majority of the braconid subfamilies are restricted to a single host order. Adeliinae, Agathidinae, Amicrocentrinae, Cardiochilinae, Cheloninae, Dirrhopinae, Gnamptodontinae, Homolobinae, Macrocentrinae, Microgastrinae, Miracinae, Orgilinae, Sigalphinae, and Xiphozelineae, where known, are exclusively endoparasitoids of Lepidoptera. Meteorideinae are primarily parasitoids of Lepidoptera (94), but unlike nearly all other braconids, they emerge from the pupa. All known Cheloninae, a group with over 700 described species, are egg-larval parasitoids (20, 94), and association of adeliines with chelonines (87, 118) enables us to predict that adeliines may also be egg-larval parasitoids. All known Aphidiinae (about 300 species) use aphids as hosts. Alysiinae and Opiinae, together comprising over 2300 described species, are endoparasitoids of cyclorrhaphous Diptera (121, 139, 140), ovipositing in the larva or egg, and emerging from the puparium. Records of nondipteran hosts are now considered erroneous. Cenocoeliinae and Helconinae (when defined very narrowly) are thus far known only as endoparasitoids of Coleoptera. Neoneurinae, a small group of about 20 species, attack Formicidae (94). Only four subfamilies (Braconinae, Doryctinae, Euphorinae, Rogadinae) attack hosts from three or more insect orders (72, 86, 94, 96, 99, 100). When Exothecinae (72, 99), or Exothecinae plus Rhyssalinae (87), are recognized as separate subfamilies, or when these genera are transferred to Doryctinae (9), Rogadinae can be defined as parasitoids of Lepidoptera.

Many of the anomalous host records found in the older braconid literature, and repeated in catalogs and other secondary sources, are now known to be incorrect. Yet the paucity of reliable host records noted by Matthews (77) is still a major limiting factor for tracing patterns of host utilization within the
various subfamilies (e.g. 16). Nevertheless, following on the pioneering studies of Griffiths (44) with dacnusines and agromyzids, several recently published works deal with the evolution of host associations in braconids. Maeto (71), for example, demonstrated considerable support for the evolution of lepidopteran host associations from coleopterous ancestral hosts in the Meteorinae (Meteorus and Zele). Identification of a macrolepidopteran suite among the Microgastrinae (74), however, has proven controversial (137), and previous reports suggesting that Miracinae are restricted to lyonetiid and nepticulid hosts (87, 121) have not been confirmed (145). Nepticulids do nonetheless appear to be used exclusively by adeliines (94) and gnamp­todontines (120). Some attention has also been given to the use of scolytid hosts by members of the genus Spathius (76). Further examination of these relationships is definitely warranted.

Recent reviews of host records of parasitoids of Diptera have shown that the largest lineage of alysiines (the Aspilota group) has diversified on phorids (35, 129, 139), and at least three major lineages within the Opinae are closely linked with their tephritid hosts (140). Suggestions that alysiines originated as parasitoids of Agromyzidae and later diversified onto other hosts (38) ignore morphological evidence that suggests that at least dacnusines are a derived lineage, and that agromyzid parasitism may therefore be specialized. Evidence for the suggestion that radiation onto tephritids from agromyzids has occurred in the Opinae (120, 122) has not yet been presented. Gauld (38) suggests that parasitism of Diptera is an evolutionary dead-end because there is no evidence of radiation from dipterous hosts onto hosts from other orders. This suggestion is somewhat misleading because host switching at the ordinal level is rare among braconid subfamilies (when they are narrowly defined as in 87), especially those containing endoparasitoids of larval endopterygotes. Host utilization by the Alysinae and Opinae (dipterous parasitoids that account for more than one-seventh of the described species of Braconidae) is also remarkably diverse; confirmed records describe at least 30 families of Diptera (139; R. A. Wharton, unpublished observations).

Shaw (95), building upon the excellent basis provided by Loan & Tobias (references in 95), developed an elaborate hypothesis to explain host diversification in the Euphorinae, which is based on adult parasitism as a new adaptive zone. From the results of an earlier phylogenetic analysis, chryso­melids were identified as the ancestral hosts from which this radiation occurred. Major host shifts in euphorines were hypothesized to take place largely among free-living, phytophagous hosts occurring in the same micro­habitat, and accidents involving host recognition were invoked to explain broad host shifts. However, euphorine hosts occur in a variety of microhabitats. Because many of these hosts are not external plant feeders, niche-shifting, which Shaw briefly alludes to for parasitoids of Psocoptera
and Scolytidae, must also occur. Shaw's explanation for accidents in host recognition within a microhabitat can also be used to explain their attraction to different microhabitats, if kairomones used for host location are host associated (127). Thus, some euphorines may be attracted to the same compounds found in a range of hosts, regardless of microhabitat. The attraction of an anthicid parasitoid (an undescribed species of *Centistes*) to the same cantharidin-baited traps that attract both anthicids and pedilids (R. A. Wharton, unpublished observations) supports the concept that cues independent of the host habitat can be used to bring euphorines into contact with different hosts.

