Life history evolution in the parasitoid Hymenoptera

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Abstract

This thesis addresses life history evolution of the parasitoid Hymenoptera. It aims to identify assumptions that should be incorporated into parasitoid life history theory and the predictions that theory should aim to make. Both two species and multi-species comparative studies as well as up-to-date phylogenetic information are employed to investigate these issues.

Anecdotal observations suggest that solitary parasitoids have narrower host ranges than closely related gregarious species. There are several possible reasons for this; for example gregarious species may be able to exploit larger bodied hosts because they can fully consume the host, which may be essential for successful pupation to occur. Comparative laboratory experiments between two closely related species of *Aphaereta*, one of which is solitary and the other gregarious, show no difference in the extent of host range. This study does, however, suggest that differences in the realized niche that each species occupies in the field may result from life history differences between the species. These differences may themselves have arisen due to solitary or gregarious development.

The first multi-species study in the thesis uses a data set, compiled for the parasitic Hymenoptera by Blackburn (1990), to address factors that may influence body size and clutch size. This study builds on previous analyses of the data (see Blackburn 1990, 1991a/b, Mayhew & Blackburn 1999) through the use of up-to-date phylogenetic information. Evidence is found that the host stage attacked by a parasitoid is associated with both body and clutch size, due to the amount of resources available for the developing parasitoids. In addition, gregarious species found at high latitudes have a reduced clutch size relative to those found at low latitudes. Several cross-species associations, which are not evolutionarily correlated, are identified: larger wasps lay smaller clutches; when attacking the same host stage, koinobionts are larger than idiobionts; temperate species are larger than tropical species (Bergmann's rule). This study supports some theoretical models and hypotheses based on other empirical studies.

A second multi-species study is carried out using a novel data set and up-to-date phylogenetic information for the Ichneumonoidea. Evidence supporting some aspects of the dichotomous hypothesis is found; for example, ectoparasitoids / idiobionts live longer than endoparasitoids / koinobionts and endoparasitoids are more fecund than ectoparasitoids. There is a trade-off between parasitoid body size and brood size, and also between fecundity and egg volume. Body size is positively correlated with development time, adult lifespan, and egg size. Host body size is positively correlated with parasitoid body size and brood size. Gregarious wasps are smaller, but attack larger hosts than solitary species and the former are more associated with external rather than internal pupation sites. Temperate parasitoids have larger geographic ranges, longer preadult lifespans and attack more host species than tropical parasitoids. Positive relationships are identified between parasitoid geographic range and a) host geographic range and b) the number of host species attacked. All of these results illustrate that several biological transitions are important regulators of life history variation within the Ichneumonoidea.

The evolutionary lability of Ichneumonoidea traits is then investigated. Influential life history traits, such as ecto- / endoparasitism, idio- / koinobiosis, body size, and solitary / gregarious development, are all conserved traits. Less conserved traits include longevity, pre-adult lifespan, geographic range, host niche and host stage attacked. The majority of variation

amongst traits was found at the family or subfamily level, suggesting that ancient evolutionary events are responsible for the majority of modern phenotypic diversity.

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Now it's all over I can finally look back on it with fond memories!

Declaration

Chapters 2-5 are presented as a series of scientific papers co-written with Dr. Peter Mayhew. In chapter 2, I carried out all the experiments; for chapter 3 the data set was obtained from Blackburn (1990), with the authors permission; I compiled the data set used in chapters 4 and 5. Dr. Mayhew assisted in the data analysis and preparation of the results for submission to journals for chapters 2-5. Chapters 2-5 are in preparation for submission (or have been submitted) to leading journals, such as '*Oikos*' and '*Entomologia Experimentalis et Applicata*'. Therefore these chapters can each be read as a self-contained whole, therefore discarding any need for a separate methods chapter. However, this layout means that there is a degree of repetition in these chapters.

Chapter 1: Introduction to life history evolution

1.1 Introduction

The aim of this thesis introduction is to provide readers with a background to the subject of life history evolution in parasitoids. A general look at life history evolution is provided in section 1.1.1, addressing the different conceptual approaches used, such as genetic and ecological. Section 1.1.2 introduces life history theories that consider several traits simultaneously, and thus represent a holistic and organism-based approach. Then, a related concept, that of the evolution of the ecological niche, is discussed (section 1.2). Empirical approaches to studying evolution are introduced in section 1.3, with particular emphasis on comparative studies. In section 1.4 there is a brief introduction to taxonomies and phylogenies and how they are constructed, which leads into section 1.5, addressing the statistical methods covered in the thesis. Various types of analyses that can be used in comparative studies are discussed, including cross-species analysis, independent contrasts, and phylogenetic lability methods. Section 1.6 introduces parasitoids, discussing their taxonomy and biology. Section 1.7 covers the evolution of parasitoid life histories and their ecological niches. Finally section 1.8 introduces the remaining chapters of the thesis.

1.1.1 Life history evolution

The main life history traits, shared by most organisms and identified by Stearns (1992), are size at birth, growth pattern, age and size at maturity, the number and sex ratio of offspring, age and size specific mortality schedules, and longevity. In an ideal world, every organism would a) reproduce many times and produce many offspring each time, b) have a high and indeterminate growth rate, c) large adult body size and d) mature quickly. Such an organism has been termed the 'Darwinian demon' (Law 1979), that is an evolutionary ideal organism, which cannot exist due to the presence of trade-offs between traits.

In 1947, Deevey noted that species differ in life history strategies, and from this became interested in studying species factors moulding their evolution. Since then many researchers have been interested in explaining aspects of life history evolution, how different traits interact and or influence one another, and how it can ultimately affect an organism's fitness. Studying life history evolution can allow one to explain reproductive rates and life-span differences between organisms, as well as to predict how populations will respond to changing environments. This incorporates aspects of natural selection, adaptation and also constraints (trade-offs). Physical constraints and / or trade-offs mean that not all life history traits are independent of one another, and this can result in organisms differing in fitness in different environments.

There are two major conceptual approaches to life history evolutionary theory: genetic and ecological. Both the genetic and ecological models have been found on occasions to produce equivalent results (see Charlesworth 1990, Roff 1994). The genetic approach utilises single-locus or two-locus models, assigns life history birth and death schedules to given genotypes, and this allows gene frequencies, their dynamic changes and equilibrium outcomes to be investigated (Anderson & King 1970), as well as using selection to explore evolutionary

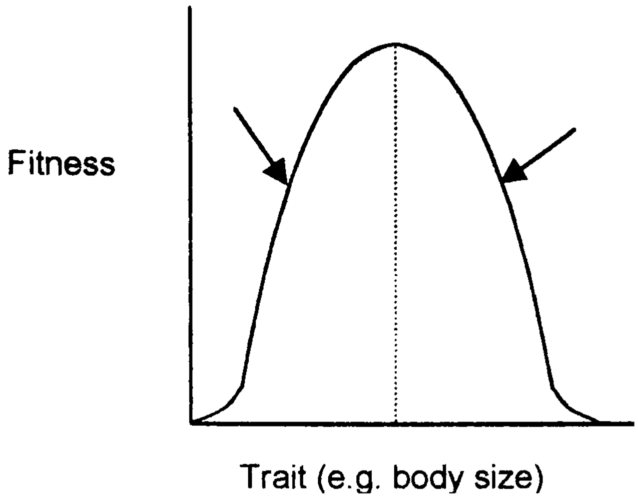


Figure 1.1: Factors affecting life-history evolution. The broken line indicates optimum fitness; arrows indicate constraints, which define the organism's fitness.

trajectories (Lande 1982). On the other hand, the ecological approach predicts the combination of life history parameters that has the optimum fitness under given conditions by using set options or trade-offs (Parker & Maynard Smith 1990, Pianka & Parker 1975). This is also known as the optimization approach.

The optimization approach identifies constraints and / or trade-offs that influence variable(s) and their state(s), that are required to produce an organisms highest level of fitness. Models are constructed that include details on a) fitness currencies, b) strategy sets, and c) constraints (Figure 1.1), some models also include details of current and future reproduction trade-offs. From this, assumptions can be made about conditions under which the observed phenotype would be optimal.

The fitness effects of traits can vary across taxa due to a) environment-specific and b) taxon-specific constraints and trade-offs. Trade-offs are where one trait can be increased only at the expense of another, such as when two traits are limited by the same resource that can only be spent once (the 'principle of allocation', Levins 1968). They are seen as a consequence of either physiological or behavioural life history decisions made by an individual.

The optimization approach is typified by studies of clutch size evolution. In 1947, Lack proposed a hypothesis for the evolution of clutch size in birds, illustrating how resources should be divided to obtain an optimal clutch size. An increase in clutch size results in each offspring receiving fewer resources, therefore decreasing individual offspring fitness. An intermediate clutch size may be better as it will produce the greatest number of surviving offspring. The optimal clutch size is thus determined by a trade-off between the number and fitness of offspring. Lack's (1947) hypothesis has been tested in birds through the manipulation of clutch size. Gustafsson and Sutherland (1988) manipulated the clutch size of collared flycatchers (*Ficedula albicollis*). When clutch size was increased there was an increase in the number of offspring fledging (see also Dijkstra *et al.* 1990, Lessells 1986, Rohwer 1985), thus illustrating that species lay smaller clutches than the most productive clutch size. Studies showing the same effect have also been carried out on insects, for example female *Callosobruchus maculatus* beetles, which lay their eggs on beans in which their larvae. They lay between 2-6 eggs on each black-eyed bean, whereas their most productive brood size is actually about 16 eggs (Wilson 1989). A commonly invoked explanation for brood sizes smaller than the Lack optimum is that organisms trade-off present for future reproduction. In turn, evidence from a range of organisms shows that such trade-offs are widespread (Stearns 1992). Thus, the testing of a model and its assumptions has led biologists to understand some of the important influences on trait evolution.

Although single trait investigations do not take into account the whole life history of an organism, they can identify how selective pressures can affect each trait in turn. However, to fully understand the life history of an organism it would be beneficial if one could simultaneously consider all of its component life history traits, and understand how those traits affect each other.

1.1.2 Multi-trait life history models

When trying to explain life history trait evolution it is easy for a theoretical model to get complex very quickly, as it initially seems that there are so many traits and factors at work influencing trait evolution. Yet in many instances those trait evolution patterns may actually be explained very simply; in other words, there may be only a few simple processes which underline much of life history variation within and across species. An example of this can be observed in mammals.

Much of the interspecific mammalian life history variation can be explained by natural selection working on a small set of ecological and physiological constraints to maximise fitness (growth, survival and reproduction). A 'fast-slow continuum' of life history traits is observed across species. Large mammals are found to have a greater longevity, reproduce later in life, produce fewer offspring of a larger body mass, and have lower juvenile and adult mortality rates in comparison to small mammals that exhibit the opposite trends for these traits. This suite of traits has been identified through many studies (see Lessells 1991, Partridge & Harvey 1988, Stearns 1992). Huxley (1932) noted that allometry, where traits depend strongly on body size, is found in many life history traits. For example, the logarithm of adult body mass is linearly related to the logarithm of longevity, gestation period and offspring size across mammal species. Harvey and Zammuto (1985) identified that mammals with a high mortality rate in relation to their body size tend to live and reproduce fast, and there may be a trade-off between reproductive efficiency and the risk of mortality.

Charnov (1991, 1993) produced a model predicting interspecific variation in many traits in female mammals. The model is based on three assumptions: a) there is a trade-off between reproduction and growth, b) growth is determinate and annual fecundity is constant, and c) once an organism has reached adulthood, mortality is constant and independent of reproduction. Mammals grow after independence from their mother, but then decide when to mature, diverting energy previously used for growth into reproduction instead. The model is successful in that it explains the vast majority of patterns already observed in mammals, yet some novel predictions are contradicted by the comparative data (Purvis & Harvey 1995). Subsequent adaptive models have also been successful in predicting the fast-slow continuum in mammals (see Charnov 2001, Harvey & Purvis 1999, Kozlowski & Weiner 1996, Purvis & Harvey 1995).

Trait associations like those found in mammals have also been identified in other groups of organisms. Gemmill *et al.* (1999) developed an optimality model for maturation time in parasitic nematodes and, using a comparative data set on mammalian gastrointestinal

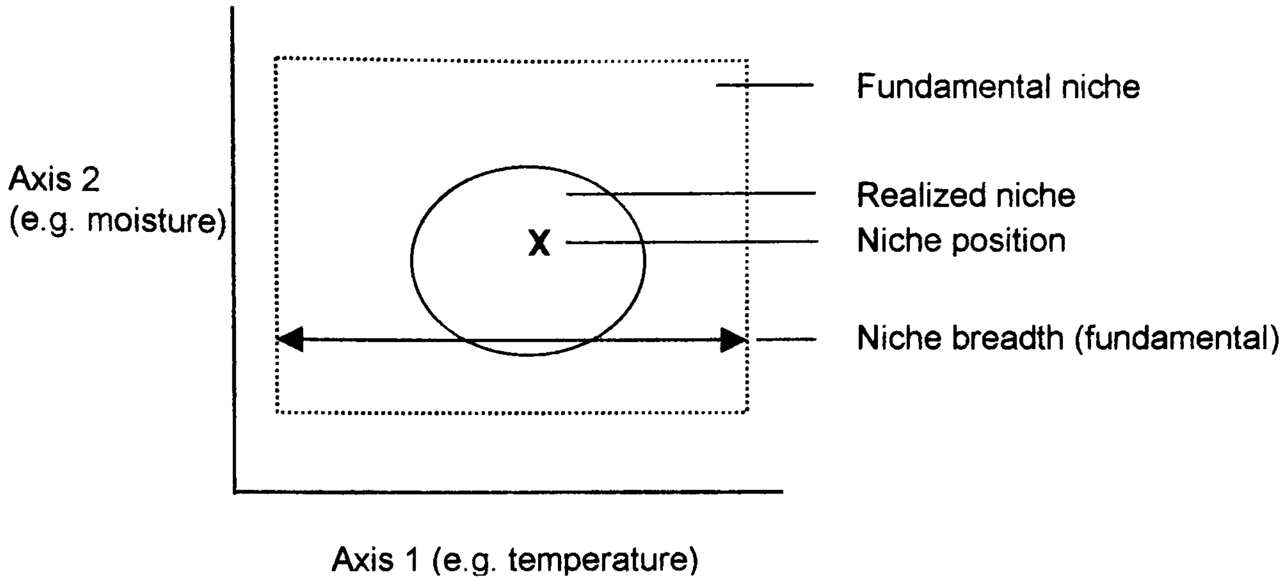


Figure 1.2: Niche diagram, illustrating the fundamental and realized niche, niche breadth and niche position.

nematode taxa, tested the models predictions. From this they identified a negative relationship between maturation time and adult mortality rate, which was the basis of Charnov's mammalian model. Franco and Silvertown (1997) also found such a relationship in flowering plants.

Other groups, for example some avian families, seem to follow certain trends displayed by the 'fast-slow continuum'. Some families of birds display slow development rates, delays in breeding, reduction of reproductive effort, but an increase in survival rates. Others show the reverse trends (Bennett & Owens 2002). However certain aspects of bird life history evolution cannot be explained by the mammalian theory. For example, altrical birds are reared to full adult size by their parents, unlike mammals. In addition, bird body size is not strongly associated with adult mortality rates, unlike mammals. In response, Charnov (2000) has recently adapted his mammalian theory for altrical birds, though the key predictions remain untested.

1.2 Ecological niche evolution

1.2.1 Defining a niche

The evolution of the ecological niche is a long-standing problem in evolutionary ecology. Species occupy a given niche or habitat and utilise the resources available there. A useful distinction is between the 'fundamental niche', which is the range of environments in which an organism can maintain a positive population growth rate, and the 'realized niche', which is the actual niche occupied in nature (see Futuyma 2001). The realized niche is a subset of the fundamental niche, which is modified through limits on dispersal and individual decision-making (see Jaenike 1990, Mayhew 1997) (Figure 1.2). Niche position refers to the average niche adopted by an organism, such as whether it is a herbivore or a carnivore (Figure 1.2). Niche breadth is a measure of how many environments a species exploits or can survive in (Gaston & Blackburn 2000) (Figure 1.2). Generalist species have adapted to utilise a wide range of resources, whereas specialists use a narrower or more isolated range of resources, or have narrower tolerances to abiotic factors than generalist species (Futuyma 2001). Specialization is often a flexible attribute of a population responding to features of its particular community, rather than an attribute of a species throughout its geographical range (Fox & Morrow 1981).

1.2.2 Niche evolution

The evolution of ecological specialization and generalization is of great interest in evolutionary biology (see Futuyma 1976, Futuyma & Moreno 1988, Mayr 1942). The principle focus has been to try to explain the presence of specialist species, which would seem to be vulnerable in the face of temporal changes in the environment. One of the earliest theoretical solutions to this problem was the concept of fitness trade-offs in different environments. For example, Levins (1968) proposed a niche breadth model that assumed a) two habitats that a species can occupy, b) a range of genotypes, which describe a species' fitness in those habitats, and c) a curve describing the (negative) relationship between fitness in habitat 1 and fitness in habitat 2. Specialists will evolve in this model a) when generalists perform less well than specialists in the specialist environment (when trade-offs are strong) and b) where one environment is more common than the other one. However, generalists can evolve if both habitats are common and if the fitness trade-off is not strong. Brown (1984) used the well-known saying 'Jack-of-all-trades, master-of-none' to apply to generalist species that evolve via this route.

Since Levin's work, a suite of theoretical models have addressed other circumstances that might favour specialist versus generalist strategies. As expected, generalist strategies are more likely to evolve in temporally heterogeneous environments, whilst specialists are favoured in environments that remain constant over time. Intraspecific competition within habitats favours generalist strategies, an intuitively sensible result as individuals have greater options on the use of different resources, some of which might be competitor-free. Interspecific competition is generally thought to favour specialism. A classic example is the character displacement of sticklebacks. In British Columbia, there are two different types of three-spined stickleback in each of the five lakes, a large benthic species that feeds on large prey in the littoral zone, and a smaller species that feeds on plankton in the open water. Each lake is hypothesized to have been colonised independently by a marine ancestor, from which an intermediate form evolved that exploited both littoral and open water habitats. A second marine invasion is thought to have caused the intermediate form to be displaced toward a benthic life strategy, whereas the second invader remained a zooplanktivore. Field experiments proved this hypothesis (Schluter 1994).

Models have also been developed that do not rely on the presence of fitness trade-offs for the evolution of specialists. Kawecki *et al.* (1997) produced a model based on the random fixation of neutral or slightly deleterious habitat-specific mutations. A population isolated in a novel habitat experiences mutations, which degrade its adaptations to the original habitat, are selectively neutral, and can be fixed by genetic drift. This can result in populations being confined to the novel habitat. For those populations located in both the original and novel habitats, a slight deleterious mutation that decreases fitness in the novel habitat can be fixed by genetic mutation. If many such mutations accumulate this may result in population extinction in the novel habitat. In this model specialization evolves due to genetic drift, and selection would favour those alleles for specialized behavioural preference, for the increasingly superior original habitat.

The ecological niche a species occupies depends on that species' adaptations to its present habitat, as well as the adaptations inherited from its ancestors. Prinzing *et al.* (2001) studied niche conservatism in higher plants in central Europe, and found that the niche position occupied by species was significantly determined by their phylogenetic position. They suggest that the niche conservatism observed in extant plants reflects the environmental conditions experienced by their ancestors. Phytophagous insects often display phylogenetic conservatism of host-plant use, for example related phytophagous species utilise similar hosts that are taxonomically, chemically, or structurally similar (see Futuyma & Moreno 1988, Janz *et al.* 2001).

The evolution of a species' niche may also depend on an interaction with its life history traits. Ecological and life history correlates of niche use have been inferred from comparative studies carried out on groups of organisms (see Bernays & Chapman 1994). Braby (2002) studied satyrine butterflies (Lepidoptera: Nymphalidae) in the wet-dry tropics of Australia, and found that certain life history traits were correlated with habitat utilisation. *Mycalesis perseus* is found in more temporary or unpredictable and adverse habitats than *M. sirius* and *M. terminus*, which are both found in more permanent habitats. The former species is known to have a smaller body size, faster developmental rate, earlier maturation time, higher fecundity, a smaller egg volume and a more flexible breeding strategy than the latter species. All these life history traits have allowed *M. perseus* to successfully exploit a more variable habitat in comparison to the other species. A study carried out on the ecological basis of life history variation in marsupials revealed that those species with a foliage-rich diet tended to have low fecundity rates in comparison to those without a foliage-rich diet (Fisher *et al.* 2001).

It is also becoming more apparent that social interactions between individuals can affect many aspects of both life history and niche evolution (Svensson & Sheldon 1998). One way for this to happen is if social interactions act as constraints on the life history and development of the organism, which in turn affects the environments it can exploit, or the most efficient way to exploit them. In chapter 2, I explore some of the consequences of social evolution on niche evolution in parasitoids.

1.3 Empirical approaches in evolutionary biology

1.3.1 General

Evolutionary biologists often hypothesize as to those factors influencing the evolution of different traits by producing theoretical models. These hypotheses or models then need to be rigorously tested, to see whether or not they are correct. From these observations clues can be found as to where the hypotheses or models may be incorrect. Empirical approaches in evolutionary biology may be divided into within-species and across-species studies. Within-species studies are typified by laboratory selection experiments. Advantages are that the experimenter can decide the level of replication, conditions can be controlled or manipulated so as to detect causative relationships, evolution can be studied as it occurs, and traits can be subjected to detailed analysis. However, within species studies are often limited by the level of variation that is shown both phenotypically and genetically, and also because conclusions are limited to the organisms in question.

Interspecific comparative studies offer an alternative approach. Comparative studies are carried out on two or more species and use the differences between species, as the results of a past experiment in evolution, to infer how processes might have occurred. Cross-species studies can be divided into two different types, two-species comparative studies and multi-species comparative studies. As all the analyses carried out in this thesis (see chapters 3, 4 & 5) are concerned with cross-species studies these will be dealt with in detail below.

1.3.2 Cross-species studies

Two-species comparative studies, as the name suggests, focus on two species and generally use experiments to gather information on various life history traits of the species of interest. Traits, some of which may not be suitable to use in broader comparisons, may be studied in detail. Using this approach allows the manipulation of at least one variable, to test whether there is a relationship between the variables of interest. Some life history traits may only be properly studied or measured in experiments, as there may not be any information available for them in the existing literature. Experiments that are well designed can eliminate confounding variables, also using closely related species can, to some degree, eliminate the problem of unaccounted for, or confounding, variables. This allows the experimenter some degree of control over the complex relationships between morphology, behaviour, or ecology that could potentially confound the results, and which are known to obscure or confuse the interpretation of cross-species studies (Price 1997). As discussed by Harvey and Pagel (1991), a study of this type only represents a single independent contrast (see section 1.5.2) between the species of interest. However, if many similar studies are carried out on various taxa then, combined, they all contribute towards addressing life history hypotheses.

Multi-species comparative studies are carried out on numerous species and are generally literature-based studies. Multi-species studies are important for inferring generality: that is, hypotheses that have been tested on several species, or indeed different populations of the same species, are not always in agreement. For example, of several studies addressing trade-offs between survival and fecundity in passerine birds, some found a trade-off present but others did not (see Bennett & Owens 2002). In cases like these it may be better to carry out multi-species comparative analyses. The variation across species is often large and allows traits to be examined that cannot, for example, be manipulated in the laboratory. Multi-species studies can therefore address the origins of trait evolution and ancient historical events. They additionally offer a higher level of replication, avoiding the major problem with two-species systems.

There are however limitations to multi-species comparative studies; certain traits are not suitable for investigation due to a lack of information about detailed differences in the ecology and behaviour of numerous species. Confounding variables may affect the associations observed between the traits of interest, although this can be overcome by incorporating these confounding variables, if they are already known, into the statistical model. However, differences in certain ecological or life history traits may not be identified by this type of study, for example in cases where biological signals are difficult to detect due to errors in the data; such errors include species misidentifications and different methods used by different authors to measure traits. In cases like these experimental studies may be better, as they can distinguish between cause and effect, suggesting relationships between variables. Two-species comparative studies are concerned with the finer details of species variation, whereas multi-species comparative analyses are interested in the broader variation observed across species. Both types of study can complement one another and be used to reconstruct evolutionary scenarios (see Janzen 1966, Thompson 1999).

1.4 Taxonomy and phylogeny

Taxonomy is the identification and classification of species. Linneaus developed the modern scientific system in the 18th century. It assigns species to a hierarchy of categories or taxonomic levels. This allows closely related species to be distinguished from one another, through morphological characteristics, and to order these species into broader taxonomic categories.

Several schools of taxonomy exist (see Ridley 1983, 1986). Pheneticists construct taxonomies based on the principle of phenotypic similarity, which includes both homologous (those characteristics attributed to shared ancestry) and analogous characters (characters that are similar but have evolved separately). Statistical methods are used to detect clusters to produce a hierarchical classification, however different cluster statistics will produce different taxonomic groupings (see Sneath & Sokal 1973). Cladists use rules devised by Willi Hennig (1966) that utilise a hierarchy of derived characters to define monophyletic groups, which are in turn taken from a hierarchy of recent common ancestry. Comparative biologists often use taxonomies derived by the evolutionary taxonomists as replacements for phylogenetic relationships. Evolutionary taxonomists base their taxonomies only on those characters that are homologous. However, this method can produce groupings that are not monophyletic. This is because homologous characters that are also synapomorphies (characters that are shared and derived) need to be used. A well-known example of this is shown in the classification of birds, crocodiles and lizards. Birds are placed within the Class Aves, and crocodiles and lizards within the Class Reptilia, even though birds and crocodiles are more closely related phylogenetically than either group is to lizards. As birds have evolved to look more different than crocodiles, they are placed in a different class, and as crocodiles look similar to lizards these two are placed in the same class. Reptiles share the same set of primitive characters and are paraphyletic (gave rise to birds and mammals) and are mistakenly united in this scheme using plesiomorphous (primitive) homologous characters.

Levinton (1988, p. 49) defined a phylogeny as the genealogical history of a group, which hypothesises ancestor-dependent relationships (Figure 1.3). The branching pattern of a phylogeny provides information on what species are closely related to one another and when species last shared a common ancestor. Some phylogenies also provide information on the timings or dates of branching events. Phylogenies can be constructed based on morphology and molecular data (for example protein, DNA), or can be based on a combination of this data to form a character matrix from which a tree can be built.

Many methods can be used to infer phylogenetic relationships between species. The maximum likelihood approach uses statistical estimates based on a model of evolutionary change to construct a tree which has the highest probability of having produced the given data under a certain set of probabilities of character change. No tree is impossible, but some trees

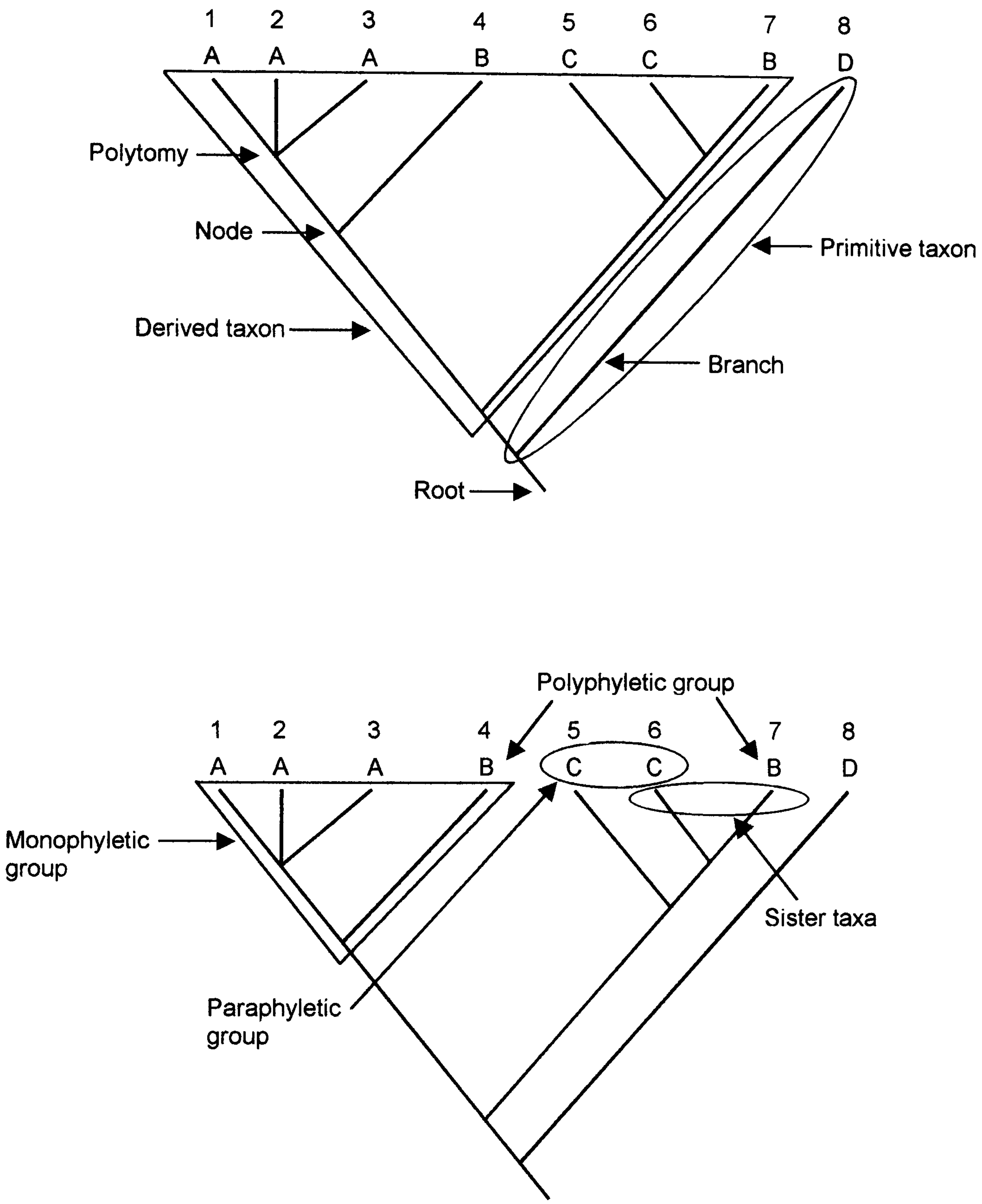


Figure 1.3: Phylogeny diagrams, illustrating various phylogenetic groupings. Numbers indicate different species, and letters indicate various traits.

are more likely than others (see Felsenstein 1973a/b). Various parsimony methods, based on Hennig's (1966) work, are used to construct phylogenies. Parsimony assumes minimum homoplasy in the data (which in turn assumes that the scientist has identified synapomorphous characters to use) and that evolution does not commonly reverse itself. Each parsimony method specifies slightly different criteria, for example 'Dollo parsimony' assumes that derived characters can only originate or evolve once in a phylogeny but can be lost many times, whereas 'Camin-Sokal parsimony' states that a derived character can evolve more than once in a phylogeny.

Bootstrapping is a method used to assess the reliability or degree of support for each branch in a tree. Using the raw character data, columns are sampled at random from the original data, and a novel dataset (known as a pseudoreplicate) is ued to estimate phylogeny. Branch support is then calculated as a proportion of the pseudoreplicate trees that include a given branch. A branch is generally said to have a high degree of support if it has a bootstrap value above 70%, because simulation studies show that such values are generally believable.

1.5 Comparative analyses used in the thesis

1.5.1 Cross-species analysis

The term "phenotypic correlation" is often used in life history studies to distinguish measurements of the phenotype from "genotypic correlations", measurements of the heritable tendency underlying them. In this thesis, the term is used instead to distinguish correlations between raw species measurements and "evolutionary correlations", which measure the tendency for evolutionary change in one trait to be correlated with change in another. Using raw species data identifies phenotypic correlations between extant life history traits and both categorical and continuous traits can be studied using standard parametric and non-parametric statistical tests (see chapters 3 & 4). Phenotypic correlations are the product of any evolutionary correlations between traits (associations between evolution in one trait and evolution in another) and can reflect evolutionary correlations relatively accurately, if there is no phylogenetic dependence in the data (Price 1997, Freckleton *et al.* 2002). However as a method to detect evolutionary correlations, it fails to take into account that closely related taxa are a product of, not only their current environment, but also of the proportion of phenotypes they have inherited from a common ancestor (see Bjorklund 1997, Westoby *et al.* 1995a/b). As a result these analyses can overestimate the number of independent evolutionary observations and inflate the level of significance, leading to Type I errors (Garland *et al.* 1992). To eliminate this problem, analyses can make use of phylogenetic information that can help identify the extent to which the raw species represent independent observations.

1.5.2 Independent contrast methods

Felstenstein (1985) introduced the independent contrast method to detect correlated evolution between traits. Estimates of phylogenetic relatedness are used to calculate, from the raw species data, differences between sister taxa, known as contrasts. Contrasts are more likely to represent independent data points than raw species values because differences between sister taxa have arisen only since two taxa last shared a common ancestor, whereas raw species data are the product of the entire history of evolutionary change back to the origins of life. Species have, in fact, only been independent of other species in the dataset since the last time they shared a common ancestor with one of them. In order to use the contrasts in regression style analyses, contrasts are calculated by assuming a Brownian (random walk) model of evolutionary change, because the variances associated with the contrasts can be estimated and then used to standardise them prior to statistical analysis. Although this method was introduced to test the significance of a correlation or regression coefficient, it is widely used as a means to evaluate the adaptive significance of traits (see Price 1997). The independent contrast method (Felsenstein 1985) has been developed further by others (see Grafen 1989, Pagel & Harvey 1989, Purvis & Rambaut 1995).

Grafen (1989) introduced phylogenetic regression (PR) as an advance over Felsenstein's original method and it displays several minor yet useful changes. First, contrasts can be calculated over soft polytomies, representing areas of uncertainty over phylogenetic relationships. Second, the regression equations of the contrasts are forced through the origin, something that was not generally recognised to be necessary in the early contrast analyses. It is required because the change in a y-variable, in response to zero change in a potential explanatory variable, must also be zero. Branch lengths in phylogenetic regression are assigned according to a counting rule (the age of the node is proportional to the log of the number of species it contains). Prior to the calculation of contrasts however, PR rescales the branches of the phylogeny using a maximum likelihood procedure to obtain the most suitable distribution of variances for regression analysis. The scaling parameter is known as ρ, and depends on a) the data set and b) the phylogenetic topology. Simulation studies have shown that this method yields valid Type I error rates and has good statistical power (Grafen 1989). Recent simulation studies show that ρ is a relatively good estimator of phylogenetic dependence when the number of species analysed is quite large, although it is biased such that small sample sizes tend to produce large ρ values (Freckleton *et al.* 2002, see chapters 3 & 5). Phylogenetic regression also allows the use of categorical as well as continuous explanatory or control variables, and may validly be used on both continuous and binary categorical response variables.

Purvis and Rambaut (1995) produced an application known as CAIC (Comparative Analysis using Independent Contrasts) that was a development of a method by Pagel & Harvey (1989). The latter method assumes that branch lengths are all equal and then contrasts are assigned an expected variance proportional to two times the fixed branch length. The effectiveness of this method at producing independent comparisons must be tested post-hoc, for example by plotting the size of the contrasts against raw species values, or against the distance of a node from the root of the tree. Purvis & Rambaut's application outputs the contrasts, which may then be visualised readily, and subjected to further analysis. The application allows alternative branch lengths to be assigned if the default equal branch lengths fail to produce independent contrasts. Evolutionary changes deep in a phylogeny can exert a disproportionately large historical impact on extant phenotypes (see Hardy & Mayhew 1998, West & Herre 1998). Therefore it is useful to examine individual contrasts to identify those which might have been influential on extant phenotypes and also why some identified contrasts come to be in the opposite direction than might otherwise be expected (see chapter 3).

1.5.3 Measures of phylogenetic lability

Phylogenetic analyses are useful as they provide researchers with information vital for interpreting both the current ecological structure and historical context of the traits of interest, and can address how much trait variation occurs at different taxonomic levels or how malleable certain traits are (see Owens & Bennett 1995). Many phylogenetic methods produce metrics that can be used to address how labile traits are. Evolutionary lability is the ease and speed with which particular traits evolve.

Nested analysis of variance (ANOVA) was originally developed in 1969 by Sokal and Rohlf, and was later adapted for use with phylogenies (see Clutton-Brock & Harvey 1977, Harvey & Clutton-Brock 1985, Harvey & Mace 1982). This method is used to describe how the total variation in a given trait is distributed amongst the various taxonomic levels used in the analysis, it finds and incorporates whatever phylogenetic effect is present in a data set, regardless of how it came about (Martins & Hansen 1996). This information can then be used to suggest which taxonomic level is the most suitable unit of analysis, or the taxonomic level at which phylogenetic independence can more or less be assumed (see chapter 5). However, the method also describes how long ago evolutionary change occurred and can therefore be used to infer rates of evolutionary change and the evolutionary lability of traits.

In 1985, Cheverud *et al.* described a method known as phylogenetic autocorrelation, which uses a technique originally developed for spatial autocorrelation analysis. This method partitions phenotypic traits into a) a phylogenetic component (that can be attributed to ancestry) and b) a specific component, which might be adaptive. It uses a linear autocorrelation model to partition the total variance in a trait, which is measured across species, into the sum of the phylogenetic and specific variances, as well as the covariance between these values of the trait. The specific component is used to test for correlated evolution between traits, whereas the phylogenetic component can be used to assess the evolutionary lability of traits.

The retention index (RI) is another metric used to ascertain a categorical trait's measure of fit to a given phylogenetic tree, that is the evolutionary lability of a trait or how easily a trait can reverse its state (Archie 1989a/b, Farris 1989). RI is a reflection of the degree of similarities that are apparent in a data set that can be retained as homologies on a tree (Farris 1989). As RI takes into account the number of taxa that have each state of a given trait, it is a good measure of phylogenetic information content (Wimberger and de Queiroz 1996). This metric is calculated using the formula:

$$\text{Character RI} = (M_i - s_i) / (M_i - m_i)$$

Here, i is the trait of interest on a tree, M_i is the maximum number of conceivable steps for the trait on the tree, s_i is the observed treelength or the reconstructed number of steps for the trait on the tree and m_i is the minimum possible treelength or the minimum conceivable number of steps for the trait on the tree. A trait is not labile if RI equals 1, whereas a RI value of 0 means that the trait is very labile (see chapter 5).

The parameter ρ, calculated using PR (Grafen 1989), reflects the degree of phylogenetic independence of a data set (whether descendants are similar to their ancestors, or whether close relatives are very different from one another) (see section 1.5.2, chapter 5). When phylogenetic dependence is present then ρ is high, approaching 1, which means that branch lengths are longest at the base of the tree. If there is no phylogenetic dependence present then ρ is low, approaching zero, and branch lengths are longest at the tips of the tree. However, there is a problem with bias when sample sizes are low (see section 1.5.2).

Pagel (1997, 1999b) was the first to use maximum likelihood techniques to test hypotheses about character evolution. This method does not require independent contrasts to be calculated, as non-independence is controlled for internally by a matrix of expected covariances among species. A benefit of this method is that it can scale phylogenetic path lengths in response to patterns in the data. Pagel's (1997, 1999b) method assumes a standard constant-variance random walk model, or a directional random-walk model. The scaling parameters κ, λ, and δ allow the testing of tempo, mode and phylogenetic associations of trait evolution respectively, the parameter λ in particular plays the same role as ρ in phylogenetic regression and gives an indication of how long ago evolutionary change occurred. Hypotheses are tested using the likelihood ratio statistic, which compares the log-likelihood of a null hypothesis model to that of an alternative hypothesis model (see chapter 2).

1.6 Introduction to parasitoids

1.6.1 Taxonomy

Parasitoids are one of the main constituents of global diversity with over 100,000 species worldwide, comprising approximately 20% of all insect species (Basibuyuk & Quicke 1995, La Salle & Gauld 1991). The majority of parasitoids are found within the order Hymenoptera (86,000 described species) (Basibuyuk & Quicke 1995) and within the order Diptera (approximately 15,000 described species) (Gaston 1991). One species of parasitoid has also been identified within the order Trichoptera (Wells 1992). The remaining parasitoids (approximately 3,000 species) are found within the orders Coleoptera, Lepidoptera and Neuroptera (Eggleton & Belshaw 1992).

The order Hymenoptera is split into the suborders Symphyta (sawflies) and Apocrita (ants, bees and wasps). The Apocrita is divided into the divisions Parasitica and Aculeata. The former division contains the majority of parasitoid species, but it also contains some non-parasitic groups like the family Agaonidae (fig wasps). The Aculeata contains a number of parasitoid species as well as the eusocial Hymenoptera.

1.6.2 Biology

Parasitoids are insects that develop as parasites of other arthropods during their immature stages, killing their hosts before becoming free-living adults (Strand 2000). Typically, the female parasitoid locates hosts and deposits eggs in, on, or near the hosts. The developing parasitoid larvae feed on these hosts, then pupate and finally emerge as adults.

Parasitoids are an interesting group of organisms to study as they have many unusual life history traits unique to the group (Godfray 1994). There is however, a lack of knowledge on the associations between their life history traits and, unlike some other groups of organisms (for example mammals and birds), there is no general theoretical model to explain or predict this life history variation. Identifying the factors which determine the life history traits and ecological niches of a given parasitoid species or group will lead to a better understanding of parasitoid diversity and their ecological importance.

The terms ectoparasitism and endoparasitism describe the feeding behaviour of the parasitoid larvae. Ectoparasitoids oviposit on or near their host and the parasitoid larvae complete development outside the host's body. Endoparasitoids oviposit into their host's body, where the developing larvae consume the host's haemolymph and / or tissues internally. Endoparasitoids normally complete their development internally to the host, but can sometimes complete development externally to the host.

Idiobionts are parasitoids that permanently paralyse their hosts, using lethal or paralysing venom at the time of oviposition, with the parasitoid larva rapidly consuming the host.

Koinobionts temporarily paralyse their host but allow it to resume development for a time post-parasitism. The parasitoid larva remains inactive until the host reaches a suitable stage for final consumption to take place.

Parasitoids are also termed either solitary or gregarious with regard to their larval development. Solitary wasps are those whereby only a single individual successfully completes development per host. Solitary parasitoid larvae display contest competition or siblicidal behaviour (Godfray 1994). Gregarious development is when several offspring can successfully complete development on each host and the larvae display scramble competition (Quicke 1997).

1.7 Parasitoid life history evolution

1.7.1 Introduction

Godfray (1994) suggested that the modern study of parasitoid life histories began with Askew's (1975) work on gall-forming and leaf-mining insects, as well as Price's (1972, 1973a, 1974, 1975) work which focused on explaining differences observed in fecundity rates of related parasitoid species attacking the same host species. There have since been numerous studies addressing the evolution of parasitoid life history traits (see Eggleton & Belshaw 1992, Gauld 1988, Shaw 1983, Shaw 1988, Shaw & Huddleston 1991, Whitfield 1992). These have lead to the identification of ecological and evolutionary processes that influence many aspects of the life histories exhibited by parasitoids, for example host range and parasitoid diversity. Several comparative analyses have been carried out to determine which hypotheses, if any held true. Some of these studies lacked rigorous statistical tests (Askew & Shaw 1986, Force 1972, Price 1972), whereas others lacked a good working phylogeny (Blackburn 1991a/b, Mayhew & Blackburn 1999).

1.7.2 The 'dichotomous hypothesis'

Haeselbarth (1979) first divided parasitoids into koinobionts or idiobionts (as defined in section 1.6.2). However Askew (1975) was the first to suggest that many parasitoid life history traits may be correlated with idiobiosis and koinobiosis or ectoparasitism and endoparasitism. The term 'the dichotomous hypothesis' (Godfray 1994) is used to describe how natural selection operates on the life history strategies of idiobionts and koinobionts to magnify their initial differences (Table 1.1). Many studies have focused on this dichotomy to try to explain life history variation amongst parasitoids (Askew 1975, Askew & Shaw 1986, Blackburn 1991a/b, Mayhew & Blackburn 1999, Price 1974, 1975, see also chapter 3 & 4). Several suggested differences however, remain only anecdotal in nature (such as diurnal verses nocturnal activity and the extent of sexual size dimorphism).

Mayhew and Blackburn (1999) carried out the first formal test of the dichotomous hypothesis on the parasitic Hymenoptera, controlling for the relatedness of species using taxonomy. They found strong evidence that ectoparasitism is associated with idiobiosis and endoparasitism with koinobiosis. Idiobiont ectoparasitism is often cited as the plesiomorphic state for most parasitoid lineages (see Belshaw *et al.* 1998, Godfray 1994, Shaw 1983), as this is the least physiologically specialized life history strategy. Koinobiont endoparasitism is said to be more specialized due to the various adaptations required; the parasitoids oviposit into a host

Table 1.1: 'The dichotomous hypothesis' showing the suite of life history traits associated with idiobiont and koinobiont parasitoids (adapted from Quicke 1997).

Idiobiont	Koinobiont
Ectoparasitoid	Endoparasitoid
Generalist	Specialist
Large eggs	Small eggs
Synovigeny	Pro-ovigeny
Oosorption	No oosorption
Wasp may choose sex of egg to match host size	No such relationship
Host concealed	Host exposed
Host stage attacked larger than wasp	Host stage attacked often smaller than wasp
Permanent host paralysis	Temporary / no host paralysis
Host-feeding common	Host-feeding uncommon
Rapid larval development	Slow / delayed larval development
Long adult lifespan	Short adult lifespan
Sexual dimorphism often pronounced	Sexual dimorphism absent / less pronounced
Mostly diurnal	Diurnal / nocturnal

and allow it to continue developing for a time post-parasitism. Therefore the developing juvenile parasitoids may have to overcome the host's internal defences to successfully develop to adulthood, and they also have to grow up in a fluid filled environment, which may cause problems for parasitoid pupation as they cannot pupate in a 'wet' environment. Endoparasitic koinobionts are therefore thought to have a narrower host range (attack a smaller number of host species) than ectoparasitic idiobionts. Hypotheses have been suggested as to how this more specialized strategy of may have arisen (Gauld 1988, Shaw 1983).

Shaw (1983) studied the evolution of endoparasitism within the Rogadinae (Hymenoptera: Braconidae) and speculate that biological adaptations resulted in a transition from ectoparasitism to endoparasitism (Figure 1.4). As ectoparasitoids are found external to the host's body, they require some form of protection from for example desiccation or predation when they are developing. Endoparasitoids on the other hand develop inside the host's body, which in itself protects the developing parasitoids. The genera *Colastes* and *Oncophanes* exhibit the least specialized strategy (ectoparasitic idiobiosis) and some species (for example *Colastes braconius*) are known to have very broad host ranges. Female parasitoids locate and permanently paralyse suitable hosts (for example late instar lepidopterous leaf-mining larvae) and lay their eggs within the leaf-mine, where the juvenile parasitoids gain some protection from the semi-concealed nature of the leaf-mine. From this primitive strategy there seems to have been a transition to koinobiont ectoparasitism, as observed in the genera *Phanomeris*, *Xenarcha* and *Rhysipolis*, these species attack middle to late instar leaf-mining lepidopteran hosts. When female wasps find a suitable host, they inject the host with venom that temporarily paralyses it. The host regains mobility and can continue to feed and grow for a time, which increases the amount of food resource available to the juvenile parasitoids. Both *Phanomeris* and *Xenarcha* species lay their eggs within the leaf-mine. However, *Rhysipolis* species attach their eggs onto the host's integument as the hosts that are attacked are very mobile and can pupate away from the leaf-mine because the cocoons they produce are very strong and provide them with adequate protection. Finally there was a transition from koinobiont ectoparasitism to koinobiont endoparasitism, which is the most specialized strategy, and is found within the genera *Clinocentrus*, *Aleiodes* and *Rogas*. Endoparasitism provides the developing parasitoids

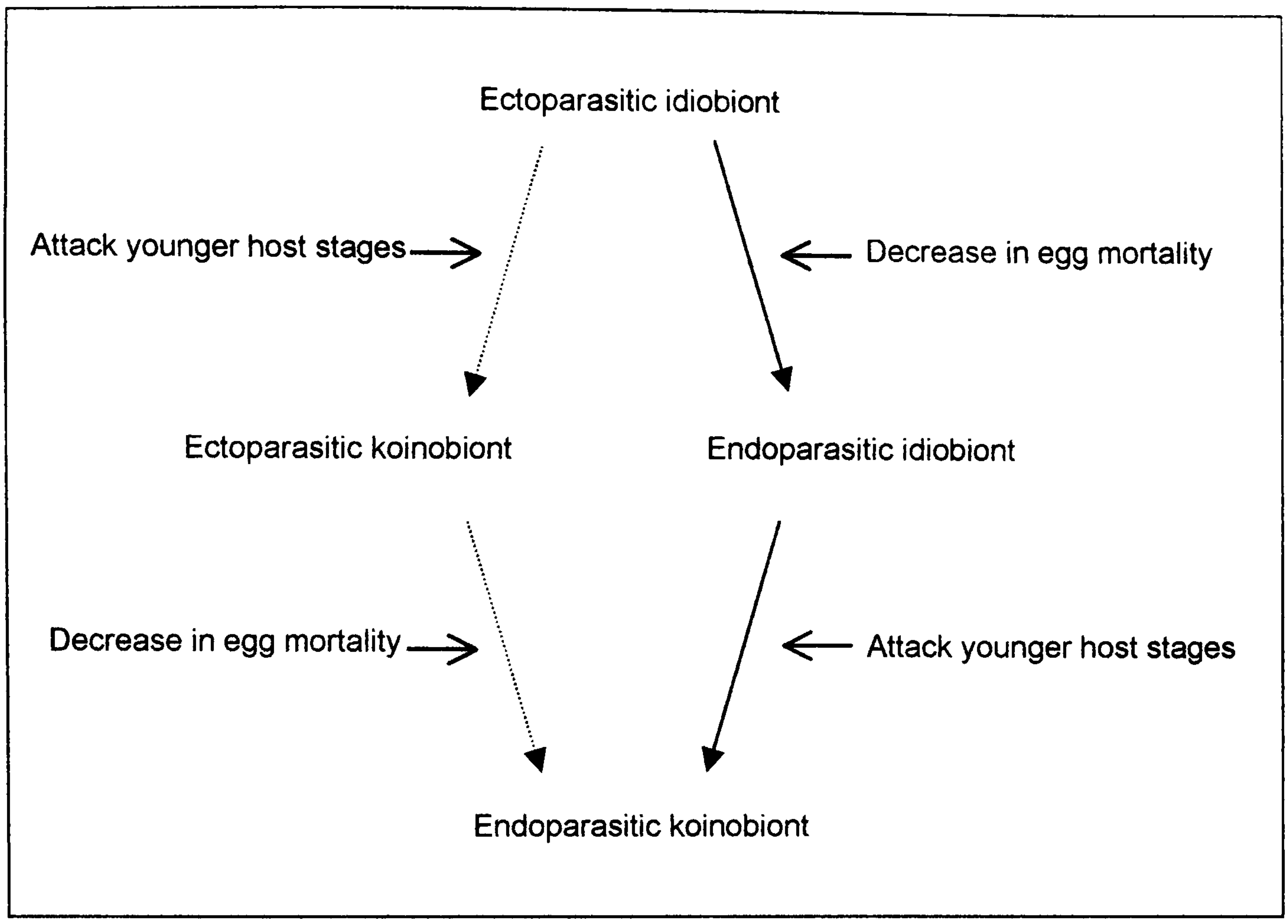


Figure 1.4: Schematic illustration of the possible evolutionary pathways from ectoparasitic idiobionts to endoparasitic koinobionts, as hypothesized by Shaw (1983) (broken lines) and Gauld (1988) (solid lines). Horizontal arrows indicate selection pressures influencing parasitoid evolution.

with improved egg concealment and protection in comparison to ectoparasitism. *Clinocentrus* attacks concealed, late instar, leaf-mining hosts, it lays eggs under the host's integument, where larval development takes place once the host has made a cocoon. However, *Aleiodes* and *Rogas* species attack early host instar larvae of Macrolepidoptera found in exposed locations. Like *Clinocentrus*, the female wasps temporarily paralyse their hosts, which allows successful parasitization to occur. Eggs are laid in the host's haemocoel, and hosts are killed when they have reached the middle instar stage. As the parasitoid larvae as placed within the haemocoel of an active host larva, they may have to avoid or overcome internal host defences to successfully complete development.