Until recently, phytophagy in the Braconidae was unsubstantiated [though earlier reports (73) do exist]. Several phytophagous species are now known or suspected, all of which are cyclostomes (27; P. Hanson, unpublished observations). The taxa involved (*Allorhogas* and *Monitoriella*) indicate that phytophagy has arisen more than once within the cyclostomes, but such hypotheses remain to be tested; further evidence of phytophagy should be looked for, particularly among the Doryctinae. Confirmation of the phytophagous habit in *Allorhogas dyspistus* (27) offers exciting opportunities for exploring the evolution of phytophagy from a parasitic or inquiline habit and for comparing this with similar developments in chalcidoids and cynipoids.

Gauld (38) has compared braconids with ichneumonids and noted several interesting differences in evolutionary pathways, particularly in utilization of certain host stages (e.g. few pupal parasitoids in braconids) and certain host taxa. Statements regarding the limited use of exophytic sawflies (38) are particularly interesting, but one should note that sawflies in general are attacked by several genera in the Exothecinae (93), Braconinae (3, 100), and Ichneutinae (72, 94). Thus, in addition to *Ichneutes*, which is a relatively small genus attacking exophytic hosts, several lineages of sawfly parasitoids exist. Improved understanding of the tropical and south temperate faunas, with their numerous potential argid and pergid hosts, could add significantly to the existing data on sawfly parasitism. At least one braconid group (Proteropini) may be restricted to these sawflies. Most Proteropini are tropical and are not described.

### Host Specificity

Ectoparasitoids are usually considered to be less host specific than endoparasitoids. The many exceptions to this general statement led Askew & Shaw (2), following Haeselbarth (46), to look for a more reliable and meaningful approach to comparisons between generalists and specialists, and to the use of the terms idiobiont and koinobiont for such purposes. Some of the more careful studies on idiobiont braconids clearly demonstrate that certain species, such as *Bracon mellitor* (85, 114) and *Colastes braconius* (93), are
broadly polyphagous while others, such as *Xenarcha* spp. (93), are notably less so. Similarly, extensive rearings of various koinobionts reveals that species such as *Lysiphlebus testaceipes* (23), *Pholetesor salalicus* (144), and *Aphaereta pallipes* (139) have decidedly broader host ranges than species such as *Cardiochiles nigriceps* (133) and *Dacnusa dryas* (47).

If koinobionts are physiologically constrained by the host milieu in which they develop, we might expect that koinobionts would be relatively more host specific than idiobionts. This expectation seems to hold true when comparing the more polyphagous species in both groups (polyphagous in the sense of number of host species attacked), because even polyphagous koinobionts are only relatively so. The hosts of *L. testaceipes* (attacking only aphids), certain *Pholetesor* species (attacking only leaf-mining Lepidoptera), and *A. pallipes* (attacking only cyclorrhaphous Diptera) are relatively restricted taxonomically, compared with those of *B. mellitor* and *C. braconius*, which attack hosts from more than one order of insects. These former species should be considered oligophagous compared with the latter. For idiobionts that permanently paralyze their hosts, host specificity, when it occurs, may be achieved primarily through narrow habitat selection (38). The failure of idiobionts to attack all seemingly susceptible hosts within a narrowly defined habitat, however, and their failure to develop equally well on all species attacked, indicates that such generalities should be made with caution.

For the Braconidae, one must cautiously use summaries of published host records (e.g. 97–101) to discern patterns in host specificity among taxa. Wide host ranges listed for several species [e.g. *Opius pallipes* (33)] are based on errors in identification of hosts and/or parasitoids, or because hosts have not been correctly associated when more than one host occurs in the same microhabitat. Similarly, available evidence for monophagy among the Braconidae (with the possible exception of some aphidiines and dacnusines) is largely a reflection of our ignorance of the true host ranges of most species. Much of our reliable information on host ranges is based on field surveys of insect pests; the host utilization of nonpest species is largely unknown. Many investigators have examined braconid host ranges through use of host exposures in an experimental setting (17, 22, 24, 64, 123), but comparative work (84, 93, 124, 129) is almost nonexistent. The multiplicity of factors that affect host suitability (132), and the ability of parasitoids to learn new cues and accept novel or less preferred hosts (26, 66, 128, 129), make such studies particularly difficult, especially for endoparasitoids.