Gauld (1988) has hypothesized alternative pathways for the life history switch from idiobiont ectoparasitism to koinobiont endoparasitism in the Ichneumonoidea, that have been influenced by shared taxonomy and ecology (Figure 1.4). Idiobiont ectoparasitism is hypothesized to be the primitive state within this superfamily, where hosts concealed in plant tissue are attacked. Pupal endoparasitoids are thought to have evolved from pupal ectoparasitoids of hosts that form flimsy cocoons that do not provide the developing parasitoids with adequate protection from predators, hyperparasitoids or environmental conditions. Endoparasitoids of pupal hosts therefore have more protection from these factors than ectoparasitoids. This added protection also allows parasitoids to expand their host range to attack hosts with naked pupae. In addition, some pupal endoparasitoids may have evolved from larval-pupal endoparasitoids. Larval koinobiont endoparasitoids may have evolved through parasitoids selecting to attack younger host stages, although these parasitoids would also have had to simultaneously evolve adaptations to cope with the internal defences of a non-paralysed host.

Koinobionts allow their hosts to continue developing for a time post-parasitism. Therefore they can exploit hosts of a relatively smaller size (or of earlier development) that would not necessarily be suitable to support parasitoid development at the time of parasitism (see Askew 1975). However, idiobionts have to attack those hosts that provide sufficient resources to sustain parasitoid development from the time of parasitization.

Host mortality schedules are hypothesized to affect parasitoid life history traits (see Blackburn 1991b, Price 1974). Parasitoids (endoparasitic koinobionts) that attack early host stages may suffer a higher degree of juvenile mortality due to corresponding high rates of juvenile host mortality. Juvenile host stages such as larvae will suffer high mortality rates because they are active stages and move around to obtain food hence they are exposed and as a result are more susceptible to, for example, predation risks or an increased risk of desiccation. Inactive or older host stages, such as pupae, do not suffer from juvenile mortality as much as larvae, as they are not active and are often concealed. Alternatively, endoparasitoids may suffer because they are competitively inferior to ectoparasitoids.

The risks of juvenile mortality can affect other parasitoid life histories; endoparasitic koinobionts may be selected to have higher fecundities and increased oviposition rates to balance out the high juvenile mortality risks. Blackburn (1991b) found that endoparasitic koinobionts are more fecund, tend to lay smaller eggs and oviposit at a faster rate than ectoparasitic idiobionts (see also Mayhew & Blackburn 1999). Ectoparasitic idiobionts may require larger eggs so that developing parasitoids have adequate resources for rapid development prior to larval feeding taking place (see Godfray 1994). Endoparasitic koinobionts however, do not necessarily require such an abundance of resources within the egg prior to hatching, as some can absorb nutrients from their host (see Shaw & Huddleston 1991) and larger eggs may be more difficult for the parasitoid wasp to successfully inject into the host.

Koinobionts have been found to have longer preadult lifespans than idiobionts (see Blackburn 1991a, Mayhew & Blackburn 1999). This can be explained by the delayed development observed in koinobionts in comparison to the immediate rapid development in idiobionts. Endoparasitoids / koinobionts have shorter adult lifespans than ectoparasitoids / idiobionts, which may be due to within-lifetime trade-offs in resource division for growth and reproduction. Some studies have revealed trade-offs between life span and reproduction, for example an increase in egg production is correlated with a decrease in mean life span in the braconid *Asobara tabida* (see Ellers 1996, Ellers & van Alphen 1997, Ellers *et al.* 2000). Alternatively it could be due to predation risks, as mentioned above (see also Gauld 1987).

Jervis *et al.* (2001) carried out a comparative analysis addressing pro-ovigeny and synovigeny in parasitoid wasps. Pro-ovigenic species are those that have all or nearly all of their eggs mature prior to the start of oviposition, whereas synovigenic species are those that continue to mature eggs throughout their reproductive life (Flanders 1950). They hypothesized that ovigeny should be linked to idio- / koinobiosis for several reasons. Producing smaller eggs means that a parasitoid can achieve a higher realized fecundity, which is the number of eggs deposited by a parasitoid (Godfray 1994). Koinobionts have shorter adult lifespans than idiobionts (Mayhew & Blackburn 1999) and this should be correlated with a higher number of mature eggs upon emergence. The oviposition rate in koinobionts is higher than for idiobionts (Blackburn 1991b) and koinobionts have longer preadult lifespans than idiobionts (Blackburn 1991a) therefore allowing more time for eggs to develop prior to adult emergence. They found that koinobionts a) produce smaller eggs, b) tend to emerge with more mature eggs, and c) have shorter lifespans than idiobionts. However, they had insufficient data available to test oviposition rates. Koinobionts have the ability to manipulate their hosts' physiology and feeding behaviour, therefore they may be better at carrying over more resources to their pupal stage and emerging with a greater complement of mature eggs than idiobionts.

1.7.3 Other trait associations

Price (1972) studied the Hymenopteran parasitoid complex of the sawfly *Neodiprion swainei* and found that there was a difference in the number of ovarioles per ovary between the parasitoid species. Wasps found to attack early host stages (eggs, young larvae) had more ovarioles per ovary than those attacking later host stages (mature larvae, pupae) (Price 1972, 1974). Comparative studies on the reproductive morphology of the Ichneumonidae revealed that mean ovariole number was correlated with host stage attacked (Price 1973b, 1975) and the number of ovarioles per ovary was correlated with the number of eggs available for oviposition (Price 1975). Parasitoids attacking younger host stages had a greater fecundity than those attacking later or older host stages. Price (1972, 1973a, 1974, 1975) suggested that this was due to immature host mortality rates and was termed the 'balanced mortality hypothesis'. This hypothesis predicts that the average realized fecundity of parasitoids, and therefore measures of potential fecundity (for example ovariole number) should balance parasitoid juvenile mortality. Potential fecundity refers to measurements of, for example ovariole numbers, used to estimate fecundity. Fecundity may be correlated with other life history traits that would affect juvenile mortality rates (Blackburn 1991b, see section 1.7.2). Price (1973b, 1975) suggested that parasitoids attacking hosts found in protected locations (e.g. leaf-mines or rolls, burrows, webs) should have a relatively low fecundity as they are relatively protected from extrinsic mortality due to the type of host niche exploited. Ichneumonid parasitoid ovariole number was inversely correlated with ovipositor length, those parasitoids attacking concealed hosts, as described above, had long ovipositors (Price 1973b).

A comparative study carried out on the parasitic Hymenoptera revealed a trade-off between fecundity and egg size (Blackburn 1991b, see chapter 4) and this has also been demonstrated in the ichneumonids (Price 1974). As predicted by some life history models (for example Smith & Fretwell 1974) those species with high fecundities had smaller eggs and higher fecundity rates, suggesting that they have allocated more resources to reproduction rather than to survival in comparison to those with lower fecundities. Blackburn (1991b) also found a positive relationship between body size and fecundity.

By far, the majority of work on parasitoid life history evolution concerns clutch size, though most of these only address intra-specific studies. Clutch size theory for parasitoids has been adapted from the Lack clutch size models (Lack 1947, see section 1.1.1), where clutch size determines the amount of resources allocated to each offspring. Theory assumes that an increase in the number of eggs laid per unit of host resource will result in a decrease in the fitness of each offspring due to density-dependent competition for resources, in other words a trade-off between clutch size and fitness (see Godfray 1987, Waage 1986). Hardy *et al.* (1992) carried out a clutch manipulation experiment on the bethylid wasp *Goniozus nephantidis*, which is an ectoparasitoid of microlepidopteran larvae. This wasp is unusual in that it guards its offspring until they pupate. Using hosts of equal weight they found that clutch manipulation had no effect on offspring survival, however it did affect offspring size. Large clutches produced smaller offspring, which resulted in a decrease in individual offspring fitness as predicted.

It has been suggested that parasitoid clutch size should decrease, due to a decrease in egg reserves, with an increase in the frequency of host encounters. A study carried out on an aquatic mymarid wasp (*Caraphractus cinctus*) demonstrated that wasps produce smaller clutch sizes when presented with a series of hosts in comparison to when the hosts are presented individually (Jackson 1966). Similar results have also been found for trichogrammatid egg parasitoids (Schmidt & Smith 1985).

Mayhew & Glaizot (2001) suggested expanding parasitoid clutch size theory to include predictions about body size and host size. These three variables are ultimately linked because the host defines the resources available for parasitoid development and an increase in clutch size, on a given host size, must result in a decrease in body size. Theory suggests that both clutch size and body size have the potential to increase with host size across species.

For solitary wasps, small clutches minimise resource wastage in offspring that will certainly fail to complete development (Mayhew & Glaziot 2001, Waage & Godfray 1985), therefore clutch size for these wasps is not expected to vary even when attacking larger hosts. However, gregarious species may be selected to increase both clutch size and offspring size when attacking larger hosts (Mayhew and Glaziot 2001). Le Masurier's (1987) *Apanteles* study found a positive relationship between host size and clutch size in gregarious parasitoids, but not solitary ones. Mayhew and Hardy (1998) also found these gregarious trends in the family Bethylidae.

Recently, it has been suggested that solitary and gregarious parasitoids may differ in life history traits other than simply clutch size (Pexton & Mayhew 2002). By definition, for solitary parasitoids only one offspring per host will emerge, whereas for gregarious species numerous offspring can emerge per host. On a host of given size, juvenile parasitoids developing solitarily will have a greater amount of resources available than parasitoids developing gregariously. Indeed, families containing gregarious species have been shown to be smaller bodied than their sister taxa that are exclusively solitary (Mayhew 1998). Studies carried out on a sister species pair of alysiine braconids have shown that the solitary species, *Aphaereta genevensis*, has a larger body size than the gregarious species, *Aphaereta pallipes* (see Mayhew & van Alphen 1999, Pexton & Mayhew 2002, see also chapter 2).

As solitary species cannot vary their final brood size their body size should be highly sensitive to host size (an increase in host size should lead to an increase in parasitoid size). This is the case for the solitary braconid wasp *Monoctonus paulensis*, which shows an increase in body size when attacking larger hosts (Mackauer & Chau 2001). However, Le Masurier (1987) found that solitary *Apanteles* species (Hymenoptera: Braconidae) that parasitized larger bodied hosts did not show an increase in body size, whereas their gregarious counterparts did. Gregarious *Apanteles* species have the ability to manipulate and increase host growth to support the developing offspring. However, solitary species are not known to do this, and hosts parasitized by solitary species are often smaller than unparasitised hosts of the same age. Solitary species that are not able to fully consume a larger host may just kill the host before it has matured any further. This is the case for the *Cotesia* species *C. rubecula* and *C. glomerata*. When they parasitize the same host species (*Pieris rapae*), *C. rubecula*, which is solitary, emerges from a half-grown caterpillar, whereas *C. glomerata*, which is gregarious, emerges from a fully-grown host (Parker & Pinnell 1973).

Theoretical and empirical work suggests that gregarious species will invest less in reproduction than solitary species (see Smith 1991). Pexton and Mayhew (2002) showed that the gregarious *Aphaereta pallipes* allocates more resources towards reproduction, which in turn reduces its longevity. On the other hand, the solitary species *Aphaereta genevensis* invests more resources towards greater fat reserves, resulting in enhanced longevity, but subsequently decreases the amount of available resources for reproduction.

The evolution of gregarious development may also allow parasitoids to exploit novel hosts. Previously unsuitable hosts may become suitable if the large parasitoid clutches laid per host overwhelm the host's immune response. Alternatively these large clutches and hence large numbers of offspring may be able to fully consume larger bodied hosts that are therefore unavailable to solitary species (see Ode & Rosenheim 1998, Streams 1971).

1.7.4 Evolution of the parasitoid niche

The main components of a parasitoids niche are a) what type of host species are attacked and at which developmental stage, b) how many host species are attacked, c) what and how many habitat types a parasitoid searches in, and d) the extent of parasitoid geographic range. The type of hosts that a parasitoid will attack is influenced by two important factors, hosts taxonomy and shared ecology (Askew & Shaw 1986, Shaw 1988). Parasitoids may attack closely related (taxonomically similar) host species because they share similar defence mechanisms and physiological properties (reviewed by Godfray 1994). Idiobiont parasitoids are unlikely to be affected by host taxonomy as much as koinobiont parasitoids, due to the lack of specialist adaptations required for the former's association with its host. Koinobionts have to develop a capacity to overcome the defence mechanisms of their hosts.

Some parasitoids attack closely related host species located in different habitats, for example the ichneumonid *Hoplismenus morulus* is known to attack a number of closely related Nymphalidae butterflies in deciduous woodland and chapparal habitats (Price 1981). It seems that the shared ecology of the Nymphalidae influences parasitoid host range. However, other studies have failed to find a link between parasitoid host range and host taxonomy, instead suggesting that aspects of host ecology are more influential than host taxonomy.

Closely related host species will more likely have similar biologies or ecologies, for example they may utilise similar feeding niches or the same host plants, and this can influence parasitoid host range. Stireman and Singer (2003) found that the host associations of tachinid parasitoids are influenced by some host morphological and ecological traits. Whether the host (caterpillar stage) attacked is hairy or smooth affects what parasitoids can successfully parasitize it, for example some parasitoids have adapted to use hairy hosts by 'projectile ovipositing' their eggs. For polyphagous parasitoids, host abundance is expected to determine which hosts are attacked. Polyphagous tachinids were shown to attack hosts that utilised broader food-plant ranges than those attacked by oligophagous tachinids. The narrowing of host ranges exhibited by oligophagous tachinids is believed to be due to parasitoids being selected for more specialised host location cues to find specialised hosts, rather than the parasitoids being limited by a hosts chemical defenses, which has previously been disproved (see Arnaud 1978).

Askew (1994) found that many ecological factors influencing host range of parasitoids of leaf-mining Lepidoptera relate to host food plant. For example, those parasitoids found to attack Nepticulidae on trees were different to those attacking the same host family on herbaceous plants. Koinobiont parasitoids were more associated with low apparency plants (for example herbs and shrubs) and idiobionts with plants of greater apparency (for example trees). Plants with higher apparency are expected to have higher levels of colonisation by herbivorous insects. Idiobionts tend to be generalists and they lack the specialized behaviour of koinobionts to locate hosts, so idiobionts tend to search opportunistically for hosts on more apparent plants. *Achrysocharoides* parasitoids only attacked hosts that mined in taxonomically similar food plants. This is because the *Achrysocharoides* species are endoparasitic koinobionts and they have adapted to exploit a specific range of hosts due to the specialist adaptations that this life history strategy requires.

The ecological host habitat is a major factor influencing host range in parasitoids of tephritid fruit flies (Hoffmeister 1992). The hosts offer two different resources for the parasitoids; they can either be attacked when they are concealed larvae inside fruits, or when they are puparia within the soil. The former stage is only available for a short length of time, whereas the latter is available for approximately 8 months. The longer a host stage exists therefore the more available it is for discovery by a parasitoid. However, it appears that the life history strategy a parasitoid adopts actually affects the ecological niche it exploits. Only ectoparasitic idiobionts were found to attack the puparium host stage, and these parasitoids were found to be polyphagous. The authors believed that these parasitoids are specialized for searching in the soil for hosts, but are not host specialists, rather they accept a range of physiologically suitable hosts. Parasitoids attacking the larval host stages inside fruits were specialized endoparasitic koinobionts that were not affected by the moist environment that the larvae inhabited, which make this habitat unsuitable for ectoparasitoids.

The niche breadth of a parasitoid refers to how many different host species a parasitoid will attack, which is determined by the habitats in which it searches for hosts. Therefore, to address the factors affecting the evolution of parasitoid niches one must explore both ecological and life history (behavioural, physiological and phylogenetic) correlates of host use.

Idiobionts or ectoparasitoids are expected to have wider host ranges than koinobionts or endoparasitoids (see section 1.7.2). There is much evidence that this is indeed the case (see Godfray 1994, Sato 1990). Askew and Shaw (1974 & 1986) studied chalcid parasitoids attacking an arboreal leaf-miner community on deciduous tress in Britain and found that idiobionts attacked approximately 2.8 times more host families that koinobionts. Sheehan and Hawkins (1991) studied both metopiine and pimpline (excluding the tribe Polysphinctini) ichneumonid wasps. Pimplinae wasps, which are idiobionts, were found to have broader host ranges when compared, at host species, genus and family taxonomic levels, to the Metopiinae wasps, which are koinobionts. Idiobiont parasitoids have been found to have approximately twice as many host species as the koinobionts attacking Tortricoidea hosts (Mills 1992). Müller *et al.* (1999) studied aphid parasitoids and found that 'mummy aphids', defined as idiobiont parasitoids whose larvae develop on dead or permanently paralysed host tissue, attacked the greatest number of host species. Primary parasitoids and hyperparasitoids, which are both defined as koinobiont parasitoids attacking living hosts, attacked the smallest number of host species. All of this implies that there are fitness trade-offs present when adopting a more specialized life history strategy (koinobiosis and / or endoparasitism) (see Gauld 1988, Shaw 1983) as assumed by Levin's (1968) model of niche evolution (see section 1.2.2).

The microhabitat that potential host species occupy may determine what parasitoids can successfully attack those hosts. Differences in the distribution and trophic relationships between parasitoid species can be a result of previous evolutionary pressures at work to minimize interspecific competition. Some parasitoid species that attack the same host species can coexist by specializing on different microhabitats. Vet and van Opzeeland (1985) studied *Leptopilina heterotoma* and *Asobara tabida*, both of which attack frugivorous *Drosophila* larvae. They exhibit differences in microhabitat or host location cues, *L. heterotoma* is attracted to a later stage of substrate decay than *A. tabida*. This temporal separation between the species means that they can coexist whilst specializing on different microhabitats. Vet *et al.* (1984a) found that two closely related braconid parasitoids, *Asobara tabida* and *Asobara rufescens*, that attack *Drosophila* species live sympatrically but are found in different microhabitats. The former species is associated with fermenting fruit, and the latter species is associated with decaying vegetation. This niche segregation eliminates competition between the two parasitoids, therefore allowing them to occupy the same host niche.

1.8 Conclusion

This thesis addresses life history evolution of the parasitoid Hymenoptera. Host range in siblicidal and non-siblicidal parasitoids is investigated experimentally in chapter 2. The parasitization success in two sister species of braconid wasp (the solitary *Aphaereta genevensis* and the gregarious *Aphaereta pallipes*) is compared using several *Drosophila* species or strains. The social interactions of the wasp species displaying these different life history strategies is expected to affect their host ranges in that gregarious species are expected to have broader host ranges than solitary species. Literature based comparative analyses are presented in chapters 3 and 4. Chapter 3 revisits a data set compiled by Blackburn (1990) on the parasitic Hymenoptera. Previous studies have already shown that body size and clutch size do not seem to form clear associations with the major life history axis of idiobiosis and koinobiosis. A comparative analysis investigates parasitoid life history traits that may affect the evolution of body size and clutch size, within the parasitic Hymenoptera, when taking into account phylogenetic relationships. A novel life history data set was compiled, along with recent phylogenetic information, on the Ichneumonoidea for chapters 4 and 5. Chapter 4 addresses associations between traits, those biological transitions that regulate life history variation and whether aspects of the host's ecological niche or life history affect parasitoid evolution. The question of trait lability is covered in chapter 5, using several different metrics to assess what types of trait are labile and whether most variation occurs at higher or lower taxonomic levels. In chapter 6 this work is discussed in relation to how it can improve parasitoid life history theory, and what future directions the field should take.

Chapter 2: Host range in solitary and gregarious parasitoids: a laboratory experiment.

Ruth E. Traynor & Peter J. Mayhew

2.1 Abstract

Social interactions within a species may affect the size of the ecological niche. We test the hypothesis that parasitoids displaying siblicidal behaviour in their larvae (solitary species) have narrower host ranges than gregarious parasitoids (with tolerant larvae). In laboratory experiments, we compare parasitization success in two sister species of braconid wasp (*Aphaereta genevensis* (Fischer), solitary, and *A. pallipes* (Say), gregarious) on eight *Drosophila* species or strains. Host species or strain is the most important factor affecting parasitization success, and some of this variation is accounted for by differences in host physiological defenses. Although two hosts are more suitable for the solitary species, and one more suitable for the gregarious species, these differences are small, and there is no consistent difference across all hosts. Wasp body size is positively correlated with parasitization success in both wasp species. This may be because body size increases oviposition success, or the motivation to oviposit. In *A. pallipes* parasitization success peaks after 3-4 days, but later in *A. genevensis*. This trend is likely to be a consequence of low life expectancy or high egg loads increasing oviposition tendency in *A. pallipes* early in life. These data suggest that social interactions between wasp larvae do not greatly affect host suitability. However, the extent of the realized niche may be affected by life history traits that differ between species but that may work in opposing directions.

2.2 Introduction

The evolution of the ecological niche is a long-standing problem in evolutionary ecology. One useful distinction is between the 'fundamental niche', which is the range of environments in which an organism can maintain a positive population growth rate, and the 'realized niche', which is the actual niche occupied in nature (see Futuyma 2001). Selection pressures and constraints on the fundamental niche include the presence of trade-offs in fitness in different environments, interspecific interactions such as competition, as well as intraspecific competition (see Futuyma 2001, Futuyma & Moreno 1988, Jaenike 1990, Schluter 2001). The realized niche is a subset of the fundamental niche modified through limits on dispersal and individual decision-making (see Jaenike 1990, Mayhew 1997). In this paper we investigate the evolution of the ecological niche in relation to intraspecific social interactions, a relatively neglected selection pressure in this context.

It is increasingly apparent that social interactions between individuals can affect many aspects of a species evolution (see Frank 1997, Hamilton 1996, Svensson & Sheldon 1998, West & Griffen 2002). In parasitoid wasps, which develop to maturity on the bodies of other arthropod species, recent work has suggested that the interactions between offspring on a host can radically affect life histories and adult behaviour. In solitary wasps, only a single individual completes development on each host, and the parasitoid larvae display contest competition. In gregarious species, several offspring can successfully develop on each host, and the larvae display scramble competition. Previous work has suggested that gregarious species tend to be smaller (Mayhew 1998, Mayhew & van Alphen 1999), lay larger clutches of eggs (Mayhew & van Alphen 1999, Mayhew & Glaizot 2001), and may also be shorter lived and more fecund (Pexton & Mayhew 2002) than solitary species, differences that are likely to be a consequence of the different types of larval interaction.

In parasitoid wasps, a major component of the ecological niche is the range of host species parasitized (see Askew & Shaw 1986, Godfray 1994, Shaw 1998, Müller *et al.* 1999). There are both empirical and theoretical reasons for believing that solitary and gregarious parasitoids might differ in the extent of their host ranges. Anecdotal observations suggest that gregarious species might have broader host ranges than closely related solitary species. For example, Wharton (1984) and Shaw & Huddleston (1991) both note that some of the endoparasitic gregarious alysiine braconids (Braconidae: Alysiinae) have been reared from a relatively large number of host species. In the braconid subfamily Microgasterinae, the solitary *Cotesia rubecula* (Marshall) is a specialist on *Pieris rapae* (L.), whilst the gregarious *C. glomerata* (L.) is a generalist on several *Pieris* species (Brodeur *et al.*1996, 1998). In addition observations on bruchid beetles, with a parasitoid-like biology, show that species with tolerant larvae have decreased oviposition specificity, implying a larger host range (Smith 1991).

Theoretically, a broader host range might be the consequence of increasing the range of suitable hosts available to gregarious parasitoids, in other words increasing the fundamental host niche. Some of the hosts parasitized by endoparasitic gregarious alysiines are very large relative to the size of the wasp (see Vet *et al.* 1993). Because they pupate internally, the host must be completely consumed prior to parasitoid pupation and this can only be achieved in a big host by increasing the number of offspring sharing the host. Therefore larger bodied hosts may be more easily exploited by gregarious species. In addition, laying several eggs may increase host suitability by helping to overwhelm the host's immune response (see Ode & Rosenheim 1988).

Gregarious parasitoids may also have larger realized niches due to individual decision making. Being generally smaller bodied, gregarious species should have shorter lifespans than related solitary species. State-dependent decision-making models suggest that expected future lifespan should negatively correlate with oviposition tendency (see Mangel 1987, Roitberg *et al.* 1993). In addition, if they allocate resources preferentially to eggs rather than survival, the resulting higher egg loads should also increase oviposition tendency (Pexton & Mayhew 2002).

In this study, we compare host suitability in two closely related species of parasitoids: *Aphaereta genevensis* (Fischer) (solitary) and *A. pallipes* (Say) (gregarious) (Hymenoptera: Braconidae: Alysiinae). Using a pair of close relatives allows us to eliminate, as far as possible, other potentially confounding biological differences. We expose both wasps to a range of potential hosts under controlled conditions, monitoring the consequences for parasitization success and wasp fitness. We hope therefore to further establish whether social interactions can modify the ecological niche in this group of organisms.

2.3 Materials and Methods

2.3.1 Cultures

A. genevensis, which has only be recorded for New York State, and *A. pallipes*, which occurs throughout the New World, are almost indistinguishable morphologically (Wharton 1977). They attack the larvae of cyclorrhaphous Diptera, developing in rotting and fermenting substrates, and emerge from the pupal host stage. The *A. genevensis* culture was initially established from a single female found on milk-cap fungi on the 4th September 1996 on the North Shore of Long Island, New York. The *A. pallipes* culture was established from a single female caught on a compost pile on the 1st October 1995 in Queens County, New York. Both species were originally reared on *Drosophila repleta*, but from 1997 have been reared on *Drosophila virilis* (Sturtevant) (Mayhew & van Alphen 1999).

A number of *Drosophila* species were used in the experiments. Although it would have been possible to widen our experiments to other fly genera, these would have required different culturing conditions, making the experiments increasingly less standardised. An advantage of using only *Drosophila* is that they display a variety of relevant traits and yet many species can be cultured under identical conditions. We chose hosts to maximise taxonomic spread, because host taxonomy is a likely constraint on the fundamental niche. Therefore each host species came from a different species group. A consequence of this was that hosts also varied in body size, another factor hypothesized to affect host range in the wasps (see section 2.2). We also selected some hosts to test the affect of host defenses on wasp success.

As *D. virilis* (Subgenus *Drosophila*, virilis group, virilis subgroup) is the normal culturing host for the wasps in the laboratory, this species was used as the control species in this study. It was obtained from Dr. Peter Chabora, Queens College, New York, in 1997. *D. melanogaster* (Meigen) (Silwood strain) (Subgenus *Sophophora*, melanogaster group, melanogaster subgroup) came from a culture in Silwood Park, UK, which was originally collected in Italy 2001. This strain has been selected for high encapsulation ability against a closely related alysiine wasp, *Asobara tabida* (Nees) (Kraaijeveld & Godfray 1997). *D. melanogaster* (York strain) came from a culture established over 20 years ago at York University (originally obtained from the Bloomington Fly Stock Centre, Indiana University) which has not been exposed to parasitoids in that time. Lack of selection pressure is known to reduce encapsulation ability over time because that ability is costly (Kraaijeveld & Godfray 1997). *D. subobscura* (Collin) (Subgenus *Sophophora*, obscura group, obscura subgroup) was obtained from a culture at Silwood Park, (originally collected from two sites in the Netherlands; the flies from the two sites were pooled together in 1984 to form a lab strain) which has been cultured for almost 20 years. This species is known to be unable to encapsulate parasitoids. *D. funebris* (Fabricius) (Subgenus *Drosophila*, funebris group, funebris subgroup) came from a culture established in 2000 at Leeds University, UK, originally collected at the Faversham pub in Leeds. The following three fly species were obtained from the Fly Stock Centre in Arizona. *D. busckii* (Coquillet) (Subgenus *Dorsilopha*) was originally collected from Costa Rica (stock number 13000-0081.0, genotype Dbus\wild-type). *D. willistoni* (Sturtevant) (Subgenus *Sophophora*, willistoni group, willistoni subgroup) was originally collected from Florida, USA (stock number 14030-0811.2, genotype Dwil\wild-type). *D. immigrans* (Sturtevant) (Subgenus *Drosophila*, immigrans group, immigrans subgroup) was originally collected from Colombia (stock number 155111-1731.0, genotype Dimm\wild-type).

Glass jars (5 cm diameter), with foam stoppers, were used to culture the parasitoids. The base of these jars contained a 2cm layer of set nutrient agar, on top of which was a dab of viscous yeast medium. Several 5-8 day old *D. virilis* larvae were added to each jar, as were 2-5 mated parasitoid females (with no prior host experience). The jars were placed in secure plastic boxes to ensure that both parasitoid species were kept separate within a single culturing room. All *Drosophila* species were kept in this culture room and were separately reared in glass bottles with foam stoppers, containing standard medium. The medium comprised of sucrose, nutrient agar, maize meal, water and dried yeast in the following weight ratios; 65: 11: 75: 612: 10. The culture room was kept at 20^{0}C, constant light and ambient humidity (experiments were carried out under these conditions).

2.3.2 Host range experiments

To standardise the host stage, only 3rd instar host larvae were used for the experiments; this stage is known from previous work to be relatively suitable for parasitoid oviposition and also has the advantage of decreasing host mortality prior to pupation. Each replicate (of which there were a total of 20 per fly and wasp species) was run for a total of 6 days because preliminary work showed that experience is required before peak oviposition activity occurs. This also enabled us to observe age-dependent affects on parasitoid reproductive success. Glass rearing tubes (2cm in diameter), containing 2 cm of agar with a dab of viscous yeast medium and a plastic stopper with air holes, were used. Each tube contained one female parasitoid wasp (which had emerged and mated within the 24 hours prior to the experiment taking place) and 20 x 3rd instar larvae of a given *Drosophila* species. For each replicate, on days 3 and 5, the female wasp was placed into a new rearing tube containing medium and novel *Drosophila* larvae (as described above). Each individual female wasp was treated as an independent replicate.

After the six-day period, the female wasp was placed into a labelled tube and killed by freezing at –20^{0}C. Rearing tubes were checked every day over the course of 50 days for emerged flies / wasps. Emerged individuals were placed in labelled tubes and killed by freezing (as mentioned above). Hind tibia length (mm) was recorded for all wasps, and thorax length (mm) was recorded for all flies. For all fly and wasp species, twenty male and twenty female individuals were dried at 70^{0}C for 4 days, and weighed. These data were used to convert fly thorax length into fly dry mass, and wasp hind tibia length into wasp dry mass. For conversion equations, we used regressions of hind tibia length (wasps) or thorax length (flies), against dry weight. If tibia length or thorax length were not significant predictors of individual dry weight, all individuals were assumed to have the mean mass of those weighed. The equations are as follows:

D. busckii; female and male dry weight = 0.063 + (0.266 x thorax length (mm)). *D. funebris*; female mean value used, and male dry weight = 0.007 + (0.310 x thorax length (mm)). *D. immigrans*; female dry weight = 0.267 + (0.059 x thorax length (mm)), and male dry weight = 0.285 + (0.194 x thorax length (mm)). *D. melanogaster* (Silwood); female and male dry weight = 0.092 + (0.243 x thorax length (mm)). *D. melanogaster* (York); female and male mean value used. *D. subobscura*; mean values used. *D. virilis*, female: mean value used; male dry weight = 0.115 + (0.223 x thorax length (mm)). *D. willistoni*; female and male dry weight = 0.136 + (0.100 x thorax length (mm)). *A. genevensis*; female dry weight = -0.09762 + (0.412 x hind tibia length (mm)), and male dry weight = -0.124 = (0.410 x hind tibia length (mm)). *A. pallipes*; female and male dry weight = -0.094 + (0.402 x hind tibia length (mm)).

The number of flies / wasps emerging per tube was recorded, as was the total number of pupae per rearing tube. After the 50 day period, all puparia were removed and examined for emergence holes, those with no emergence holes were dissected to see if there was a failed fly / wasp inside. This allowed us to record the actual number of fly pupae that gave rise to wasps.

2.3.3 Statistical Analysis

Data analysis was carried out using general linear modelling in GLIM (Numerical Algorithm Group, Oxford). Binomial error variance was assumed for proportion data and Poisson error variance was assumed for count data. Statistical models were constructed by stepwise subtraction from a full model, which included all potential explanatory variables for which we had data, starting with the least significant terms. Significance was assessed by the change in deviance under both binomial errors and Poisson errors by a chi-square test. Only significant terms remained in the model, which was then termed 'the minimal adequate model'. The appropriateness of binomial and Poisson errors was assessed by a heterogeneity factor. This factor is equal to the residual deviance divided by the residual degrees of freedom. If the heterogeneity factor was greater than 1.3, this indicates overdispersion, and the model was rescaled using the value of Pearson's χ^2/df (Crawley 1993).

One potential pitfall of our data is that the same individual wasp was used to gather three successive data points, as each wasp aged over the first six days of its life. These are potential pseudoreplicates and should not be treated as independent in any analysis. To avoid pseudoreplication we only analysed data from one of the time periods in any one analysis, or pooled all the data from each wasp individual into a single replicate. To investigate the effect of wasp age we used the non-parametric within-subject Friedmann test, which controls for relatedness amongst observations. Regression analysis was performed to test whether fly body mass (mg) was significantly affecting the proportion of pupae successfully parasitized by each wasp species. These two analyses were implemented in SPSS. Where necessary, we applied sequential Bonferroni correction (Rice 1989) to the significance values to control for multiple comparisons (Table 2.1). To test whether host phylogenetic relatedness was a significant factor affecting wasp species success, we constructed a cladogram by clustering species groups according to Grimaldi (1990) and subgenera according to Tatarenkov *et al.* (1999). The mean proportion of pupae successfully parasitized for each wasp species (Table 2.1) was 'hung' on the cladogram. Significance was assessed by a χ^2 test. The analysis was performed in the 'Continuous' software package (Pagel 1997, 1999a). We used a likelihood ratio test to compare the log-likelihood of a null model (where λ was set to zero) to that of the alternative model (where λ was set to its maximum likelihood value). The parameter λ, when set to zero, indicates that species are independent (1 indicates species values are maximally dependent on phylogeny).

2.4 Results

2.4.1 Proportion of pupae from which wasps emerged

Across all fly species, the proportion (mean±SEM) of pupae successfully parasitized was similar for both wasp species (0.076±0.037 and 0.038±0.017 for *A. genevensis* and *A. pallipes* respectively). Fly species on its own was highly significant ($\chi^2_7 = 367.40$, $P < 0.001$) but wasp

Table 2.1: Mean±SEM per wasp species of the proportion of fly pupae parasitized successfully, and the general linear model of this data, sample size of 20 fly pupae per replicate tube, and 20 replicate wasps per host and wasp species combination. (*$P<0.05$ **$P<0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction over the entire table, rejecting the null hypothesis that there are no significant results in the table. By chance 4.2 significant results are expected, but 19 are found.

Fly species	*A. genevensis*	*A. pallipes*	Explanatory variables		
			Wasp species	Female mass (mg)	Interaction
D. busckii					
Day 1-2	0.032±0.012	0.157±0.025	(X^2_1=22.750**)	X^2_1=2.713	(X^2_1=19.590**)
Day 3-4	0.062±0.019	0.169±0.033	X^2_1=7.556*	X^2_1=0.006	X^2_1=7.980*
Day 5-6	0.109±0.032	0.028±0.011	X^2_1=4.432*	X^2_1=4.954*	X^2_1=2.191
Overall	0.056±0.138	0.123±0.131	(X^2_1=11.820**)	X^2_1=0.001	(X^2_1=13.220**)
D. funebris					
Day 1-2	0.178±0.039	0.193±0.059	X^2_1=0.290	X^2_1=8.571*	X^2_1=0.144
Day 3-4	0.290±0.048	0.330±0.059	X^2_1=0.676	X^2_1=0.037	X^2_1=0.788
Day 5-6	0.332±0.055	0.222±0.041	X^2_1=1.032	X^2_1=1.738	X^2_1=1.852
Overall	0.256±0.039	0.243±0.042	X^2_1=0.005	X^2_1<0.001	X^2_1=0.005
D. melanogaster (York)					
Day 1-2	0.112±0.042	0.072±0.018	X^2_1=2.136	X^2_1=3.201	X^2_1=2.159
Day 3-4	0.224±0.049	0.199±0.052	X^2_1=2.032	X^2_1=0.043	X^2_1=2.372
Day 5-6	0.218±0.048	0.132±0.038	X^2_1=4.654*	X^2_1=2.409	X^2_1=4.095*
Overall	0.184±0.037	0.104±0.018	X^2_1=6.399*	X^2_1=2.741	X^2_1=6.305*
D. melanogaster (Silwood)					
Day 1-2	0.003±0.012	0.004±0.013	X^2_1=0.481	X^2_1=1.044	X^2_3=7.423
Day 3-4	0.019±0.014	0.005±0.005	X^2_1=1.466	X^2_1=8.611*	X^2_1=0.242
Day 5-6	0.006±0.004	0.063±0.063	X^2_1=2.994	X^2_1=2.505	X^2_1=1.042
Overall	0.020±0.006	0.028±0.008	X^2_1=0.983	X^2_1=0.056	X^2_1=1.178
D. subobscura					
Day 1-2	0.058±0.021	0.045±0.026	X^2_1=1.256	X^2_1=0.698	X^2_1=2.459
Day 3-4	0.117±0.044	0.092±0.022	X^2_1=0.805	X^2_1=2.373	X^2_1=0.802
Day 5-6	0.253±0.056	0.101±0.029	X^2_1=10.990**	X^2_1=3.353	X^2_1=8.762*
Overall	0.178±0.033	0.074±0.013	X^2_1=11.280**	X^2_1=2.718	X^2_1=9.227*
D. virilis					
Day 1-2	0.160±0.050	0.280±0.059	χ^2_1=2.122	χ^2_1=0.270	χ^2_1=3.181
Day 3-4	0.338±0.058	0.307±0.057	X^2_1=0.190	X^2_1=0.207	X^2_1=0.093
Day 5-6	0.301±0.048	0.241±0.046	X^2_1=0.591	X^2_1=1.691	X^2_1=0.156
Overall	0.270±0.038	0.277±0.045	X^2_1=0.040	X^2_1=0.878	X^2_1=0.719
D. willistoni					
Day 1-2	0.023±0.012	0.012±0.007	X^2_1=1.337	X^2_1=4.755*	X^2_1=0.306
Day 3-4	0.040±0.014	0.059±0.015	X^2_1=0.262	X^2_1=1.800	X^2_1=2.164
Day 5-6	0.007±0.005	0.031±0.011	X^2_1=2.932	X^2_1=0.931	X^2_1=2.180
Overall	0.024±0.007	0.032±0.007	X^2_1=0.551	X^2_1=1.417	X^2_1=1.724

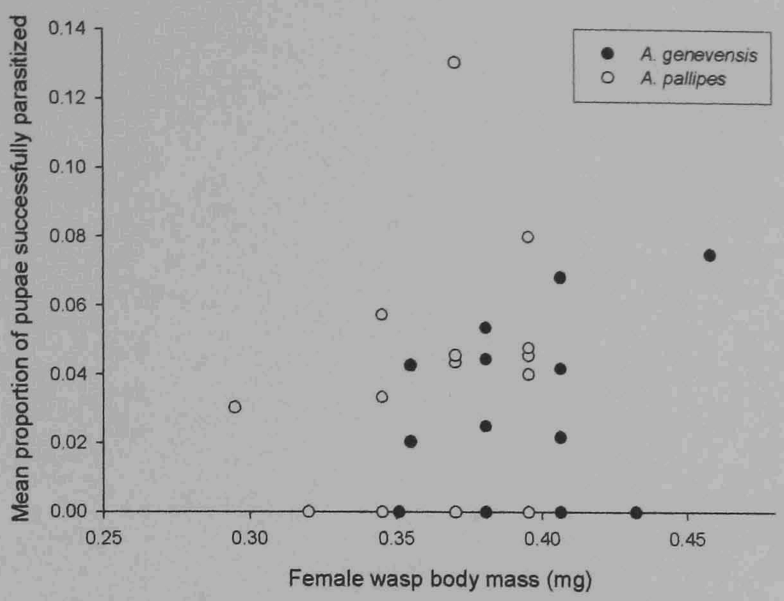


Figure 2.1: Female wasp body mass (mg) against overall mean proportion of pupae successfully parasitized for *D. melanogaster* (York).

Table 2.2: Age-dependent effects on the success of wasp parasitization (Friedmann test). Rank values (italics); mean±SEM.

Wasp species	Day 1-2		Day 3-4		Day 5-6		df	P
A. genevensis	*1.77*	0.09±0.01	*2.08*	0.16±0.02	*2.15*	0.18±0.02	2	<0.001
A. *pallipes*	*1.86*	0.12±0.015	*2.24*	0.17±0.017	*1.90*	0.12±0.015	2	<0.001

species was not ($\chi^2_1 < 0.001$, $P > 0.1$). The best hosts overall were *D. virilis* (control) and *D. funebris* (Table 2.1). *D. immigrans* was the least suitable host, failing to produce a single wasp. Female dry mass was included in the minimum adequate model ($\chi^2_1 = 5.03$, $P < 0.05$): the proportion of pupae successfully parasitized was positively correlated with female dry mass (for example Figure 2.1). There was also a significant interaction between fly and wasp species ($\chi^2_7 = 23.810$, $P < 0.05$). *A. genevensis* parasitized more *D. melanogaster* (York) and more *D. subobscura* than *A. pallipes*. However, *A. pallipes* parasitized more *D. busckii* than *A. genevensis* (Table 2.1). Fly species was a significant factor ($\chi^2_2 = 45.70$, $P < 0.001$) explaining the differences in parasitization success for those fly species specifically selected for their varying encapsulating abilities (*D. melanogaster* (Silwood and York strains) and *D. subobscura*).

Host body size was not a significant predictor of the parasitization success in either *A. genevensis* (F = 0.03, df = 2, $P = 0.959$) or *A. pallipes* (F = 0.698, df = 2, $P = 0.436$) (Figure 2.2). There was no significant affect of host phylogeny on the parasitization success of either wasp species. For *A. genevensis* the maximum likelihood estimate of $\lambda = 0.117$, $\chi^2 = 0.06$, df = 1 and $P = 0.82$. For *A. pallipes* the maximum likelihood estimate of $\lambda = 0$, $\chi^2 = 0$, df = 1 and $P = 1$.

Age-dependent effects were significant for both wasp species (Table 2.2). *A. genevensis* successfully parasitized the greatest number of pupae on day 5-6 and was the least successful on day 1-2. *A. pallipes* successfully parasitized the greatest number of pupae on day 3-4 and was the least successful on day 1-2. Wasp species was a significant factor ($\chi^2_1 = 4.81$,

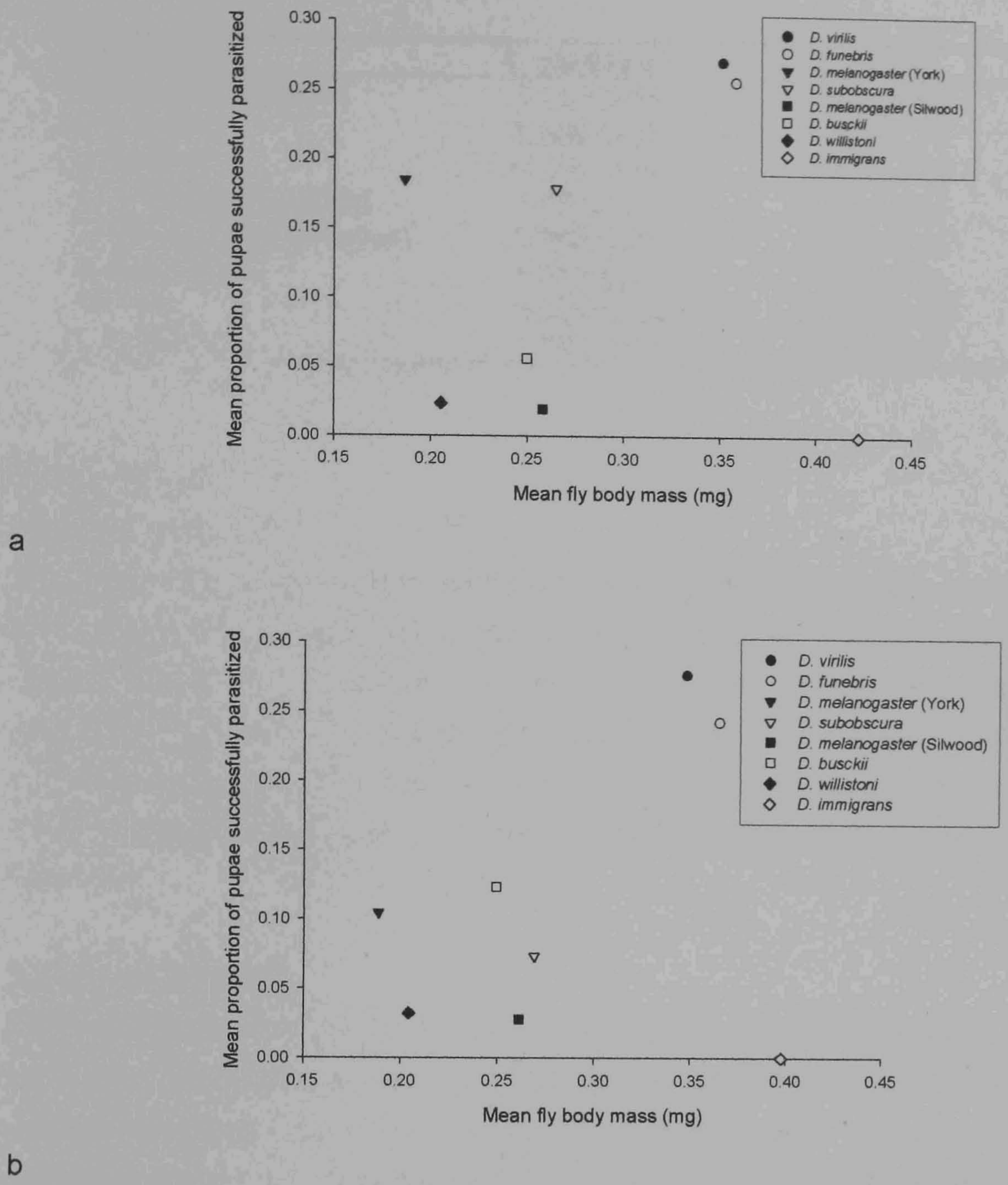


Figure 2.2: Mean proportion of fly pupae that successfully gave rise to a) *A. genevensis* offspring and b) *A. pallipes* offspring, across different fly species or strains.

$P < 0.05$) on day 5-6, explaining the differences in parasitization success between the two wasp species. However, there was no significant effect of wasp species on day 1-2 ($\chi^2_1 = 2.88$, $P > 0.01$) or on day 3-4 ($\chi^2_1 = 0.27$, $P > 0.01$).

2.4.2 Number of parasitoid offspring produced

For total offspring produced per individual wasp, over all hosts, the minimum adequate model contained female dry mass ($\chi^2_1 = 5.44$, $P < 0.05$), fly species ($\chi^2_7 = 273.70$, $P < 0.001$) and wasp species ($\chi^2_1 = 12.01$, $P < 0.001$), but no interaction terms. *A. pallipes* produced a greater number of offspring than *A. genevensis* (Table 2.3), there was a positive relationship between number of offspring produced and female dry mass, and again *D. virilis and D. funebris* were the best hosts, in terms of number of wasp offspring produced (Table 2.3). For brood size, over all hosts, wasp species was the only significant factor ($\chi^2_1 = 14.730$, $P < 0.001$), with *A. pallipes* producing larger broods than *A. genevensis*.

Table 2.3: Mean±SEM of the number of offspring (brood size) per wasp species.

Fly species	*A. genevensis*	*A. pallipes*
Fly species combined	5.713±2.05	7.556±2.95
D. busckii	2.950±0.63	6.450±0.71
D. funebris	12.050±1.67	18.650±4.59
D. melanogaster (York)	7.700±1.60	6.200±1.04
D. melanogaster (Silwood)	0.900±0.26	0.600±0.18
D. subobscura	5.050±0.38	3.550±0.52
D. virilis	16.000±2.32	21.850±3.10
D. willistoni	1.050±0.30	2.650±0.67

2.5 Discussion

2.5.1 Main findings

The main finding of this study is that host species affects parasitization success similarly in two sister species of parasitoids that differ in larval behaviour. Although some hosts are more suitable for the solitary species, and one more suitable for the gregarious species, these differences are small. In addition, wasp size and age are important explanatory variables explaining wasp success, suggesting they may be important predictors of the realized niche. Below we put these results in the context of previous work, before discussing how they can be furthered.

2.5.2 Current findings

The most suitable host species for both wasps were *D. virilis* and *D. funebris*. The least suitable host was *D. immigrans* and the other host species were of intermediate suitability. Host body size cannot explain this as the largest hosts could be either highly suitable or completely unsuitable, and the two traits were not significantly correlated overall. Host taxonomic affiliation is also unable to explain host suitability for the wasps. Encapsulation ability does seem to explain some of the variation in success. A strain of *D. melanogaster* that has been selected for high encapsulation ability was of low suitability for both wasps. However, both wasps were more successful on a control strain of *D. melanogaster*, as well as on the closely related *D. subobscura*, which is known to be unable to encapsulate parasitoids. Therefore physiological features of the host, such as host defense capability, can account for some of the variation in fundamental host niche. What exactly affects host suitability in the other species examined is presently unknown, but possible factors include host defense responses and other physiological traits, as well as a species' apparency to searching female parasitoids.

Two hosts are more suitable for the solitary species, whereas one host is more suitable for the gregarious species. We hypothesized that a) larger hosts would be more suitable for the gregarious species than the solitary species; b) hosts with vigorous immune responses would be more suitable for the gregarious than the solitary species; c) gregarious species would have increased oviposition motivation than the solitary species due to high egg load and low life expectancy. We found that *D. busckii* was more suitable for the gregarious than the solitary species, but that *D. melanogaster* (York) and *D. subobscura* were more suitable for the solitary species. There was no overall suggestion that oviposition motivation was generally higher in the gregarious species. Interpreting the differences we observe is currently problematic. *D. busckii* is a relatively small species, but its encapsulation ability is unknown. *D. melanogaster* (York) and *D. subobscura* are known or inferred to have low encapsulation abilities. We do not know why *A. genevensis* should perform relatively better on these hosts, although the differences are small. In contrast, wasp species performance was not different on the host chosen for its high encapsulation ability. It is possible that the differences represent evolved species-specific adaptations (or exaptations) to particular hosts or wasps. All hosts used are cosmopolitan species, so are certain to be encountered in the native geographic ranges of the wasps. However, use of different microhabitats in nature may limit the actual encounter rates with these species (see Vet & Janse 1984, Vet *et al.* 1984).

The effect of wasp size on wasp performance was positive. A likely reason is that larger bodied wasps contain more eggs in both species (Pexton & Mayhew 2002). State-dependent models of behaviour show that higher egg loads should increase oviposition tendency and several studies have provided confirmation of this (Godfray 1994). An additional reason for the trend may be that larger wasps are better able to reach, subdue or oviposit into hosts. Larger wasps have longer ovipositors so might be able to reach or search for hosts more effectively. Larger wasps may also be better able to overcome behavioural or other host defenses. Such defenses have been show in a number of species. For example, Rotheray and Barbosa (1984) noted that host handling time increased with an increase in host size when they studied *Brachymeria intermedia* attacking pupae of the gypsy moth. The percentage of male gypsy moth parasitism was greater than that of female moth parasitism, the male moths were smaller than the female moths and were not as aggressive towards the parasitoids as the female wasps were. Kouamé and Mackauer (1991) found that aphids attacked by *Ephedrus californicus* kicked to prevent parasitism and that larger aphids were more successful at preventing parasitism. It is possible that such defense reactions are also size related in our hosts and that larger wasps are better able to overcome them.

The effects of wasp body size on performance may have implications for the host ranges of solitary and gregarious species. Gregarious species are generally smaller bodied than solitary relatives. This should then mean that body size has the effect of decreasing realized host range by virtue of generally lower performance. However, it is possible that other factors counterbalance this. Gregarious species may have larger egg loads and lower life expectancies than solitary species of the same size, which could increase oviposition motivation and overall performance in gregarious species. The effects of age on performance may reflect this: *A. pallipes* reached peak performance earlier in life than *A. genevensis* and this may indicate a generally higher motivation to oviposit. Overall in our experiments there is no indication that the wasp species differed in overall performance.