Thorough host-range testing for parasitic Hymenoptera used in biological control may be desirable for some taxa. The magnitude of the task, however, indicates that most of these efforts might be better directed towards a consideration of the predictive capabilities of our existing knowledge (13) and a careful examination of what it is we really want to test. For example, given
the relative success rate of those braconids that have already been used in biological control, and considering the possibility that none of them are monophagous, monophagy should not be used as a criterion for biocontrol use, especially in temporary agroecosystems (49).

Exposed and Concealed Hosts and Associated Oviposition Behavior

Although nearly all ectoparasitic braconids attack concealed hosts, endoparasitoids are nearly equally divided between those that develop on concealed hosts and those that develop on exposed hosts. Among endoparasitoids, most macrocentrines, orgilines, and helconines, and many agathidines, microgastrines, opiines, and alysiines have long ovipositors that may be used to reach concealed hosts. Some of these species (notably alysiines and opiines) drill or push the ovipositor directly through the substrate (82, 129, 139). Others (e.g. the agathidine Alabagrus stigma) slither their long ovipositors between leaf sheaths. Several species simply probe preexisting holes and feeding tunnels to reach their hosts (10, 32). The abdomen itself may be adapted to reach concealed hosts (93, 129, 139), thus precluding a long ovipositor. Among the ectoparasitoids are many braconines and doryctines that drill through solid wood to reach their host. This process often takes more than half an hour (88), increasing the possibility of both intra- and interspecific encounters during oviposition (28). Ectoparasitoids that oviposit through less solid substrates, such as rolled leaves, may probe repeatedly with the ovipositor to locate the host (93).

An exceptionally large number of endoparasitic braconids are egg-larval parasitoids (20, 94), and this pattern tends to occur in well-defined lineages, as noted above for Cheloninae. Egg-larval parasitism is also known in the Alysinae, Helconinae, Ichneutinae, Microgastrinae, and Opiinae. Shaw & Huddleston (94) suggest that the egg-larval habit may occur throughout the helconine tribe Brachistini, but sufficiently detailed records have been published for only five species. Egg-larval parasitism in the Adeliinae (14) has not yet been confirmed (but see above discussion under patterns in host utilization), nor are there any published data on its occurrence in Sigalphinae (94), despite reports to the contrary (121). The latter is of interest because of the suggestions (94, 122) that the presence of a carapace-like abdomen is correlated with oviposition into hard structures such as eggs. Shaw & Huddleston (94) discuss several factors that may have contributed to the evolution of egg-larval parasitism in braconids.

SPECIES RICHNESS IN TROPICAL AND TEMPERATE REGIONS

Much has been written about species richness of ichneumonids in tropical and temperate regions, and there have been several attempts to explain the
anomalous patterns observed (37, 52). Little, however, has been said about
the Braconidae. If the pattern in Ichneumonidae is not simply a sampling
artifact, then the Braconidae offer an interesting comparison. In the Brac-
onidae, latitudinal gradients are very much taxon dependent, and several
different patterns are apparent. Both the idiobiont Braconinae and koinobiont
Agathidinae (large subfamilies containing many colorful, diurnal species) are
exceptionally speciose in the tropics, and both have more genera in tropical
than in temperate regions (86, 97, 100). Sharkey (91), for example, recorded
93 species of the New World genus Alabagrus (Agathidinae) between the
tropics of Cancer and Capricorn. This is nearly equal to the entire agathidine
fauna in America north of Mexico, which contains nine genera (72). The
subfamily Alysiinae, by comparison, is known for its temperate and boreal
diversity (44, 98, 139). Sampling bias is a potential problem when comparing
tropical and temperate alysiines because descriptive work has focused
primarily on collections from the Holarctic region. Thus, most of the species
of Asobara, a group that has radiated extensively onto tropical Drosophilidae,
are undescribed. Nevertheless, almost half the described Alysiinae from the
Holarctic region belong to a group (the Dacnusini) that is nearly absent in the
tropics. Collections from the tropics have failed to indicate the presence of a
similarly large tropical group that is poorly represented in the temperate
region.