We have taken as our primary measure of performance the number of host pupae that gave rise to wasps. This was used because the primary variable of concern was host range (which hosts give rise to wasps). In addition, we needed a variable in which to fairly compare a solitary and a gregarious species. Since the two have distinct clutch size strategies that also have consequences for offspring body size, these are not suitable comparative indicators of performance across species. However, within species they might indicate differential performance across hosts. To examine this, we took one of these measures, namely the number of offspring produced (per host and per individual wasp). Results generally confirmed prior findings. The gregarious species produced larger broods per host individual, but brood size was host species specific. Consequently, host species that were heavily parasitized also gave rise to more wasp offspring.

2.5.3 Analytical issues

Several analytical and experimental issues arise from our work. First, although we exposed both wasp species to a variety of *Drosophila* hosts, chosen for their different biologies, because we used only a single host genus, the total range of biologies to which the wasps were exposed may still be relatively slim. It may be that we did not select host species that were phylogenetically distinct enough from one another. However, using hosts from the same genus allowed us to control for a number of design features that may have affected wasp performance, such as the medium on which they had to search for hosts. It may be that using a still wider variety of hosts would reveal important features of the fundamental niche, such as whether a solitary species can successfully parasitize them. This would merit future investigation.

Second, although the wasps were exposed to numerous *Drosophila* hosts, they were only exposed to one host species at any time, meaning that the wasps were not able to choose which host species to parasitize. Conducting host choice experiments might identify differences in host preference between the solitary and gregarious wasp species, therefore distinguishing differences between the fundamental niche of both wasp species. Patch exploitation experiments may also detect fundamental niche differences in host searching behaviour and microhabitat use between these wasp species.

Thirdly, we realise that field studies are useful in that they can provide information on a species realized niche, but recognise that laboratory studies are also important and complementary in that they can identify aspects of a species fundamental niche. Although laboratory conditions are artificial they can be both highly controlled and easily manipulated, therefore decreasing the risk of the observations being due to confounding variables, something that field studies can less rigorously control for.

Fourth, the experimental results may be affected by wasp confinement through self-superparasitization. This is when a parasitoid attacks a host that she has already parasitized (Waage 1986) and can result in a parasitoid wasting both time and eggs (Hubbard *et al.* 1987, Waage 1986). This could easily have occurred as each individual parasitoid was only provided with a total of 20 host larvae per two-day period. If self-superparasitization did occur this could have been either an advantage or a disadvantage to parasitization success. A disadvantage, in the case of the solitary wasp species, is that if there were two parasitoid larvae developing per individual host, then both developing parasitoids might destroy each other. Therefore the female wasp would have wasted both time and eggs. However, there may also be an advantage to self-superparasitization in solitary parasitoids, placing two eggs in a host may mean that the host's defense system is saturated and one parasitoid offspring can successfully develop to adulthood, which may allow the parasitoid to exploit novel hosts. Another artefact of confinement is that of a finite food resource for the developing host larva. If this resource is exhausted the host larvae may not reach an optimal size for parasitoid development to successfully take place.

Another issue that should be raised is that the fly cultures' suitability for successful parasitization may have evolved. Those host species, which may have been regularly exposed to parasitoid attack in the field and hence survived, may have lost their ability to defend themselves against parasitoid attack due to the absence of parasitoid exposure whilst in culture.

2.5.4 Conclusions

As discussed by Harvey and Pagel (1991) our study represents a single independent contrast between the two wasp species being studied and therefore cannot be used alone to confirm or reject the hypothesis that gregarious parasitoid species have broader host ranges than solitary species. This hypothesis may eventually be rejected or accepted if many similar studies are carried out using similar systems.

In conclusion, our study suggests that the host ranges of a pair of parasitoid species that differ in larval behaviour are broadly similar, but that their use of hosts may be affected by life history traits that differ between wasp species. Future work should investigate how these traits translate into actual host use in the field.

Chapter 3: A comparative study of body size and clutch size across the parasitoid Hymenoptera

Ruth E. Traynor and Peter J. Mayhew

3.1 Abstract

Across animal species, body size and clutch size often form part of a suite of associated life history traits, exemplified by the "fast-slow continuum" in mammals. Across the parasitoid Hymenoptera however, a major axis of life history variation is the development mode of the larva (koinobiosis versus idiobiosis), and body size and clutch size do not seem to form clear associations with this major axis. We use a large comparative data set and the latest phylogenetic information to explore hypotheses that might explain the variation in body size and clutch size across species in parasitoids. We find evidence for three novel evolutionary correlations: changes in the stage of host attacked (for example egg, larva, pupa) by the parasitoid significantly predicts changes in both body size and clutch size, whilst in gregarious species changes to higher latitudes are associated with reduced clutch size. We also find a number of hypothesized cross-species (phenotypic) associations that we cannot demonstrate are the result of evolutionary correlations: large bodied species in our data tend to lay small clutches; koinobionts are larger than idiobionts attacking the same host stage; tropical species are smaller than temperate species (Bergmann's rule). Our results provide support for theoretical models of trait evolution in parasitoids, whilst the associations between latitude and life history may help explain why species richness in the family Ichneumonidae peaks at intermediate latitudes. Our results also show the continuing value of phylogenetically-based comparative analyses and demonstrate that recent work on parasitoid phylogenetics has produced significant benefits for our understanding of life history evolution.

3.2 Introduction

The explanation of life history variation across species remains one of the major challenges in evolutionary ecology. In recent years considerable progress has come from the interplay of interspecific comparative studies, which describe the associations between traits across taxa, and theoretical models that attempt to predict those associations. Perhaps the most notable studies have concerned mammals, where a fast-slow continuum of traits exists; large bodied species have long lifespans, suffer low adult mortality, mature late, have low fecundity, small litters, and large offspring that suffer low juvenile mortality. Small-bodied species have the opposite characteristics (see Harvey & Purvis 1999). Some adaptive models (Charnov 1991, 1993, Kozlowski & Weiner 1996) have had notable success in predicting this suite of associations (see Harvey & Purvis 1999, Purvis & Harvey 1995). Some of the mammalian associations have also been found in other organisms, such as parasitic nematodes (Gemmill *et al.* 1999) and angiosperms (Franco & Silvertown 1997), though other groups such as birds differ in substantial ways that demand alternative models (see Bennett & Owens 2002, Charnov 2000).

Parasitoids are insects that develop to maturity by feeding on the body of another host arthropod, eventually killing it. The parasitoid Hymenoptera (wasps) are one of the most species-rich components of terrestrial ecosystems; about 77,000 species have been described (Mayhew 1998 using data from Brown 1982), and they may comprise 20% of all insect species (La Salle & Gauld 1991). They also display enormous variation in life history traits that begs explanation (Godfray 1994). Despite much study on intraspecific variation, the associations between traits across species are still relatively poorly known, and as yet no general theoretical model has attempted to predict or describe such variation. In this study we describe novel interspecific associations between traits that should promote understanding of the causes of life history variation in this group and help the development of theory.

Previous comparative work on the parasitoid Hymenoptera has revealed that development mode is a major predictor of a suite of life history traits (see Askew & Shaw 1986, Godfray 1994, Jervis *et al.* 2001, Mayhew & Blackburn 1999, Müller *et al.* 1999, Quicke 1997, Sheehan & Hawkins 1991). Specifically, koinobionts, which allow their host to continue to develop after parasitization, have long development times, tend to be endoparasitic, have short adult lifespans, a high fecundity, lay small eggs, emerge with many eggs matured, and have narrow host ranges. Idiobionts, which permanently paralyze their hosts, have the opposite traits. One could consider koinobionts to have "slow" larvae but "fast" adults, and idiobionts to have "fast" larvae but "slow" adults. Unsurprisingly then, the suite of inter-related traits seen in mammals is not found in parasitoids (Blackburn 1991a). Interestingly, not only is parasitoid body size not associated with most other traits, unlike in mammals (Blackburn 1991a), but it is also not strongly associated with development mode (Mayhew & Blackburn 1999). Correlates of clutch size have not yet been investigated in large-scale interspecific studies. This begs the question of what does control the variation in these two life-history traits that are such central components of variation in other groups.

We test hypotheses, derived both from knowledge of parasitoid biology and from studies on other organisms, that have not yet received tests in a large cross-species comparative study in this group:

1. Body size and clutch size might be associated with the stage of host attacked (for example egg, larva, pupa). Theoretical models of interspecific variation (Mayhew & Glaizot 2001) have suggested that both clutch size and body size have the potential to increase with host size across species. In addition, interspecific comparative studies on two parasitoid taxa, the braconid genus *Apanteles* (Le Masurier 1987) and the family Bethylidae (Mayhew & Hardy 1998), have shown that both these trends occur. However, these studies could only examine relationships between close relatives: in addition all these parasitoids attack a single host stage (the host larva).
2. When controlling for host stage attacked, clutch size and body size might be negatively correlated. Intraspecific studies have shown that, when the size of the host is controlled, larger clutches result in smaller bodied individuals because offspring must compete for limited resources (Hardy *et al.* 1992). In addition, families that contain gregarious species (where more than one individual can develop from each host) tend to be smaller bodied than their sister taxa that are exclusively solitary (Mayhew 1998). However, gregarious development is only a crude indicator of actual clutch size, and the latter study could not examine relationships at finer taxonomic levels.

3. After controlling for the stage of host attacked, koinobionts might have larger bodies or lay larger clutches than idiobionts. Since koinobionts allow their hosts to continue to develop for some time after parasitization, the host should in general be larger when the parasitoid completes development than for idiobionts. Koinobionts may exploit this advantage in two ways: by having more offspring per host (increased clutch size) or by increased individual offspring fitness per host (increased body size). Previous comparative studies have failed to support a direct relationship between development mode and body size (Mayhew & Blackburn 1999), but the host stage attacked is a possible confounding variable.
4. Body size and clutch size might be positively correlated with latitude. The positive correlation of body size with latitude (Bergmann's rule) has been described in a number of taxa (see Gaston & Blackburn 2000), although there are significant exceptions amongst the insects. Clutch size increases strongly with latitude in birds (Cardillo 2002) but has not been extensively investigated in other taxa. Neither hypothesis has been tested in parasitoids, yet latitudinal effects on life history hold the potential to explain much of the variation across species.

3.3 Methods

3.3.1 Data

We used a data set that has been the material for three previous comparative studies (Blackburn 1991a/b, Mayhew & Blackburn 1999, Appendix 1). The data comprise information on 474 parasitoid wasp species derived from the published literature prior to 1990. Since initial investigations of this data set produced few positive results, it was criticized, quite rightly, due to it being a 'very sparse representation of a very diverse group of wasps, with a rather poorly resolved taxonomy' (Godfray 1994, p. 320). The implication was that, if only the data had been more complete and standardized, more significant associations would have emerged. However, a further investigation of the data by Mayhew and Blackburn (1999) provided evidence for a number of hypothesized associations, suggesting that the data are at least good enough for major axes of life history variation to be identified. The implication now is that the associations hypothesized in the earlier studies were genuinely absent. Given that these data are now known to contain useful information, we feel it is important to ask more questions from them, especially about variables that are so far unexplained.

In addition, there has been much recent work on the phylogenetic relations of parasitoid wasps. In our comparative analyses we use both the traditional taxonomy used in the earlier analyses as well as information from recent phylogenetic studies. Differences in outcome allow us to judge the sensitivity of results to phylogenetic assumptions, as well as the added value of this recent phylogenetic work.

The variables investigated here are:

Body length (mm): excluding antennae and ovipositor.

Clutch size: the mean number of parasitoid offspring completing development per individual host.

Solitary or gregarious development: solitary development is where the mean clutch size as defined above is one, gregarious development where it is greater than one.

Development mode: idiobiont or koinobiont

Geographic distribution: Temperate or tropical.

Host stage attacked: Species were classified as those ovipositing into eggs, nymphs, larvae, pre-pupae, pupae, adults or any combination of these. In the independent contrast analyses (see below) several of these categories were not sufficiently well represented to enable contrasts to be calculated, and we only considered the following stages: eggs, nymphs, larvae, prepupae, pupae, and adults.

3.3.2 Analysis

Both continuous variables were $\log_{10}$ transformed prior to analysis to meet statistical assumptions. Hypotheses were first tested by analysis of the raw data across species. Such "phenotypic associations" allow one to predict something about the value of one species trait in our data given knowledge of another trait. Phenotypic correlations are the product of any evolutionary correlations between traits (associations between evolution in one trait and evolution in another). Phenotypic correlations can reflect evolutionary correlations relatively accurately if there is no phylogenetic dependence in the data, such that trait values in each species are relatively independent of those in others (Freckleton *et al.* 2002, Price 1997). However, if there is a degree of phylogenetic dependence in the data, phylogenetic information needs to be incorporated into the analysis to detect evolutionary correlations, therefore to allow this we used the Phylogenetic Regression (PR) (Grafen 1989).

Phylogenetic Regression is an independent contrast method that calculates, from the raw species data, sets of contrasts that represent differences between sister-taxa in the phylogeny, and are evolutionarily independent. To adopt an appropriate evolutionary model, which is important if evolutionary correlations are to be detected (see Freckleton *et al.* 2002, Harvey & Rambaut 2000, Price 1997), PR scales the branch lengths of the phylogeny using a parameter, ρ, estimated from the data and the phylogenetic topology. The value of ρ should reflect the degree of phylogenetic independence of the data. Recent simulation studies show that ρ is a relatively good estimator of phylogenetic dependence when the number of species analyzed is quite large, as it is in our study (Freckleton *et al.* 2002).

When there is a significant phenotypic correlation but a non-significant evolutionary correlation, possible reasons include: a) reduction in power in the phylogenetic analysis, b) an inappropriate evolutionary model in the phylogenetic analysis, c) phylogenetic dependence in the data, meaning that cross species analysis does not accurately reflect evolutionary correlations (see Mayhew & Pen 2002). In the latter case (c) evolutionary changes deep in the phylogeny can exert a disproportionately large historical impact on extant phenotypes (for example Hardy & Mayhew 1998, West & Herre 1998). To examine whether such explanations apply, it is useful to examine individual contrasts, first to see which particular events have been historically influential in this way, and second to examine how some contrasts come to be in the opposite direction to that expected from the cross species analysis. Phylogenetic Regression does not allow us to examine the contrasts, so instead we re-ran the analysis through an alternative software package that does (CAIC, Purvis & Rambaut 1995). CAIC cannot run all the types of general linear model we wished to perform, and does not automatically scale the branch lengths of the phylogeny to search for appropriate evolutionary models, hence our overall preference for PR. We applied the equal branch length option to generate contrasts and then identified contrasts of interest, the source of which we then investigated in the raw data. In all cases, analyses that were non-significant using PR were also non-significant using CAIC.

3.3.3 Phylogenetic assumptions

We performed phylogenetic analyses using the traditional taxonomy used in earlier analyses of the data (see Blackburn 1991a/b, Appendix 2) and also by constructing composite cladograms from recent analyses of phylogeny. If several phylogenetic analyses had been attempted on a group and there was a lack of consensus between them, we took two alternative approaches; we first constructed a "conservative" cladogram (Appendix 3), representing only relationships that are considered robust, and collapsing uncertainties into soft polytomies. Second, we used only the most highly resolved tree available in an attempt to maximize power (Appendix 4). In both cladograms, where no phylogenetic estimates were available for a group, we used information from the taxonomy.

The basal branches of the conservative tree are taken from Figure 4 of Ronquist (1999a). Chrysidoidea relationships are from Figure 5 of Ronquist (1999a). Ceraphronoidea relationships are taxonomy based, as are the Evanoidea, the Platygasteroidea, and the Proctotrupoidea. Chalcidoidea relationships are also taxonomy based, apart from the Eulophidae, which are based on Figure 5 of Gauthier *et al.* (2000). The Cynipoidea are based on Figure 2c of Ronquist (1999b). Braconidae relationships are taken from Figure 1a of Dowton *et al.* (2002). The Ichneumonidae are taken from Figure 8 of Belshaw and Quicke (2002).

The more resolved tree differs from the conservative tree only in the following areas: the basal relationships are taken from Figure 9 of Dowton and Austin (2001), the Chalcidoidea are based upon Noyes (1990), and the microgastroids (Braconidae) are based on Figure 5 of Dowton and Austin (1998).

The number of nodes in these different estimates of phylogeny are 166, 190, and 209 for the taxonomy, the conservative phylogeny, and the resolved phylogeny respectively. This represents the maximum number of contrasts that could be made in the data, if all variables were represented for all species.

3.4 Results

3.4.1 Body size, clutch size and host stage attacked

There was a significant association between body size and host stage attacked across species (Kruskal-Wallis test, $\chi^2 = 88.61$, df = 12, $P < 0.001$), and in all the PR analyses (Table 3.1). Across species, parasitoids attacking eggs or nymphs had the smallest bodies whilst parasitoids attacking prepupal host stages had the largest bodies (Figure 3.1). The phylogenetic regressions produced values of ρ ranging from 0.370 to 0.389, indicating moderate phylogenetic effects. PR estimates also showed that parasitoids attacking eggs and nymphs had the smallest

Table 3.1: Phylogenetic regression results for body size, clutch size, and host stage attacked (* $P < 0.05$ **$P < 0.001$). Numbers denote regression estimates or ρ values (italics). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r - response variable, e – explanatory variable, c – control variable. E – egg, N – nymph, L – larva, Pr – prepupa, P – pupa, A – adult, Cs - clutch size, S – solitary, G – gregarious, I – idiobiont, K - koinobiont, Te – temperate, Tr - tropical. Unless otherwise stated all analyses were carried out using the full data set.

Analyses	Taxonomy	Conservative cladogram	Resolved cladogram
Body size (r) and host stage attacked (e)	*0.379***	*0.370****	*0.389****
	0.000 E	0.000 E	0.000 E
	-0.101 N	-0.070 N	-0.182 N
	0.120 L	0.268 L	0.156 L
	0.205 Pr	0.364 Pr	0.289 Pr
	0.109 P	0.261 P	0.179 P
	0.027 A	0.065 A	0.046 A
Clutch size (r) and host stage attacked (e)	*0.082* *	*0.045* *	*0.082* *
	0.000 E	0.000 E	0.000 E
	-0.435 N	-0.384 N	-0.334 N
	-0.125 L	-0.106 L	-0.099 L
	0.504 Pr	0.550 Pr	0.541 Pr
	0.047 P	0.039 P	0.048 P
	-0.133 A	-0.169 A	-0.070 A
Body size (r) and clutch size (e)	*0.379*	*0.352*	*0.476*
	0.002 Cs	-0.006 Cs	0.002 Cs
Body size (r), clutch size (e), host stage attacked (c)	*0.419*	*0.192*	*0.500*
	-0.023 Cs	-0.023 Cs	-0.018 Cs
Body size (r), solitary / gregarious development (e)	*0.379*	*0.352***	*0.476*
	0.000 S	0.000 S	0.000 S
	-0.028 G	-0.035 G	-0.028 G

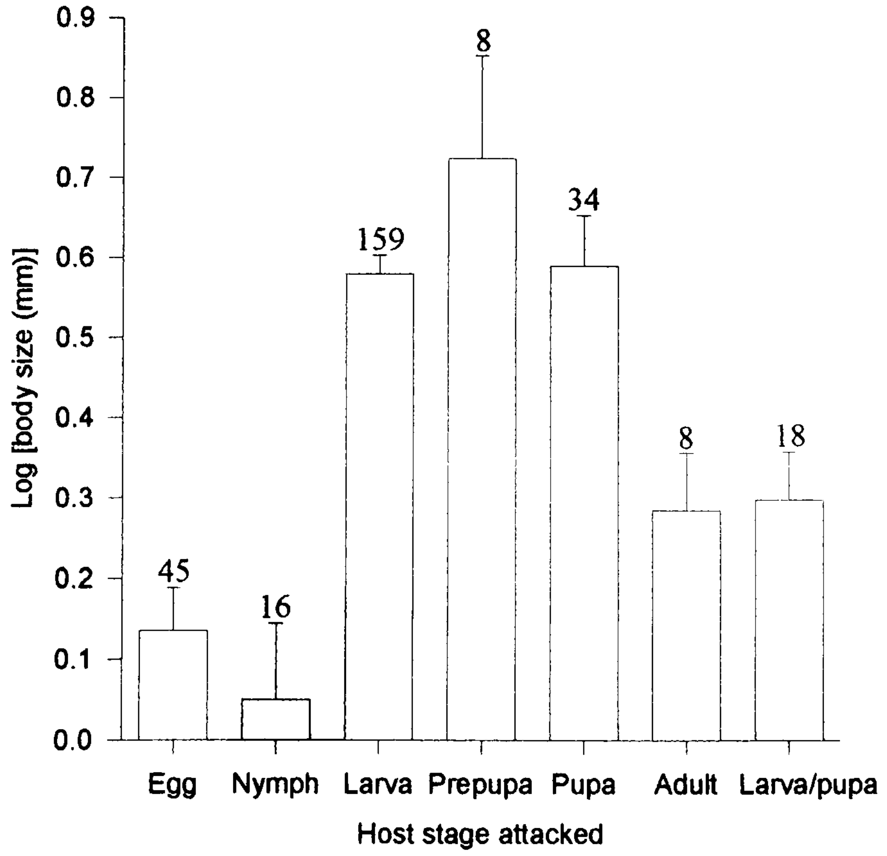


Figure 3.1: Mean (+SEM) log body size against host stage attacked across species. Numbers indicate sample sizes.

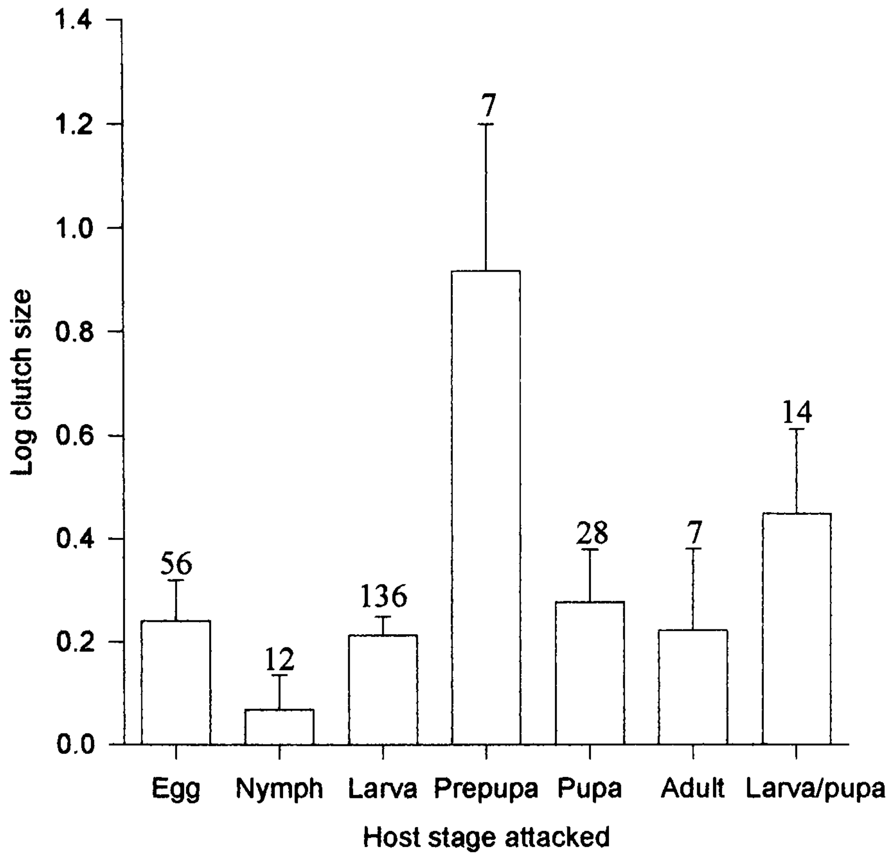


Figure 3.2: Mean (+SEM) log clutch size against host stage attacked across species. Numbers indicate sample sizes.

bodies, whilst those attacking pre-pupae had the largest bodies (Table 3.1).

Across species, there was a significant association between clutch size and host stage attacked (Kruskal-Wallis test, $\chi^2 = 26.20$, df = 11, $P = 0.006$). This relationship was also significant in all PR analyses (Table 3.1). Across species, parasitoids attacking nymphal host stages laid the smallest clutches and parasitoids attacking prepupal host stages laid the largest (Figure 3.2); egg, larval, pupal and adult parasitoids tended to lay similarly sized clutches. The PR analyses produced values of ρ ranging from 0.045 to 0.082 indicating very weak phylogenetic effects. PR estimates also showed that parasitoids attacking nymphs laid the smallest clutches, whilst parasitoids attacking prepupae laid the largest clutches (Table 3.1).

Across species, there was a significant negative association between clutch size and body size (Spearman $R = -0.211$, $n = 221$, $P = 0.002$). However, none of the PR analyses were significant (Table 3.1). Values of ρ (ranging from 0.352 to 0.476) indicate moderate phylogenetic effects. Investigation of CAIC contrasts revealed a strongly negative contrast at the root of the tree, which is likely to have been historically influential on the cross-species result. Unexpected contrasts were found in the conservative phylogeny between *Mesochorus agilis* (Mesochorinae) and *Lophyroplectus oblongopunctatus* (Scolobatinae) (Ichneumonidae), and between species of Cremastinae and Metopiinae (Ichneumonidae) within the resolved phylogeny. In both cases there have been large changes in body size without any change in clutch size (all species are solitary). Variation in host size seems a likely reason. The above analysis was repeated controlling for host stage attacked, a possible confounding variable. Across species, there was a significant interaction between clutch size and host stage attacked on body size ($F = 2.31$, df = 8, 190, $P = 0.022$); relationships were more negative for larval and pupal parasitoids than for others (Figure 3.3). However, all phylogenetic regressions remained non-significant (Table 3.1). Again phylogenetic effects were apparent, with values of ρ ranging 0.192 to 0.500.

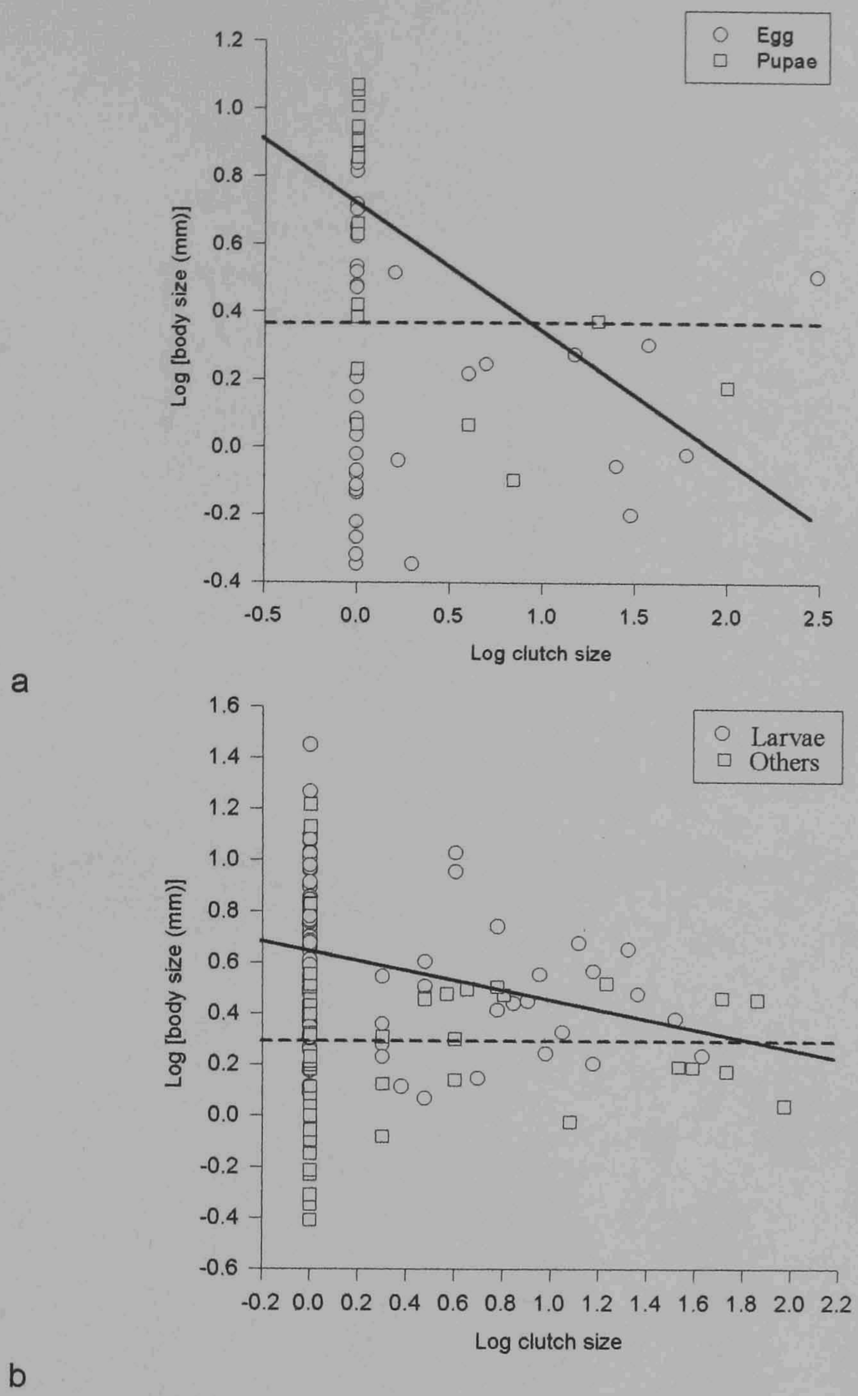


Figure 3.3: Log body size against log clutch size across species. Solid lines are regressions for (a) egg parasitoids, and (b) larval parasitoids. Dotted lines are regressions for (a) pupal parasitoids, and (b) parasitoids attacking other host stages.

Across species, solitary species had larger bodies than gregarious species (t-test, t = 2.95, df = 219, P = 0.001), but all PR analyses were non-significant, with ρ values ranging from 0.352 to 0.476. One contrast influential in the cross species result was found at the root of the tree; higher taxa with larger bodies tended to be solitary. One unexpected negative contrast involved species within the subfamily Encyrtinae (Chalcidoidea: Encyrtidae). Some of the gregarious species within this subfamily have very large body sizes in comparison to the solitary species. This is likely to be due to variation in host size: the large bodied gregarious species attack larval/pupal host stages, which are amongst the largest host stages attacked.

Across species, a significant interaction emerged between solitary and gregarious development and host stage attacked on body size (Figure 3.4). Solitary parasitoids have much larger bodies than gregarious ones attacking larval and pupal host stages. However, solitary parasitoids attacking both larval and pupal host stages have smaller body sizes than gregarious ones. When controlling for host stage attacked, solitary / gregarious development now significantly affected body size in one (Conservative cladogram, F = 2.43, df = 5, 83, P = 0.041),

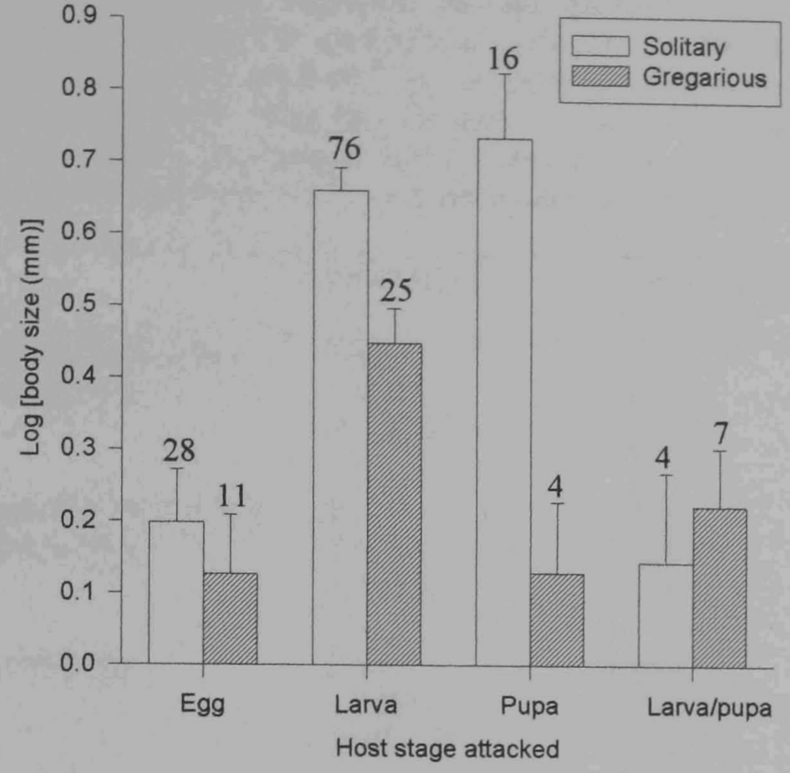


Figure 3.4: Mean (+SEM) log body size against host stage attacked, for solitary and gregarious wasp species. Numbers indicate sample sizes.

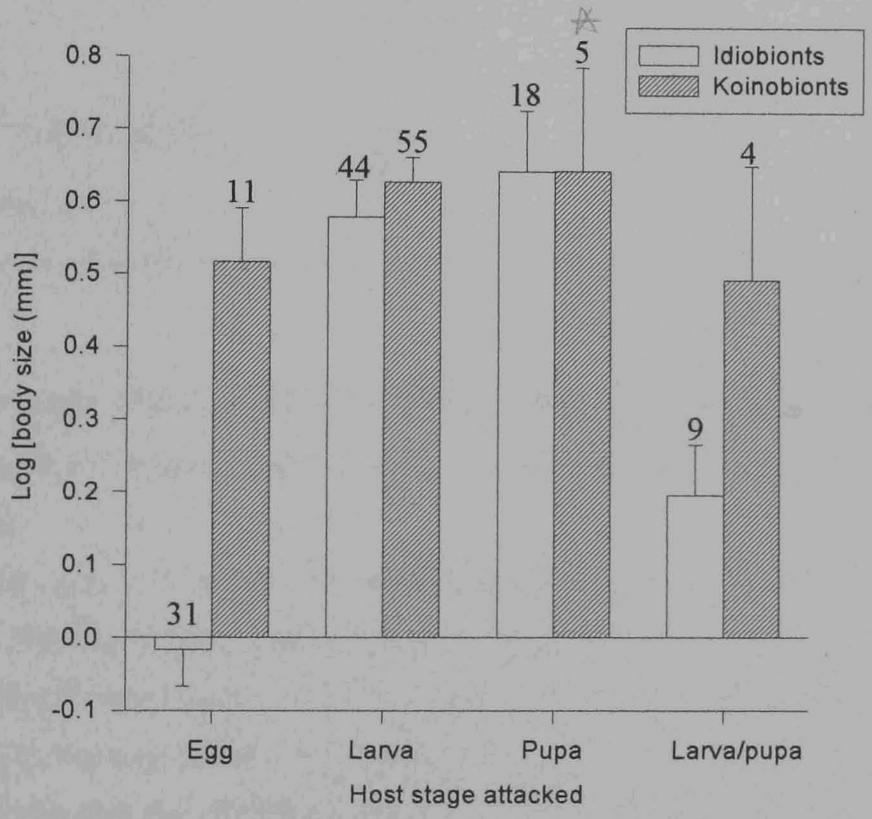


Figure 3.5: Mean (+SEM) log body size against host stage attacked, for idiobiont and koinobiont wasp species. Numbers indicate sample sizes.

but not the other two PR analyses, although these two were much more significant than previously.

3.4.2 Body size, clutch size and development mode

Across species, when controlling for host-stage attacked, there was a significant effect of development mode on body size (F = 6.32, df = 1, 194, P = 0.013) and also a significant interaction (F = 3.42, df = 6, 194, P = 0.003). Here koinobionts are larger bodied than idiobionts

Table 3.2: Phylogenetic regression results for body size, clutch size, development mode, and latitude (* $P < 0.05$ $^{**}P < 0.001$). Numbers denote regression estimates or ρ values (italics). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r - response variable, e – explanatory variable, c – control variable. E – egg, N – nymph, L – larva, Pr – prepupa, P – pupa, A – adult, Cs - clutch size, S – solitary, G – gregarious, I – idiobiont, K - koinobiont, Te – temperate, Tr - tropical. Unless otherwise stated all analyses were carried out using the full data set.

Analyses	Taxonomy	Conservative cladogram	Resolved cladogram
Body size (r), development mode (e), host stage attacked (c)	*0.526*	*0.260*	*0.526*
	0.000 I	0.000 I	0.000 I
	-0.040 K	0.022 K	-0.046 K
Clutch size (r), development mode (e), host stage attacked (c)	*0.100*	*0.055*	*0.111*
	0.000 I	0.000 I	0.000 I
	0.081 K	0.035 K	0.052 K
Body size (r), geographic distribution (e)	*0.334*	*0.288*	*0.334*
	0.000Te	0.000Te	0.000Te
	-0.022 Tr	-0.032 Tr	-0.018 Tr
Body size (r), geographic distribution (e) (Ichneumonidae species only)	*0.399*	*0.003*	*0.045*
	0.000 Te	0.000 Te	0.000 Te
	0.050 Tr	0.087 Tr	0.084 Tr
Clutch size (r) and geographic distribution (e)	*0.045*	*0.037*	*0.082*
	0.000 Te	0.000 Te	0.000 Te
	0.120 Tr	0.292 Tr	0.291 Tr
Clutch size (r) and geographic distribution (e) (gregarious species only)	*0.009*	*0.002**	*0.002**
	0.000 Te	0.000 Te	0.000 Te
	0.298 Tr	0.292 Tr	0.291 Tr

on a given host stage (Figure 3.5), but mainly in egg and larval-pupal parasitoids. However, there was no significant effect in any of the PR analyses, with ρ values ranging from 0.260 to 0.526 (Table 3.2).

Within the egg parasitoids, influential positive CAIC contrasts were found at the root, with koinobionts having larger body sizes than idiobionts. An unexpected contrast, in which idiobionts increased in size relative to koinobionts, was found in the family Encyrtidae. The only koinobiont within this group has a very large clutch size, which may account for it having such a small body size in comparison to the idiobionts. For larval parasitoids, influential contrasts in the expected direction were found between the Rogadinae species and also between species of Braconinae (Ichneumonoidea: Braconidae). A contrast in the opposite direction was found within a subsection of the Ichneumonidae (subfamilies Mesochorinae, Porizontinae, and Scolobatinae). The koinobionts have smaller bodies than the only idiobiont species (*Olesicampe ratzeburgi*), which is very large (11.50 mm). This wasp is known to attack very large bodied hosts. A similar contrast is found between the Pimplinae and Cryptinae (Ichneumonidae). Two idiobiont species (*Rhyssa persuasoria* and *Pseudorhyssa maculicoxis*) are influential here, both using very large insect larvae as hosts. For pupal parasitoids, an influential contrast was found between species of Chalcidoidea. Two species within the tribe Entedontini (Chalcidoidea: Eulophidae: Entedoninae) provided the first unexpected contrast. The *Chrysocharis* species

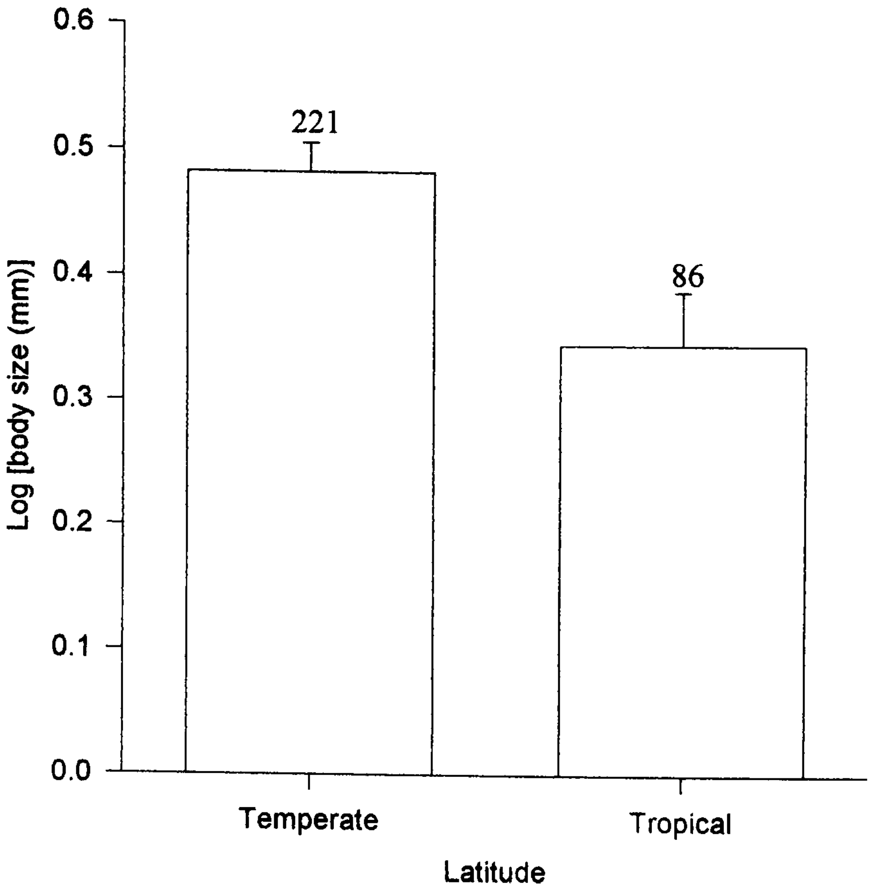


Figure 3.6: Mean (+SEM) log body size against latitudinal distribution, for all species. Numbers indicate sample sizes.

(1.49 – 1.89 mm) and *Pediobius acanthi* (1.62 mm) are idiobionts and a koinobiont respectively, all with similar body sizes. Another unexpected contrast was found in the subfamily Cryptinae (Ichneumonidae). Here *Agrothereutes adustus* has a slightly larger body size (8.25 mm) than the koinobiont species (4.25 – 7.50 mm). There was no effect of biosis on clutch size after controlling for host stage attacked, either across species (F = 0.21, df = 1, 183, P = 0.641) or in the PR analyses, where ρ values range from 0.055 to 0.111 (Table 3.2).

3.4.3 Body size, clutch size and latitude

Across species there was a significant association between body size and latitude, with larger bodies associated with temperate as opposed to tropical species (Kruskal-Wallis test, χ^2 = 9.08, df = 1, P = 0.003) (Figure 3.6). The relationship was however not significant in any PR analyses, with a range of ρ values from 0.288 to 0.334 (Table 3.2). A contrast in the expected direction was found at the root of the tree. A contrast in the opposite direction was found between Bethylidae species, the temperate species range from 1.33 – 3.50 mm in body length, whereas a tropical species (*Pristocera rufa*) is 6.05 mm long. *Pristocera rufa* attacks a weevil species that is 10 – 14 mm long (Baker 1976), whereas the other bethylid species in this contrast have very small hosts, up to 4mm in length (Mayhew and Hardy 1998). Another unexpected contrast is between the Braconinae species, which vary in clutch size, and this could confound the effect of latitude on body size. Another unexpected result is between two species of *Comperiella* (Chalcidoidea: Encyrtidae: Habrolepidini), the temperate species (*Comperiella bifasciata*) is 0.61 mm and the tropical species (*Comperiella unifasciata*) is 1.30 mm long. Both species are solitary therefore differences in host size are the likely reason for this contrast.

Because previous work has suggested that the large-bodied Ichneumonidae are more

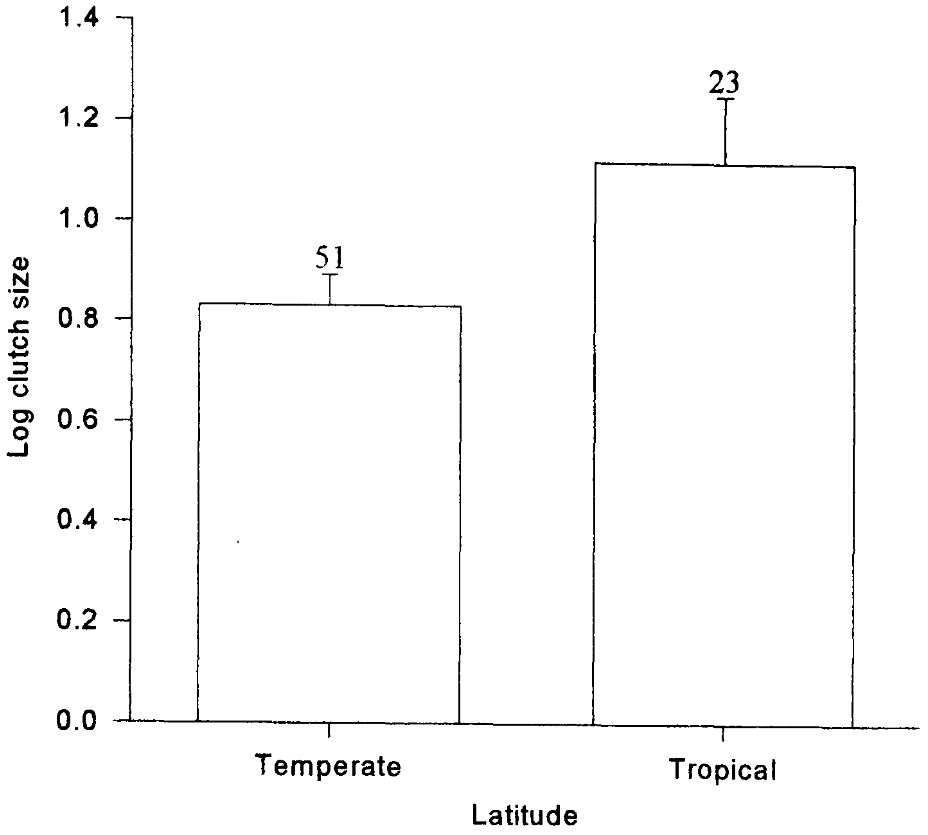


Figure 3.7: Mean (+SEM) log clutch size against latitudinal distribution, for gregarious species. Numbers indicate sample sizes.

species rich in some temperate than tropical latitudes, the cross-species result could simply be the result of sampling more ichneumonids at low latitudes. To test this possibility, we repeated the analysis without any ichneumonids. Across species there was still a significant association between body size and latitude, with larger bodies associated with temperate as opposed to tropical species (Kruskal-Wallis test, $\chi^2 = 5.08$, df = 1, $P = 0.024$). A cross-species analysis, with only the Ichneumonidae, was marginally non-significant but in the same direction (Kruskal-Wallis test, $\chi^2 = 2.97$, df = 1, $P = 0.085$). In PR, this relationship is also not significant (Table 3.2).

Across all species, clutch size was not significantly associated with latitude (Kruskal-Wallis test, $\chi^2 = 0.62$, df = 1, $P = 0.300$), although the relationship approached significance when only gregarious species were considered (Kruskal-Wallis test, $\chi^2 = 3.17$, df = 1, $P = 0.075$) (Figure 3.7). PR analyses for all species considered together are non-significant (Table 3.2). However, when analysing the subset of gregarious species, significance was obtained in the conservative and resolved phylogenies, whereas when using the taxonomic levels the result was marginally non-significant (Table 3.2). In all cases larger clutches are found in tropical species than in temperate species.

3.5 Discussion

3.5.1 General findings

The major finding of this study is that clutch size and body size are strongly associated with host stage attacked both in extant species phenotypes and in terms of evolutionary correlations. The evolutionary association between clutch size and latitude is also significant, for gregarious species. A number of other hypothesized trait associations are found across species, explaining more of the existing phenotypic variation, but without evidence that these are due to consistent evolutionary correlations. Instead, a few evolutionary events may have had disproportionate historical effects on present phenotypes. Below we discuss the implications of our findings for studies of life history evolution, and for comparative studies in general.

3.5.2 Body size, clutch size and host stage attacked

We have found that both body size and clutch size are associated with host stage attacked both across species and in phylogenetic analyses. This is to our knowledge an entirely novel finding. Parasitoid species attack a wide variety of different host types, both different taxonomic groups and / or species of different size, different host stages, and in different ecological niches (Gauld & Bolton 1988, Quicke 1997). Theoretical models (see Mayhew & Glaizot 2001), predict that the size of the host is a critical influence on both clutch size and body size across species: host size influences body size because it ultimately limits the amount of resource available for developing offspring, and hence also regulates the clutch sizes allocated to hosts by females. Solitary species by definition cannot vary their final brood size and hence their body size should be highly sensitive to host size, increasing with host size across species. Even gregarious populations, experiencing different average host sizes, may be selected to increase both the clutch size and the body size of offspring on larger hosts (Mayhew & Glaizot 2001).

Two previous comparative analyses provide evidence for these trends in the braconid genus *Apanteles* and the family Bethylidae respectively (Le Masurier 1987, Mayhew & Hardy 1998). In both, taxa body size and clutch size are positively correlated with host size as predicted by theoretical models. In the present study we have a much larger data set covering the taxonomic breadth of the parasitoid Hymenoptera, but we do not have information on the body sizes of the host species involved. However, unlike the above studies, host stage attacked varies widely in our data and is recorded. Some associations are concordant with expectations based on the relative sizes of the host stages; the largest body and clutch sizes are associated with relatively late host stages (prepupae) and the smallest bodies and clutches are associated with attacking eggs or the nymphs of hemimetabolous insects such as aphids, mealybugs and scale insects, which in general are very small.

Unexpected results are that some egg parasitoids are very large-bodied or lay large broods. These are koinobionts, which allow their hosts to grow considerably after maturation; for example, *Copidosoma* species (Encyrtidae) lay in host eggs but the offspring emerge from fully developed host larvae, and several hundred can develop polyembronically from a single host: these are amongst the largest brood sizes in any parasitoid. In addition, parasitoids attacking adult insects are not generally the largest bodied and do not lay the largest clutches. In fact, adult parasitism is rather rare amongst the parasitoid Hymenoptera and the host species concerned are not large: in our data they include braconids of the subfamily Euphorinae such as *Microctonus hyperodae*, which parasitizes the adult of the argentine stem weevil, and *Microterys flavus* (Encyrtidae), a parasitoid of scale insects.

Variation in body size is generally much more reflective of the size of the host stage attacked than clutch size (Figure 3.1, 3.2). For example, egg parasitoids are very much smaller than larval, prepupal and pupal parasitoids. In contrast, average clutch sizes are very similar for egg, larval, pupal and adult parasitoids. Theoretical models predict that body size will be much more responsive to variation in host size in species that display contest competition amongst their larvae (solitary species) than species that display scramble competition amongst their larvae (gregarious species). In our data the majority of species are solitary, and this is probably representative of the parasitoid Hymenoptera as a whole (see Mayhew 1998), so contest competition between larvae seems a likely reason for this result.

An alternative type of explanation might be that there are selection pressures on body size or clutch size that depend on the stage of host attacked but are independent of its size. For example, clutch size might be modified in response to the host's immune system, which might be more efficient in larvae than in eggs. Our data should now stimulate studies comparing the fitness consequences of body size and clutch size in parasitoids attacking different host stages.

Interestingly, in a previous comparative study of body size and clutch size (Mayhew & Hardy 1998), evolutionary correlations were non-significant over the entire phylogeny, but were significant over different parts of it, indicating perhaps that clutch size and body size differ in their evolutionary lability (see Strand 2000). In the present study, both variables are significantly correlated with host stage attacked over the entire phylogeny. One possible reason for this difference is that important changes in both variables occurred at the origin of major groups, which were not represented in the previous study. Intuitively, this seems likely, since the major groups of parasitoid Hymenoptera represent contrasting body and clutch sizes (for example Ichneumonoidea versus Chalcidoidea). These results therefore cast doubt on the generality of previous results on the lability of these traits, though they remain valid for bethylids.

Previous comparative work across families (Mayhew 1998) suggested that body size and clutch size were negatively evolutionarily associated, as expected if they trade-off for a given host size. In this study we find a negative correlation between the traits across species, but fail to find a significant evolutionary correlation, even after controlling for host stage attacked. One possible reason for the difference in our results is that the data of Mayhew (1998) represented all families, but did not investigate relationships between close relatives. In contrast, the present study does contain many contrasts between members of the same genus or closely related genera, but does not represent all major higher taxa. It is likely that differences in clutch size or body size, between close relatives, are also the result of confounding variables, which we are unable to control for here. This indicates that any association between body size and clutch size is probably dependent on a number of other variables (host stage attacked, host species size, development mode) remaining constant.