HOST SELECTION

The continuum of behavioral and physiological steps leading to successful
parasitism has been fully elaborated (e.g. 128, 130–132) from the outline
provided in the classic work by Salt (89). These steps can be conveniently
separated into those involving the adult and its search for hosts (host selection)
and those involving development of the immature parasitoid. Studies on host
selection and on the physiological interaction between host and parasitoid
provide a sound mechanistic basis for understanding the complex interplay of
environmental factors and evolutionary constraints that have determined how
the various patterns of braconid host associations have evolved (38, 93,
127–129). Numerous reviews cover the topic of host selection and use
braconids as major examples (39, 80, 124, 131, 134).

Bracon mellitor, an ectoparasitic, polyphagous species and Microplitis
croceipes, an endoparasitic, oligophagous species, provide an interesting
contrast. Both have relatively short life cycles (1, 115) and are multivoltine.
Both species will search for hosts in cotton, but their host ranges normally
do not overlap. Successive generations of B. mellitor develop through the
season on a series of alternating hosts and host plants. Different hosts and
host plants are used in different parts of its range (85, 114). Additionally, B.
mellitor can successfully develop on both coleopterous and lepidopterous
larvae occurring in the same microhabitat (flower head) and can attack hosts
in flower heads, buds, and stems (114). *M. croceipes* also searches a variety of host plants but attacks a very narrow range of hosts in the noctuid genera *Heliothis, Helicoverpa,* and *Schinia* (64, 81).

As each of these parasitoids moves through the behavioral continuum from host-habitat finding to host location, associative learning of chemical cues (65, 135) provides a mechanism for explaining the location of susceptible hosts feeding on different host plants. Because both species can learn novel cues, learning ability alone is insufficient for explaining differences in host selection. These differences must therefore be examined in terms of the short-range, key stimuli that anchor associative learning during the transition from host finding to host acceptance (128). Although considerable information has now been published on the nature of kairomones and other cues used by braconids to locate habitats and hosts (29, 79, 131), little is known about the specific key stimuli responsible for the observed differences in host specificity among species. We also know very little about the breadth of responses an individual is capable of, or how switching between different chemical cues actually takes place in nature (13, 55, 65, 84, 128) (see discussion of euphorine hosts above). Responses of naive females are particularly important for identification of the key stimuli that delimit host ranges (128).

Lewis et al (66) have argued that greater plasticity at the long-range phase of the foraging sequence is a general phenomenon. Unfortunately, most recent studies involving Braconidae treat only relatively long-range (or more precisely, intermediate range) chemical cues that are useful primarily for distinguishing suitable substrates within a habitat (29, 65, 111). Cues used to identify major habitat types of interest to the parasitoid may involve abiotic factors such as humidity, light, and spatial patterns rather than or in addition to kairomones (130, 138). These have received the least amount of attention because of the difficulties in experimental design.

Sufficient information is now available on cues used in short-range host location to begin looking for evolutionary trends in host-location patterns; the work by Vet & Van Alphen (129) is an excellent model for future studies. Many of the cues used by braconids are chemical, but vibratory cues are commonly used by opiines and alysiines (40, 129, 139). Although this feature may be basic to alysiines and opiines, the use of such cues may not be limited to these groups. Vibratory cues are known for many organisms that attack concealed victims (11), and such cues may be more widely used in braconids than is currently realized. The chemical interplay between host and parasitoid [including the sequestering of plant allelochemicals (5) and the reduction in output of potential kairomones by feeding intermittently or flicking away frass] also provides fertile grounds for coevolutionary studies.

As so ably demonstrated in recent models of foraging behavior (66, 128)
and as indicated by many older findings, the physiological state of the parasitoid (well fed, mated, etc) affects her searching behavior. The need to feed at flowers, for example, may either defer or assist host location depending on whether the species attacks hosts on or in flowers. Traits such as synovigenesis (progressive maturation of eggs after adulthood) are intimately associated with adult feeding behavior because synovigenic species presumably need nutrients for egg maturation. In addition to feeding at plants, synovigenic braconids may obtain nutrients from homopteran exudates (76) or by host feeding (53). Host feeding and synovigenesis are commonly associated with an idiobiont, ectoparasitoid existence in braconids (87, 94). While such comparisons are interesting, koinobions may also be synovigenic, and at least some koinobiont braconids also host feed (19, 53). Synovigenic koinobiosis is well known in the Rogadinae (93), Opiinae (82), and Aphidiinae (21). The occurrence of proovigenesis in koinobiont braconids is largely inferential, based on egg size and number of eggs per ovariole in studies such as those of Iwata (50). Dissections of ovarioles in several koinobionts suggest that there are different levels of synovigenesis rather than a strict dichotomy between synovigenic and proovigenic species. Proovigenesis may be a functional rather than a morphological characteristic for those individuals with a short field life and a large egg load.