3.5.3 Body size, clutch size and development mode

We expected, as others have speculated (Godfray 1994), that body size would be related to development mode, because of the ability of koinobionts to allow their hosts to grow after parasitization. Mayhew and Blackburn (1999) failed to detect an evolutionary correlation between the two traits, but one possible confounding variable is the host stage attacked, which is highly variable across both koinobionts and idiobionts. After controlling for this, there is a significant association across species between development mode and body size, with koinobionts being larger than idiobionts attacking a given host stage. There is also a significant interaction, with the largest difference being amongst egg parasitoids. This makes intuitive sense, as the potential for hosts to increase in size is greatest if early host stages are attacked. However, once again there is no evidence that this is the result of a consistent evolutionary correlation. Examination of the contrasts revealed that variation in the size of the host species is likely to be the cause of the unexpected contrasts, like that found within the Ichneumonidae attacking larval host stages. There is no evidence that clutch size is related to development mode. This suggests that any fitness advantage of koinobiosis is not reaped through an increase in clutch size, but may be reaped though an increase in body size.

3.5.4 Body size, clutch size and latitude

We speculated that latitude might explain some of the variation in body size and clutch size in parasitoids, as it does in several other organisms. Our data on latitude are very crude, since species are simply coded in a binary fashion as either temperate or tropical. However, in many ways, this crude classification is powerful as it ensures that any contrasts are between species that differ markedly in the latitudinal extent of their ranges (see Cardillo 1999, 2002). Although we found a positive relationship between body size and latitude (Bergmann's rule) across species, this was not replicated in the phylogenetic analyses. At least some of the contrast variation is due to differences in clutch size and host size: for example in the Bethylidae.

Although there was not a significant across-species relationship between clutch size and latitude when all species were considered, the relationship did approach significance in the phylogenetic analyses. In a number of groups, such as the Ichneumonidae, clutch size is evolutionarily conserved and is nearly always one (solitary groups) (Mayhew 1998). If solitary species are removed from the analysis, such that we only consider gregarious species, which are generally regarded as having labile clutch sizes (Godfray 1994), then the significance of all analyses increases, and two of the phylogenetic regressions are now significant. Interestingly, the direction of this relationship (temperate species lay smaller clutches than tropical ones) is the opposite to that found in birds, but is that expected from the body size trends if clutch size and body size trade-off together.

Recently, there has been some interest in explaining latitudinal gradients in species richness by considering latitudinal gradients in life history traits. Specifically, if life history traits vary with latitude, they might in turn affect speciation or extinction rates at different latitudes, and hence species richness (Cardillo 2002). In this respect it is interesting that one group of parasitoids, the Ichneumonidae, which are generally large bodied and solitary, have often been observed to be less species rich in tropical than in some temperate latitudes (see Gaston & Blackburn 2000, Godfray 1994). Our studies raise the possibility that selection on life history traits, such as body size and clutch size, might contribute towards this trend. Previous work on explaining the lack of tropical ichneumonid diversity has concentrated on factors, such as host density declining in the tropics, that are rather general to parasitoids. However, there is good evidence that the decline in tropical diversity seen in ichneumonids is not general to all parasitoids (see Hanson & Gauld 1997). Explanations focussing on traits particular to ichneumonids should hold much more prospect of success. Large body size and small clutch size are two such traits.

3.5.5 Analytical issues

Our analyses have implications for comparative methodology and for research on the phylogenetic relationships of parasitoid wasps. One argument for not carrying out phylogenetic comparative analyses is that they generally give the same answer as cross-species analyses (see Ricklefs & Starck 1996). However, several of our analyses give significant results across species, but not when phylogeny is taken into account. In many cases values of ρ are moderately high (although never very high), indicating some phylogenetic dependence. In contrast, where there is agreement between cross-species and PR analyses, the values of ρ are often very small, indicating a lack of phylogenetic dependence. In addition, we even find one case of a significant phylogenetic analysis when the cross species analysis is non-significant! Therefore use of phylogeny is justified. Another reason to abandon phylogenetic analysis is if there is no phylogenetic dependence in the data (see Abouheif 1999). However, phylogenetic dependence is not absent from our data.

The earlier studies on the current data have been criticized due to the fact that only a poorly resolved taxonomy was used. This has the effect of lowering power, and also of possibly introducing bias if the taxonomy is not an accurate reflection of phylogeny. We have conducted analyses including the most up-to-date phylogenetic information. The result has been to improve the power of the analyses, since the number of nodes over which we can calculate contrasts has increased. The relationship between body size and host stage attacked is only marginally significant using taxonomy, but is highly significant in both analyses using phylogenetic evidence. In addition, the relationship between clutch size and latitude in gregarious species is significant in both analyses incorporating phylogenetic studies, but is marginally non-significant using taxonomy alone. Thus, only about a decade of phylogenetic work has produced significant benefits for comparative studies (as long as these studies are better representative of phylogeny than the taxonomy alone).

3.5.6 Conclusion

Finally, we put the present results in a wider context. In many organisms adult body size is probably determined by organisms deciding on the optimal time to divert resources away from growth and into reproduction (see Charnov 1993, Gemmill *et al.* 1999, Kozlowski & Gawelczyk 2002, Kozlowski & Weiner 1996, Stearns 1992). In these cases variation in mortality rates are likely to be the most important factor causing variation in maturation time, and hence body size. In contrast, with some possible exceptions (see Harvey *et al.* 2000), studies to date suggest that the most important biological factors affecting parasitoid body size are the size of the host when it is finally consumed, which ultimately limits how large a parasitoid larva can grow, and the clutch size per host, which affects how many offspring the host must be divided between. Both these are parental optimization decisions. These selection pressures, although different from those in many other organisms, may not be unique to parasitoid Hymenoptera; many other insects develop by consuming small highly depletable resource patches, and the possibility remains that body size and clutch size in many other insects, and hence a large proportion of the planet's species, are determined in much the same way.

Chapter 4: A comparative analysis of life history evolution across the Ichneumonoidea (Hymenoptera)

Ruth E. Traynor & Peter J. Mayhew

4.1 Abstract

1. A large comparative data set and recent phylogenetic information are used to investigate associations between life history traits across the Ichneumonoidea (Hymenoptera), a species rich superfamily of parasitoids.
2. A degree of support for the dichotomous hypothesis is found; idiobionts / ectoparasitoids have one suite of life history traits and koinobionts / endoparasitoids have an opposing suite of traits. Adult ectoparasitoids / idiobionts live longer than adult endoparasitoids / koinobionts, and endoparasitoids are more fecund than ectoparasitoids. Across species, koinobionts are more associated with hosts found in exposed locations, whereas idiobionts are more associated with hosts in semi-concealed locations. No evidence is found to suggest that idiobionts / ectoparasitoids have broader host ranges, shorter preadult lifespans, or larger eggs than koinobionts / endoparasitoids.
3. Trade-offs are identified between parasitoid body size and brood size, and between fecundity and egg volume. Positive relationships are found between parasitoid body length and a) preadult lifespan, b) adult longevity and c) egg size.
4. Parasitoid and host body sizes are positively correlated. Brood size is found to be positively associated with host body length across species, when parasitoid body length is controlled for. Solitary species are larger, but are associated with smaller hosts than gregarious species. Gregarious species are more associated with external rather than internal pupation sites.
5. Several variables are correlated with geographic range; parasitoids that are studied more frequently have larger known geographic ranges. After controlling for the degree of study, geographic range is positively associated with a) temperate versus tropical distribution, b) host geographic range and c) the number of host species attacked. Across species, temperate parasitoids have longer preadult lifespans than tropical parasitoids and larger parasitoids have larger geographic ranges.
6. Parasitoids that have been studied more attack more host species. After controlling for the degree of study, temperate parasitoids are found to attack more host species than tropical parasitoids, as do parasitoids with larger geographic ranges. Species attacking larval host stages attack the smallest number of host species, whereas those attacking nymphal host stages attack the greatest number of host species.
7. Our results suggest that several biological transitions regulate life history variation in the group; between i) endoparasitism and ectoparasitism, ii) koinobiosis and idiobiosis, iii) hosts with different ecological niches and life histories.

4.2 Introduction

Evolutionary ecologists are interested in explaining interspecific life history variation across species and this has been addressed in a number of ways. Theoretical models are used to formulate hypotheses which can identify constraints and selective pressures, and to predict associations identified in comparative studies, which investigate inter-correlations between traits. In return, comparative studies can suggest assumptions or predictions that theory should aim to meet. Comparative studies on mammalian life history traits (for example Gittleman 1986, Harvey & Clutton-Brock 1985, Harvey & Zammuto 1985, Read & Harvey 1989, Wootton 1987) have been used to construct theoretical models successfully predicting variation across many life history traits (see Charnov 1991, 1993, 2001, Kozlowski & Weiner 1996). In many instances, body size has been identified as an important correlate of life history variation for both vertebrates and invertebrates (see Calder 1984, King 1989, Stearns 1989). However, most groups of organisms lack a single life history model that can successfully predict or explain life history variation across a number of traits.

Parasitoids are insects that, whilst free living as adults, develop to maturity by feeding on and killing an arthropod host. Parasitoids have long been known as very good study subjects for addressing life history evolution (see Godfray 1994, Harvey *et al.* 2000, Harvey & Strand 2002), as they normally obtain their resources for development from a single source, the host. They are extremely diverse and exhibit much greater developmental variation than any other arthropod group (Strand & Grbic 1997).

Previous studies on interspecific parasitoid life history variation have mainly addressed the evolution of two traits, namely idiobiosis / koinobiosis and ectoparasitism / endoparasitism (the dichotomous hypothesis) (for example Gauld 1988, Mayhew & Blackburn 1999, Shaw 1983, Shaw & Huddleston 1991, Whitfield 1992). Idiobionts are parasitoids that permanently paralyse their hosts, using lethal or paralysing venom at the time of oviposition, with the parasitoid larva rapidly consuming the host. Koinobionts temporarily paralyse their host but allow it to resume development for a time post-parasitism. The parasitoid larva remains inactive until the host reaches a suitable stage for final consumption to take place. Ectoparasitoids oviposit on or near their host and the parasitoid larvae complete development outside the host's body. Endoparasitoids oviposit into their host's body, where the developing larva consumes the host's haemolymph and / or tissues internally. Endoparasitoids normally complete their development internally to the host, but can sometimes complete development externally.

Comparative evidence suggests that idiobiosis is associated with ectoparasitism, and koinobiosis with endoparasitism (see Mayhew & Blackburn 1999). Various studies also suggest that idiobionts / ectoparasitoids have lower fecundity (Blackburn 1991b, Price 1974), shorter preadult lifespan (Blackburn 1991a), larger eggs (Godfray 1994, Mayhew & Blackburn 1999, Shaw & Huddleston 1991), more concealed hosts (Gauld 1988, Godfray 1994, Quicke 1997), longer adult lifespan (Mayhew & Blackburn 1999) and a broader host range than koinobionts / endoparasitoids (Askew & Shaw 1986, Müller *et al.* 1999, Sato 1990, Sheehan & Hawkins 1991).

Blackburn (1991a,b) found that parasitoid preadult lifespan and egg size were correlated with body size, that more fecund taxa laid smaller eggs than less fecund taxa and that there was a positive correlation between adult body size and fecundity, when controlling for egg size. He also found temperate parasitoid species had longer preadult lifespans than tropical species. However, many traits were not correlated to body size in the way seen in other taxa.

Askew (1994) stated that host range is the most variable biological life history trait of parasitoids, where the majority of species are not host-specific. Instead many are polyphagous, exploiting hosts from different orders in similar habitats, whereas others may be restricted to a single host genus or family. The three most important determinants of host range in parasitoids have been identified as mode of development, phylogeny, and shared ecology (see Shaw 1994, Strand & Obrycki 1996). Koinobionts are hypothesized to have narrower host ranges than idiobionts (see Askew & Shaw 1986) and this was found to be the case by Sheehan and Hawkins (1991) as well as by Shaw (1994). Phylogenetic history has been used to predict which taxa are suitable as hosts for a given parasitoid species (Gauld 1986).

Other work has focused on parasitoid body size and clutch size in relation to host size. Families containing gregarious species have been shown to be smaller bodied than their sister taxa that are exclusively solitary (Mayhew 1998). Comparative studies have revealed that within, the braconid genus *Apanteles* (Le Masurier 1987), host size is positively correlated with both clutch size and body size in gregarious species, this result was also found in the Bethylidae by Mayhew and Hardy (1998). Some theoretical models (Mayhew & Glaziot 2001) predict this observed outcome.

The largest superfamily within the Hymenoptera is that of the Ichneumonoidea. It is estimated that more than 150,000 species are found within its two extant families: the Braconidae and the Ichneumonidae (Belshaw *et al.* 1998). The Ichneumonoidea are model organisms in evolutionary biology (Godfray 1994, Quicke 1997) and already have a great wealth of information available, as many are biological control agents (Greathead 1975). Several higher level phylogenetic hypotheses have been put forward for the Braconidae and Ichneumonidae (see Belshaw *et al.* 1998, Belshaw *et al.* 2003, Dowton 1999, Dowton & Austin 1998, Dowton *et al.* 1998, Quicke *et al.* 2000). The Ichneumonoidea are suitable for a comparative study, as phylogenetic estimates are available for each family, as well as a wealth of life history information available in the literature.

Comparative work by Blackburn (1991a/b) across the whole parasitoid Hymenoptera has been criticised by Godfray (1994, p. 320) as a 'very sparse representation of a very diverse group of wasps, with a rather poorly resolved taxonomy'. It was suggested that a more complete and standardised data set would have led to more significant associations being found. The current data set fulfils these criteria better than Blackburn's data set, includes novel variables (host size, host range, and geographic range data) and can provide us with more useful information on life history evolution. We use both traditional taxonomy and recent phylogenetic information. Differences in outcome allow us to judge the sensitivity of the results to the phylogenetic assumptions, as well as the added value of the recent phylogenetic work.

We test the following life history hypotheses on a large data set for the Ichneumonoidea: derived from a) knowledge of parasitoid biology and b) studies of other organisms.

1. Idiobiosis / koinobiosis and ectoparasitism / endoparasitism have been identified as important life history traits that predict a suite of other parasitoid life history traits, known as the dichotomous hypothesis (see Askew 1975, Askew & Shaw 1986, Godfray 1994, Jervis *et al.* 2001, Mayhew & Blackburn 1999). Idiobionts / ectoparasitoids should be more associated with more concealed hosts, a greater number of host species, shorter preadult lifespan, longer adult lifespan, lower fecundity and larger eggs than koinobionts / endoparasitoids.
2. We expect to find allometric relationships between egg volume and body size (see Charnov 1991, 1993, Kozlowski & Weiner 1997). We expect to find a trade-off between egg volume and fecundity (see Blackburn 1991b, Strand 2000), where a reduction in egg size will lead to an increase in fecundity.
3. Body size and brood size trade-off against each other and are positively correlated with host size (see Hardy *et al.* 1992, Mayhew & Glaziot 2001, see also chapter 3).
4. Parasitoid geographic range / distribution might be correlated with several parasitoid life history traits. There may be a positive correlation between parasitoid body size and latitude (Bergmann's rule, see Gaston & Blackburn 2000). Preadult lifespan is expected to be longer at lower temperatures, for example in temperate rather than tropical areas (Blackburn 1991a). Parasitoid geographic range may increase with latitude (Rapoport's rule) (see Stevens 1989), as found in birds in the Holarctic region (Cardillo 2002).
5. Parasitoid host range is expected to be greater for ectoparasitoids / idiobionts rather than for endoparasitoids / koinobionts (see Askew & Shaw 1986, Hawkins 1994), as the latter parasitoids are in more intimate contact with their hosts for longer periods of time, which is likely to necessitate a greater degree of specialization. The resource fragmentation hypothesis (see Janzen 1981, Janzen & Pond 1975) suggests that specialized species should be less abundant in the tropics, therefore we may expect host range to increase towards the tropics. Parasitoid geographic range may also affect host range, with parasitoids with larger geographic ranges attacking a wider range of hosts.

4.3 Methods

4.3.1 Data

The data set comprises information for 382 Ichneumonoidea parasitoid species, representing 26 braconid subfamilies and 25 ichneumonid subfamilies (Table 4.1, Appendix 5). The data was derived mainly from the published literature, although some parasitoid and host adult body length data were obtained through the measurement of specimens at the Natural History Museum, London. Parasitoid species were chosen for investigation by meeting certain criteria. Several research papers had to be available for them, and to achieve a good taxonomic spread we tried to represent as many subfamilies as possible. Literature searching was eventually called to a halt due to time limitations and diminishing returns.

Table 4.1: Number of species representing different subfamilies in the data.

Family Braconidae		Family Ichneumonidae	
Agathidinae	21	Acaenitinae	2
Alysiinae	13	Adelognathinae	5
Aphidiinae	18	Agriotypinae	16
Blacinae	3	Anomaloninae	2
Braconinae	15	Banchinae	4
Cardiochilinae	2	Campopleginae	32
Charmontinae	3	Collyriinae	1
Cheloninae	12	Cremastinae	5
Doryctinae	8	Cryptinae	20
Euphorinae	11	Ctenopelmatinae	6
Exothecinae	6	Diplazontinae	6
Gnamptodontinae	1	Eucerotinae	2
Helconinae	7	Ichneumoninae	13
Homolobinae	1	Labeninae	1
Hormiinae	2	Mesochorinae	2
Ichneutinae	2	Metopiinae	6
Macrocentrinae	4	Neorhacodinae	1
Microgasterinae	47	Ophioninae	2
Microtypinae	2	Orthopelmatinae	2
Miracinae	2	Pimplinae	26
Opiinae	17	Poemiinae	1
Orgilinae	2	Rhyssinae	2
Pambolinae	1	Stilbopinae	3
Rhysipolinae	3	Tryphoninae	6
Rhyssalinae	2	Xoridinae	2
Rogadinae	9		

The variables investigated are as follows:

Egg volume (mm^3): Calculated from the equation

$$\text{Egg volume} = 4/3\pi \times a \times b^2$$

Where a = half the egg length and b = half the maximum egg width, which assumes an ovoid egg shape (see Blackburn 1991b).

Preadult lifespan (days): Total number of days for egg, larval and pupal development.

Parasitoid adult body length (mm): Excluding antennae (and ovipositor where necessary).

Adult longevity (days): The mean longevity per parasitoid species.

Brood size: The mean number of parasitoid offspring completing development per individual host.

Fecundity: The maximum number of eggs reported to be laid by an individual of the species.

Parasitism: Ectoparasitoids oviposit on or near their host and the parasitoid larvae complete development outside the host's body. Endoparasitoids oviposit into their host's body, where the developing larvae consume the host's haemolymph and or tissues internally. Endoparasitoids normally complete their development internally to the host, but can sometimes complete development externally to the host.

Solitary or gregarious development: Solitary wasps are those whereby only a single individual successfully completes development per host. Gregarious development is when several offspring can successfully complete development on each host.

Development mode: Idiobionts permanently paralyse their hosts, using lethal or paralysing venom at the time of oviposition, with the parasitoid larva rapidly consuming the host. Koinobionts temporarily paralyse their host but allow it to resume development for a time post-parasitism. The parasitoid larva remains inactive until the host reaches a suitable stage for final consumption to take place.

Pupation site (4 states): Inside the host's body, under the host's body (for example mummified aphid), inside the host's puparium but outside it's body, external to the host's body and puparium; it was also recorded as 2 states either inside the host's body or external to the host's body.

Parasitoid geographic range (km^2): A list of countries that each species was recorded from in the literature. The area (km^2) for each country was obtained from the national geographic society at http://plasma.nationalgeographic.com/mapmachine/countryprofiles.html and the total area of the list of countries that each parasitoid was recorded from was calculated.

Parasitoid geographic distribution: Temperate species are located in countries that are found north of 23.5^0N or south of 23.5^0S. Tropical species are located in countries that are found between 23.5^0S and 23.5^0N. Species found in both temperate and tropical countries were recorded as such.

Parasitoid mean latitude: Calculated by dividing the maximum plus the minimum absolute latitude, of the countries where the parasitoid is found, by two.

Host stage attacked (6 states): Egg, nymph, larva, prepupa, pupa, adult; it was also recorded as 15 states which included combinations of the above host stages (see Appendix 5).

Host exposure: Exposed hosts are fully exposed and occupy no structural refuges, semi-concealed hosts are those that have a slight refuge within their shelter but remain susceptible to parasitoid attack (for example leaf-miners), and concealed hosts are those that are physically protected and generally well concealed (for example borers).

Host niche: External, leaf-miner, leaf-roller, web-spinner, casebearer, galler, borer, root feeder, predator, nest, in vegetation or leaf litter, pollen feeder, in stored grain, decaying plant material, frugivore, saprotroph.

Host adult body length (mm): Excluding antennae (and ovipositor where necessary).

Host geographic range (km^2): Compiled per host species from the parasitoid literature, as defined in parasitoid geographic range.

Parasitoid host range: The total number of host species recorded per parasitoid species. Taken from the literature used in this study.

Degree of study: The total number of pages recorded per parasitoid species. Taken from the literature used in this study, a page is counted if it mentions the parasitoid species of interest. Some parasitoid species have been studied more frequently than other species, for example those used for biological control, or those with a wider geographic range. This variable is used as a control variable.

4.3.2 Analysis

All the continuous variables (except mean latitude) were $\log_{10}$ transformed prior to analysis to meet statistical assumptions (see Garland *et al.* 1992).

Hypotheses were first tested by analysis of the raw data across species. To test the associations between a) two continuous variables the Pearson or Spearman's rank correlation was used, b) two categorical variables a Pearson Chi-squared test was carried out, c) a continuous and a categorical variable, a t-test or Kruskal-Wallis test was carried out, d) two continuous variables (controlling for a continuous variable for both), Partial correlation was carried out and d) a continuous and categorical variable (controlling for either a continuous or categorical variable) a two-way ANOVA was carried out. Cross-species analyses allow one to predict something about the value of one species trait in the data set given knowledge of another trait. Any evolutionary correlations between traits (associations between the evolution in one trait and the evolution in another trait) produce these phenotypic correlations. Phenotypic correlations can reflect evolutionary correlations relatively accurately if the data has no phylogenetic dependence, such that trait values in each species are relatively independent of those in others (Freckleton *et al.* 2002, Price 1997). However, if there is a degree of phylogenetic dependence in the data then phylogenetic information needs to be incorporated into the analysis, in order to detect evolutionary correlations. For this Phylogenetic Regression (PR) (Grafen 1989) was used.

Phylogenetic Regression (PR) is an independent contrast method that calculates, from the raw species data, sets of contrasts that represent differences between sister-taxa in the phylogeny, and are evolutionarily independent. To adopt an appropriate evolutionary model, which is important if evolutionary correlations are to be detected (see Harvey & Rambaut 2000, Freckleton *et al.* 2002, Price 1997), PR scales the branch lengths of the phylogeny using a parameter, ρ, estimated from the data and the phylogenetic topology. In order to adopt the appropriate model of evolution, the parameter should reflect the degree of phylogenetic independence of the data.

Control variables, as in any ANOVA or regression, can only have an affect on the response variable in PR analysis. However, confounding variables sometimes affect both the response and explanatory variables. For example, this was the case when we studied how host geographic range affects parasitoid geographic range, controlling for the degree of study. In such cases the 'residual' values were calculated and used instead of the 'normal' log values for the explanatory variable. The 'residual' values were calculated by fitting the PR slopes through the cross-species data for the variable concerned. The calculations are given below.

Taxonomic PR analysis: log parasitoid geographic range – (log parasitoid geographic range (0.495) x log degree of study); log host geographic range – (log host geographic range (0.217) x log degree of study); log host range – (log host range (0.313) x log degree of study). Composite cladogram PR analysis: log parasitoid geographic range – (log parasitoid geographic range (0.514) x log degree of study); log host geographic range – (log host geographic range (0.239) x log degree of study); log hosts range – (log host range (0.306) x log degree of study).

Unless otherwise stated all analyses, both across species and in the PR, were carried out on the full species data set, where information for the required variables was available.

Sequential Bonferroni correction (Rice 1989) was carried out separately for the a) cross-species, b) taxonomic PR, and c) composite cladogram PR analyses. This method assumes that, for each test carried out in each type of analysis, the same null hypothesis (that there are no significant results as a whole) is being tested. The correction reduces the critical level of significance when multiple comparisons are carried out because of the increased chance of a Type I error (a false positive). In the results section, tests that are significant prior to sequential Bonferroni correction are not significant afterwards, unless otherwise stated in the test or tables. As 66 tests were carried out in the cross-species analysis, one would expect 3.3 tests to be significant at $P < 0.05$ by chance alone, but 15 are found. As 83 tests were carried out in the taxonomic and composite cladogram PR analyses, one would expect 4.15 tests per analysis to be significant at $P < 0.05$ by chance alone, for the taxonomic analysis 11 are found, and for the composite cladogram analysis 12 are found.

4.3.3 Phylogenetic assumptions

We performed phylogenetic analyses using traditional taxonomy (Appendix 6) and by constructing a composite cladogram from recent phylogenetic analyses (Appendix 7). However, taxonomic information was used for those groups that had no phylogenetic estimates available. To construct the composite cladogram we searched for those studies which had cladograms that were a) well supported (with high bootstrap values), b) well resolved (with few polytomies) and c) had the greatest required taxonomic coverage.

For the composite cladogram, the Braconidae subfamily phylogeny is taken from Figure 1a of Dowton *et al.* (2002). This figure was chosen, as it is a relatively complete subfamily phylogeny (although it is missing the Microtypinae and the Rhysipolinae) based on molecular and morphological data and published with few polytomies. There are however two exceptions within this figure. Firstly, the Homolobinae and Microtypinae are placed as sister taxa according to Figure 1 of Belshaw et al. (2003). Secondly, in order to include the Rhysipolinae we used Figure 5 of Zaldivar-Riveron *et al.* (2004). Therefore the group containing Rogadinae, Hormiinae, Pambolinae, Rhysipolinae, Doryctinae, Braconinae, Exothecinae and Gnamptodontinae is instead taken to be an unresolved polytomy.