**PHYSIOLOGICAL INTERACTION BETWEEN ENDOPARASITOIDS AND THEIR HOSTS**

One of the most exciting and rapidly expanding fields of braconid research is in the physiological interactions between host, parasitoid, and associated viruses (7, 25, 36, 54, 62, 103, 132, 133). Much of the literature to date is roughly divided into studies that analyze specific factors responsible for physiological and behavioral alterations in the host, and those that examine the nature of these alterations in parasitized hosts. Although as yet we have little comparative data for the Braconidae, with most of the work limited to a few species in the Aphidiinae, Cardiochilinae, Cheloninae, Euphorinae, Microgastrinae, and Opiinae, some trends are worth noting.

After the female parasitoid determines the suitability of the internal milieu (42, 48) and lays her egg(s), the host's immune system must be dealt with. Teratocytes, nonparalyzing venoms (or secretions from the reproductive tract and associated glands), microorganisms (primarily viruses), protection or disguise of the egg surface, and secretions by the developing larva are among the factors implicated in the suppression of the host immune system in Braconidae. The precise roles and interactions are still being elucidated, and Vinson (132) provides an excellent review of this subject. The occurrence of most of these factors within the same microgastrine species (e.g. *M. croceipes*)
indicates the complexity of the host regulatory process and the problems involved in attempting to treat these factors (or their effects on the host) as separate entities.

Teratocytes are found in the Aphidiinae, Euphorinae, Cardiochilinae, Cheloniae, Helcinae, Macrocentrinae, Meteorinae, and Microgastrinae (94). Dahlman & Vinson (25) recently reviewed the function, embryonic origin, and terminology of teratocytes in parasitic Hymenoptera, and numerous earlier works are cited therein. Differences in the embryological origin of the teratocytes have been critically analyzed: those of Macrocentrus, Trioxys, Aphidius, Lysiphlebus, and Diaeretiella originate from the polar bodies, and those of Ephedrus, Praon, microgastrines, and euphorines originate from serosal delamination (119). These differences may be helpful in placing the secretory function of the undelaminated serosa of opiines (61) in an evolutionary context.

The precise role of teratocytes is still a matter of some debate. Ingestion clearly occurs in some braconid species, but this may occur subsequent to the other activities because teratocytes secrete substances that may play a role in developmental alteration, immune suppression, and/or nutrition (25, 58).

The limited amount of research on the nonparalyzing venoms of braconids suggests that venoms are important in facilitating the function of polydnaviruses (57, 104, 112, 113, 133). This is in apparent contrast to polydnavirus-bearing ichneumonids, whose venom gland products seem to be unnecessary for successful parasitism. Additional comparative work is needed, given recent findings that the dependency on venom by Microplitis demolitor varies between host species, and that there is a definite dosage-dependent response (109). These findings also suggest that host ranges may be bounded to some extent by venom activity and that venom quality is thus important in the evolution of host associations. Venom-gland products have an additional role in the discrimination of previously parasitized hosts, at least in Ascogaster reticulatus (146).

The recently characterized polydnaviruses are recorded as symbionts of both braconids and ichneumonids (36, 105), but the gross morphology of the viruses found in these two families is noticeably different (105, 107). In the Braconidae, their occurrence has been confirmed only in Cardiochilinae, Cheloniae, and Microgastrinae (106–108). The presence of similar particles in these three subfamilies affirms the grouping of these braconids in current classifications (e.g. 87) and can be used to predict the presence of polydnaviruses in their putative sister groups Adeliinae, Khoikhoiinae, and Miracinae. Further, if polydnaviruses are intimately involved in the evolution of the microgastroid complex to which these subfamilies belong, then an understanding of the evolution of this association in braconids will provide a
test for the various hypotheses (14, 15, 75, 87, 121) regarding delineation of this complex. Some variation in the polydnaviruses of microgastrines has already been observed (106). Although very few species have been examined to date, those viruses with several nucleocapsids per envelope are thus far known only from Cotesia and other genera grouped by Mason (74) near Cotesia. Those with one nucleocapsid per envelope occur in Apanteles sensu stricto, Pholetesor, and Microplitis (106, 108; R. A. Wharton, unpublished observations).

Although polydnaviruses have been implicated in nearly every aspect of the physiological interaction between host and parasitoid (31, 36, 132), much uncertainty still remains concerning the viruses’ mode of action. Comparisons between those parasitoids of Lepidoptera that have polydnaviruses and those that do not [e.g. Rogadini (92)] should prove interesting. Most of the physiological research on braconids that lack polydnaviruses, however, has been on parasitoids of Diptera, Coleoptera, or Hemiptera (especially aphids) (17, 61, 62; citations in 94 under Aphidiinae and Euphorinae).

It has become increasingly common to find viruses and other microorganisms intimately associated with parasitoids, and braconids are no exception. Microorganisms associated with the reproductive tract of braconids have been known for a long time (56), but aside from the polydnaviruses, little is known about their distribution and function.

**Larval Feeding and Development**

The need to overcome the host’s immune mechanism and the need to obtain sufficient nutrients for successful development are common to all endoparasitoids. There is tantalizing evidence that different species accomplish the tasks in different ways, perhaps reflecting broad evolutionary patterns (4). The complex nature of the interactions within a species, however, makes comparisons across taxa extremely difficult. Of particular concern are the variations observed when different hosts or different host stages are attacked by the same species (26, 109).

Developmental times for a few idiobiont braconids are impressively short [as little as 6 days from oviposition to adult emergence in some Bracon and Habrobracon (51)]. The rates recorded for several koinobionts reared under ideal conditions are also quite short; several complete development in less than 10 days (8, 67, 115). Developmental times of 2–3 weeks are more commonly reported for both idiobionts and koinobionts, however, and seem to be the norm for nondiapausing individuals. Suggestions that idiobiont larvae feed or develop more quickly than koinobionts (94, 142), based on the observation that koinobionts allow their hosts to develop, remain virtually untested. Factors involved in host regulation do result in prolonged development for some koinobionts (4, 54, 62), but the comparison is usually made
with unparasitized hosts rather than with hosts attacked by idiobionts. Moreover, paralyzing venoms can act as long-term preservatives (6), so the need for ectoparasitoids to develop quickly, especially if they are concealed, is not immediately apparent. Because developmental times are heavily temperature dependent, most of the existing literature can be used only for crude comparisons.

With the exception of the Opiinae, Alysiinae, and the endoparasitic Rogadini, most koinobiont braconids emerge from their hosts to pupate. A final ectoparasitic stage has now been recorded for several of these endoparasitoids. Although its origin is unknown, this stage may originally have evolved to counteract problems of anoxia in concealed hosts (94). The distribution of an ectoparasitic stage among endoparasitic braconids may be both taxon dependent and host-habitat dependent. Shaw & Huddleston (94) provide an excellent discussion of the differences between Microgastrus and Microplitis in this regard. Additional careful observations are needed, especially on species attacking concealed hosts.

PROGENY ALLOCATION

Most braconid species are solitary, but several are gregarious (with two or more individuals normally emerging from a single host). Gregarious species often represent distinct evolutionary lineages, as in the rubens group of Meteorus (71), the genera Aphaereta (139) and Habrobracon, and certain Microgastrinae (74, but see 137). Gregarious parasitism also occurs sporadically, with closely related species differing as much in their biology (solitary vs gregarious) as in their morphology (68, 141). The number of progeny produced per oviposition may vary considerably within a species (63, 78), and at least some of the hormiines and rhyssalines are only facultatively gregarious (59). Brood care has been described for a species of Cedria (8), and a distinctive group of species within Macrocentrus is polyembryonic.

Gregarious parasitism may simply be a means of radiating onto larger hosts, and Le Masurier (63) has reviewed optimal clutch size models as they relate to some of the gregarious species of Microgastrinae. Le Masurier found support for Godfray’s (41) model, which focuses on the issue of parent-offspring conflict (thus addressing the subject of larval tolerance). He also recognized, however, the constraints imposed by our poor understanding of microgastrine phylogeny.

Some solitary species can clearly deposit more than one egg per ovipositional event, even though only one egg will develop (90, 110). If this behavior is more common than widely supposed, it would readily explain the development of so many different gregarious lineages in braconids and other families of parasitic Hymenoptera. It also has a serious impact on how
experiments should be designed to measure the ability of females of solitary species to discriminate between parasitized and unparasitized hosts (see reviews in 125, 126). Studies that only measure the number of parasitoid eggs present in each host, rather than the number of ovipositional events, may underestimate host discrimination ability.

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140 WHARTON


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