The Ichneumonidae subfamily phylogeny (for the Xoridinae, Labeninae, Collyriinae, Acaenitinae, Eucerotinae, Cryptinae, Ichneumoninae and Adelognathinae) is taken from Belshaw and Quicke (2002). There are however two exceptions. Firstly, the Diplazontinae, Pimplinae, Poemiinae and Rhyssinae are placed within a clade according to Figure 33 of Wahl and Gauld (1998) as each of these subfamilies are split up in many locations according to Figure 8 of Belshaw and Quicke (2002). However, the Acaenitinae remained as the sister group to the Collyriinae according to Figure 8 of Belshaw and Quicke (2002) rather than being included within this polytomy. This is to reduce the number of polytomies within the phylogeny. Secondly, the Agriotypinae are placed as sister group to the clade containing the Pimpliformes and Ichneumoniformes according to Figure 1 of Belshaw et al. (2003), as the Agriotypinae are not included in Figure 8 of Belshaw and Quicke (2002). The section of Figure 8 of Belshaw and Quicke (2002) (mentioned above) is chosen as it is fairly well resolved, unfortunately the remainder of the phylogeny is less well resolved, and also has low bootstrap values. The phylogeny for the remaining subfamilies (the Campopleginae, Cremastinae, Ophioninae, Anomaloninae, Banchinae, Mesochorinae, Ctenopelmatinae, Metopiinae, Neorhacodinae, Tryphoninae, Stilbopinae and Orthopelmatinae) is taken from Figure 3 of Quicke et al. (2000). This is used to try to resolve as much of the subfamily level of the phylogeny, this phylogeny is a strict consensus tree based on two previous cladograms and it has high bootstrap values.

The number of nodes for these two different estimates of phylogeny are 515 and 551 for the taxonomy and the composite cladogram respectively, which represents the maximum number of contrasts that could be made in the data, if all variables were represented for all species. Although the cladogram potentially gives more power (more nodes) the increase in power is modest, as most phylogenetic studies have been conducted at subfamily level. However, one would expect them to give a more accurate depiction of phylogeny than taxonomy itself.

4.4 Results

4.4.1 General findings

Table 4.2: The number of parasitoid species associated with each host order.

Host order	Braconidae	Ichneumonidae
Lepidoptera	125	75
Hymenoptera	8	45
Diptera	29	9
Coleoptera	25	8
Hemiptera	18	0
Trichoptera	0	16
Araneae	0	6

Table 4.3: Parasitoid adult body lengths (mm) in the data set.

Body length (mm)	Braconidae	Ichneumonidae
Mean±SEM	3.215±0.143	7.735±0.353
Median	2.9	7.1
Range	0.7 to 11.87	2.4 to 28.15

Table 4.4: Numbers of braconid and ichneumonid species exhibiting different life history trait states.

Life history traits	Braconidae	Ichneumonidae
Ectoparasitism	24	57
Endoparasitism	102	65
Idiobiosis	13	36
Koinobiosis	86	39
Solitary larval development	90	68
Gregarious larval development	24	9
Temperate distribution	108	117
Tropical distribution	6	6
Temperate & tropical distribution	44	22
Egg host stage attacked	12	4
Nymph host stage attacked	1	2
Larva host stage attacked	122	78
Prepupa host stage attacked	0	4
Pupa host stage attacked	0	21
Adult host stage attacked	6	0

Both the braconids and ichneumonids included in the data most frequently attack hosts within the order Lepidoptera (Table 4.2). Braconids frequently attack hosts within the Diptera, Coleoptera and Hemiptera. Ichneumonids frequently attack Hymenopteran hosts, as well as Trichoptera hosts. The ichneumonids range from 2.4 to 28.15mm in length, with a mean of 7.735 mm, whereas the braconids range from 0.7 to 11.87mm in length, with a mean of 3.215mm (Table 4.3). The majority of braconids studied are endoparasitoids and koinobionts, whereas there are approximately even numbers of ichneumonids displaying both ecto- and endoparasitism and idio- and koinobiosis, and the majority of braconids and ichneumonids are solitary in development (Table 4.4). Both families are poorly represented by tropical species, and both families mostly attack larval host stages, the ichneumonids are the only species found attacking pupal host stages, whereas the braconid species are the only ones found attacking adult host stages (Table 4.4).

Table 4.5: The number of species exhibiting different states of parasitism and biosis.

	Idiobiosis	Koinobiosis	Total
Ectoparasitism	34	10	44
Endoparasitism	7	105	112
Total	41	115	156

4.4.2 The dichotomous hypothesis

The dichotomous hypothesis states that koinobiosis is associated with endoparasitism and idiobiosis with ectoparasitism. There are more ectoparasitic idiobionts than either ectoparasitic koinobionts or endoparasitic idiobionts and the majority of endoparasitoids are koinobionts (Table 4.5). There is a significant association between ecto- / endoparasitism and idio- / koinobiosis across species (Pearson, χ^2 = 82.245, df = 1, $P < 0.001$), which remains significant after sequential Bonferroni correction. There is a significant relationship between these variables in the PR analyses when the explanatory variable is a) koinobiosis / idiobiosis and b) ectoparasitism / endoparasitism (Table 4.6). As expected koinobiosis is more associated with endoparasitism than ectoparasitism, and idiobiosis with ecto- rather than endoparasitism.

There is no association between ecto- / endoparasitism and the number of host species attacked either across species (t-test, t = -0.416, df = 215, P = 0.678) or for either PR analysis (Table 4.6). When controlling for the degree of study, there is no significant relationship between ecto- / endoparasitism and the number of host species attacked for the PR analyses (Table 4.6). There is no relationship between idio- / koinobiosis and the number of host species attacked either across species (t-test, t = 0.524, df = 147, P = 0.601) or for either PR analysis (Table 4.6). When controlling for the degree of study, there is no association between idio- / koinobiosis the number of host species attacked across for either PR analysis (Table 4.6). Ecto- / endoparasitism is not significantly associated with host exposure either across species (Pearson, χ^2 = 9.706, df = 2, P = 0.08) (Table 4.7) or for either PR analyses (Table 4.6). Across species, idio- / koinobiosis is significantly associated with host exposure (Pearson, χ^2 = 11.093, df = 2, P = 0.004) (Table 4.7), although the results for both PR analyses are not significant (Table 4.6). Across species koinobionts are found to attack exposed hosts more frequently than idiobionts, which attack approximately equal numbers of semi-concealed and concealed hosts.

There is a significant association between ecto- / endoparasitism and host niche across species (Pearson, χ^2 = 52.380, df = 15, $P < 0.001$) (Table 4.8, Figure 4.1), which remains significant after sequential Bonferroni correction. However no relationship is found for either PR analysis (Table 4.9). Ectoparasitic species frequently attack hosts in exposed locations as well as attacking casebearers and borers. Endoparasitoids most frequently attack exposed hosts, borers and leaf miners. A significant association is found between development mode and host niche across species (Pearson, χ^2 = 47.414, df = 15, $P < 0.001$) (Table 4.10, Figure 4.2), which remains significant after sequential Bonferroni correction. No association is found for either PR analysis (Table 4.9). Koinobionts most frequently attack exposed hosts, but also attack borers, whereas idiobionts most frequently attack casebearers.

Table 4.6: Results of the PR for the dichotomous hypothesis, host exposure, and host range. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Development mode: I – idiobiont, K – koinobiont; Host exposure: Ex – exposed, Sc – semi-concealed, C – concealed; Parasitism: Ec – ectoparasitism, En – endoparasitism; D – the degree of study.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitism (r) and development mode (e)	156	_0.500*_ 0.000 I 0.228 K	**6**	_0.539**_ 0.000 I 0.253 K	**19**
Parasitism (r) and host exposure (e)	239	_0.334_ 0.000 Ex 0.027 Sc 0.034 C	**14**	_0.370_ 0.000 Ex 0.013 Sc 0.041 C	**29**
Development mode (r) and parasitism (e)	156	_0.213*_ 0.000 Ec 0.544 En	**18**	_0.213 *_ 0.000 Ec 0.506 En	**34**
Development mode (r) and host exposure (e)	166	_0.165_ 0.000 Ex -0.063 Sc -0.082 C	**24**	_0.165_ 0.000 Ex -0.064 Sc -0.070 C	**38**
No. host spp. attacked (r) and parasitism (e)	217	_0.030_ 0.000 0.007 En	**73**	_0.045_ 0.000 0.030 En	**101**
No. host spp. attacked (r) and development mode (e)	149	_0.030_ 0.000 -0.112 K	**56**	_0.037_ 0.000 -0.123 K	**79**
No. host spp. attacked (r) parasitism (e), degree of study (c)	217	_0.030_ 0.000 0.367 D -0.068 En	**80**	_0.030_ 0.000 0.363 D -0.057 En	**108**
No. host spp. attacked (r), development mode (e), degree of study (c)	149	_0.055_ 0.000 0.422 D -0.104 K	**61**	_0.067_ 0.000 0.418 D -0.126 K	**84**

Table 4.7: Distribution of ecto- / endoparasitoids and idio- / koinobionts attacking hosts found at different levels of exposure.

Life history trait	Host exposure			
	Exposed	Semi-concealed	Concealed	Total
Ectoparasitism	18	31	27	76
Endoparasitism	71	42	50	163
Total	89	73	77	239
Idiobiosis	9	22	16	47
Koinobiosis	52	29	38	119
Total	61	51	54	166

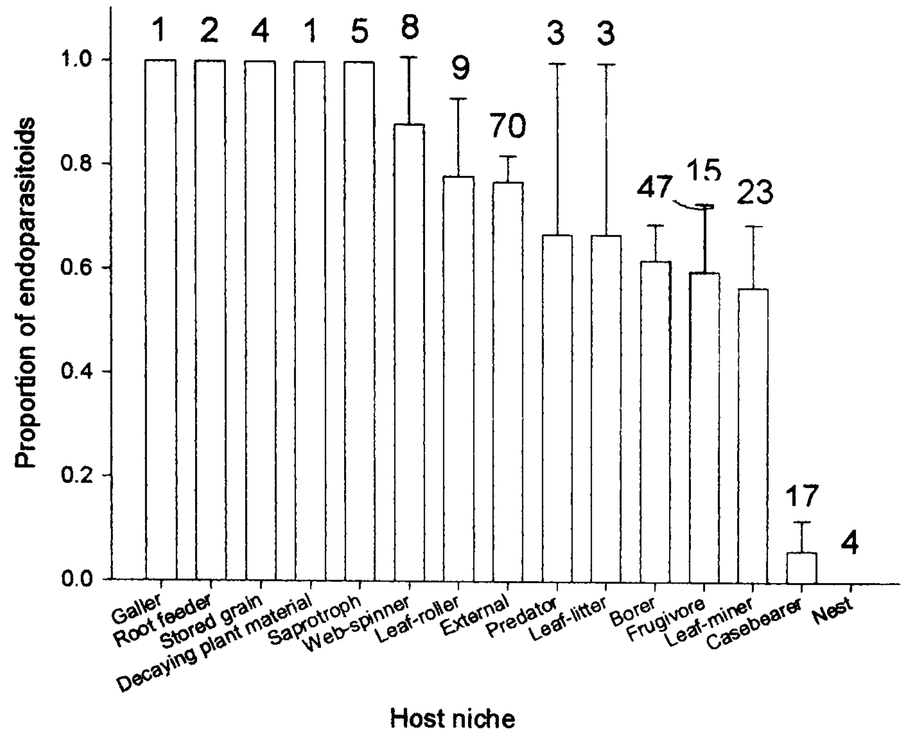


Figure 4.1: Proportion (+SEM) of endoparasitoids associated with each host niche. Numbers indicate sample sizes.

Table 4.8: Distribution of ectoparasitoids and endoparasitoids attacking hosts located in various niches. Zeros indicate niches where the state of parasitism was not recorded for any wasp species.

Niche	Ectoparasitoids	Endoparasitoids	Total
Exposed	16	54	70
Leaf miner	10	13	23
Leaf roller	2	7	9
Web-spinner	1	7	8
Casebearer	16	1	17
Galler	0	1	1
Borer	18	29	47
Root feeder	0	2	2
Predator	1	2	3
Nest	4	0	4
Leaf litter	1	2	3
Pollen feeder	0	0	0
Stored grain	0	4	4
Decaying vegetation	0	1	1
Frugivore	6	9	15
Saprotroph	0	5	5
Total	75	137	212

Table 4.9: Results of the PR for the dichotomous hypothesis and host niche. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable. Host niche: ex – exposed, lm – leaf miner, lr – leaf roller, w – web spinner, cb – casebearer, ga – galler, bo – borer, rf – root feeder, pd – predator, ns – nest, ll – leaf litter, pf – pollen feeder, sg – stored grain, dv – decaying vegetation, fr – frugivore, sp – saprotroph.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitism (r) and host niche (e)	225	*0.318*	**7**	*0.325*	**18**
		0.000 ex		0.000 ex	
		-0.002 lm		-0.026 lm	
		0.101 lr		0.063 lr	
		0.045 w		0.054 w	
		-0.253 cb		-0.207 cb	
		0.178 ga		0.171 ga	
		0.058 bo		0.046 bo	
		0.048 rf		0.029 rf	
		0.000 pd		0.000 pd	
		-0.018 ns		-0.054 ns	
		-0.087 ll		-0.134 ll	
		-0.056 pf		-0.081 pf	
		0.000 sg		0.000 sg	
		0.049 dv		0.030 dv	
		0.004 fr		0.028 fr	
		-0.104 sp		-0.073 sp	
Development mode (e) and host niche (r)	157	*0.150*	**15**	*0.150*	**29**
		0.000 ex		0.000 ex	
		-0.022 lm		-0.039 lm	
		-0.068 lr		-0.086 lr	
		0.088 w		0.102 w	
		-0.556 cb		-0.507 cb	
		0.144 ga		0.110 ga	
		-0.054 bo		-0.075 bo	
		0.000 rf		0.000 rf	
		0.000 pd		0.000 pd	
		0.116 ns		0.045 ns	
		-0.376 ll		-0.361 ll	
		0.000 pf		0.000 pf	
		0.000 sg		0.000 sg	
		-0.008 dv		-0.041 dv	
		-0.012 fr		0.006 fr	
		-0.329 sp		-0.228 sp	

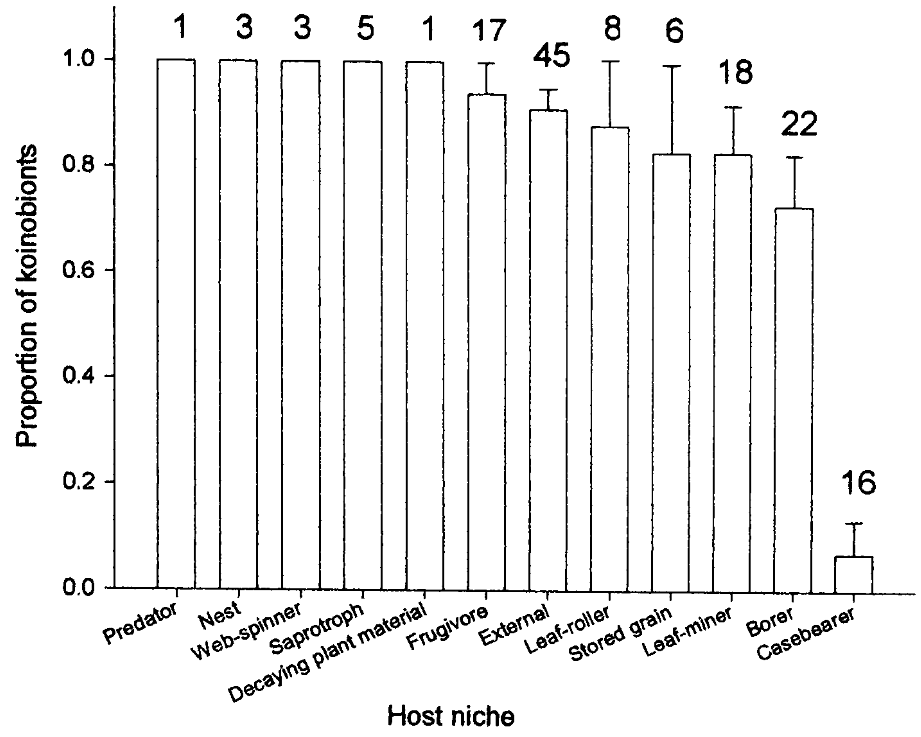


Figure 4.2: Proportion (+SEM) of koinobionts associated with each host niche. Numbers indicate sample sizes.

Table 4.10: Distribution of idiobionts and koinobionts attacking hosts located in various niches. Zeros indicate niches where the state of biosis was not recorded for any wasp species.

Niche	Idiobionts	Koinobionts	Total
Exposed	4	41	45
Leaf miner	3	15	18
Leaf roller	1	7	8
Web-spinner	0	3	3
Casebearer	15	1	16
Galler	0	0	0
Borer	6	16	22
Root feeder	0	0	0
Predator	0	1	1
Nest	0	3	3
Leaf litter	0	0	0
Pollen feeder	0	0	0
Stored grain	1	5	6
Decaying vegetation	0	1	1
Frugivore	1	16	17
Saprotroph	0	5	5
Total	31	114	145

Table 4.11: Results of the PR for the dichotomous hypothesis, preadult lifespan and adult longevity. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Development mode: I – idiobiont, K – koinobiont; Parasitism: Ec – ectoparasitism, En – endoparasitism; Parasitoid distribution: Te – temperate, Tr – tropical, B –temperate and tropical.

Analyses	Species	Taxonomy		Composite cladogram	
Preadult lifespan (r) and development mode (e)	31	*0.165* 0.000 I -0.043 K	**13**	*0.150* 0.000 I -0.021 K	**24**
Preadult lifespan (r) and parasitism (e)	40	*0.135* 0.000 Ec -0.057 En	**16**	*0.122* 0.000 Ec -0.057 En	**29**
Preadult lifespan (r), parasitism (e), parasitoid distribution (c)	34	*0.037* 0.000 Te -0.051 Tr -0.134 B -0.027 En	**10**	*0.045* 0.000 Te -0.063 Tr -0.146 B -0.023 En	**22**
Preadult lifespan (r), development mode (e), parasitoid distribution (c)	26	*0.135* 0.000 Te -0.052 Tr -0.125 B 0.028 K	**7**	*0.003* 0.000 Te -0.081 Tr -0.159 B 0.015 K	**17**
Parasitoid longevity (r) and parasitism (e)	76	*0.067** 0.000 Ec -0.197 En	**37**	*0.055* 0.000 Ec -0.196 En	**51**
Parasitoid longevity (r) and development mode (e)	59	*0.135*$^{**(**)}$ 0.000 I -0.307 K	**29**	*0.135** 0.000 I -0.330 K	**41**

Preadult lifespan is not significantly associated with ecto- / endoparasitism across species (t-test, t = 0.177, df = 38, P = 0.446) or for either PR analysis (Table 4.11). In the PR analysis, there is no significant association between these variables when controlling for parasitoid distribution (Table 4.11). Preadult lifespan is not significantly associated with idio- / koinobiosis either across species (t-test, t = 1.177, df = 29, P = 0.249) or in either PR analyses (Table 4.11). When controlling for parasitoid distribution in the PR analyses, there is no significant effect of idio- / koinobiosis on preadult (Table 4.11).

Parasitoid adult longevity is significantly associated with ecto- / endoparasitism across species (t-test, t = 2.831, df = 74, P = 0.006) and in the taxonomic PR analysis (Table 4.11). Parasitoid adult longevity is significantly associated with idio- / koinobiosis across species (t-test, t = 3.664, df = 57, P = 0.001) and in both PR analyses (Table 4.11). Ectoparasitoids and idiobionts live longer than endoparasitoids and koinobionts.

Egg volume is not significantly associated with ecto- / endoparasitism across species (Kruskal-Wallis test, χ^2 = 3.202, df = 1, P = 0.074) or for either PR analyses (Table 4.12). However, when controlling for fecundity, there is a significant effect of parasitism on egg volume both across species (F = 14.622, df = 1, P = 0.001) and in both PR analyses (Table 4.12), with endoparasitoids having smaller eggs than ectoparasitoids. Egg volume is not significantly associated with idio- /

Table 4.12: Results of the PR for the dichotomous hypothesis, egg size, fecundity. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Parasitism: Ec – ectoparasitism, En – endoparasitism; Development mode: I – idiobiont, K – koinobiont; Plt – parasitoid adult body length; F – fecundity.

Analyses	Species	Taxonomy		Composite cladogram	
Egg volume (r) and parasitism (e)	53	*0.581* 0.000 Ec -0.619 En	**22**	*0.729* 0.000 Ec -0.424 En	**35**
Egg volume (r) and development mode (e)	36	*0.729* 0.000 I -0.428 K	**14**	*0.998* 0.000 I -0.068 K	**25**
Egg volume (r), parasitism (e), parasitoid body length (c)	50	*0.581* 0.000 1.371 Plt -0.613 En	**20**	*0.676* 0.000 0.279 Plt -0.322 En	**33**
Egg volume (r), development mode (e), parasitoid body length (c)	34	*0.611** 0.000 1.419 Plt -1.040 K	**13**	*0.769* 0.000 1.458 Plt -0.418 K	**24**
Egg volume (r), parasitism (e), fecundity (c)	27	*0.776 ** 0.000 -0.501 F -1.185 En	**11**	*0.859** 0.000 -0.586 F -0.924 En	**20**
Egg volume (r), development mode (e), fecundity (c)	16	*0.729** 0.000 -0.567 F -1.401 K	**6**	*0.165* 0.000 -0.581 F -1.821 K	**12**
Fecundity (r) and parasitism (e)	51	*0.235** 0.000 Ec 0.380 En	**28**	*0.224* 0.000 Ec 0.373 En	**29**
Fecundity (r) and development mode (e)	55	*0.235* 0.000 I 0.204 K	**28**	*0.270* 0.000 I 0.227 K	**34**

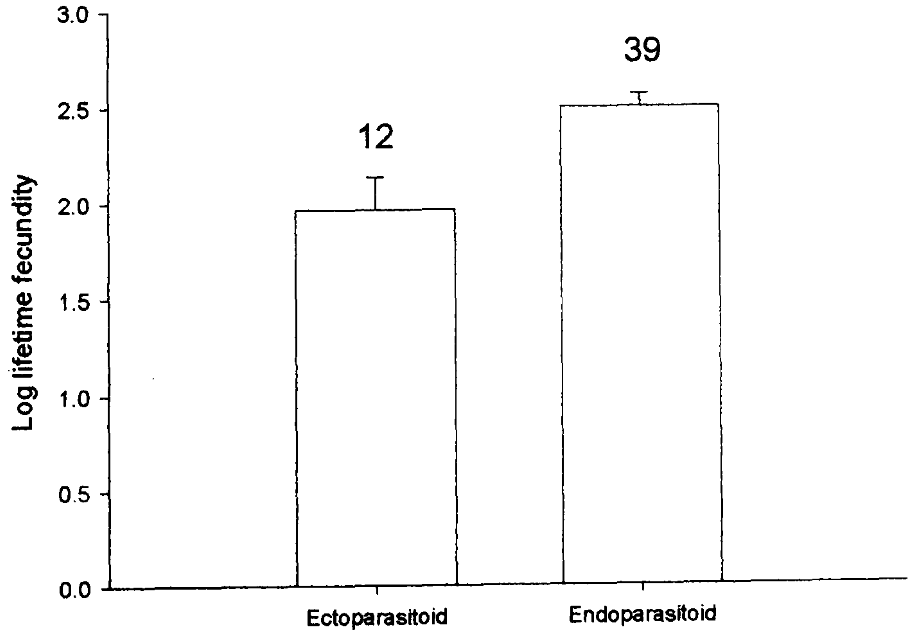


Figure 4.3: Mean (+SEM) lifetime fecundity for ecto- and endoparasitoids. Numbers indicate sample sizes.

koinobiosis across species (t-test, *t* = -1.430, df = 31, *P* = 0.163) or for either PR analyses (Table 4.12).

When controlling for parasitoid adult body length, there is a significant association between these variables for the taxonomic PR analysis (Table 4.12). When controlling for fecundity, there is a significant effect of idio- / koinobiosis on egg volume across species (*F* = 6.466, df = 1, *P* = 0.025), where koinobionts have larger eggs than idiobionts (although there are only two idiobiont species compared with 14 koinobiont species included in the analysis). A significant association is also present in the taxonomic PR analysis, again koinobionts have smaller eggs than idiobionts (Table 4.12).

Fecundity is significantly associated with ecto- / endoparasitism across species (t-test, *t* = -3.326, df = 49, *P* = 0.002) (Figure 4.3) and also for the taxonomic PR analysis (Table 4.12), where endoparasitoids are more fecund than ectoparasitoids. However, fecundity is not significantly associated with idio- / koinobiosis either across species (t-test, *t* = -1.087, df = 37, *P* = 0.284) or for the PR analyses (Table 4.12).

4.4.3 Trade-offs and allometries

Trade-offs

The relationship between parasitoid body length and brood size across species is marginally non-significant (Spearman R = -0.179, N = 109, *P* = 0.063). There is a significant negative association in the taxonomic PR analysis (Table 4.13), between parasitoid body length (response variable) and brood size (explanatory variable). However, when brood size is the response variable and parasitoid body length is the explanatory variable, there is no significant result for either PR analysis (Table 4.13). When controlling for host body length, there is a significant negative association between parasitoid body length and brood size across species (Partial correlation coefficient = -0.364, df = 93, *P* < 0.001), which remains significant after sequential Bonferroni correction. However, there is no significant association between parasitoid body length (response variable) and brood size (explanatory variable) for either PR analysis (Table 4.13). When controlling for host body length, there is a significant association between brood size (response variable) and parasitoid body length (explanatory variable) for the taxonomic PR analysis (Table 4.13).

Egg volume is not associated with fecundity across species (Pearson, R = 0.151, N = 26, *P* = 0.462) or for either PR analysis (Table 4.13). When controlling for parasitoid body length, there is a significant negative association between egg volume and fecundity across species (Partial correlation coefficient = -0.550, df = 24, *P* = 0.004), but not for either PR analysis (Table 4.13).

Allometries

There is no significant association between parasitoid body length and the degree of study across species (Spearman R = -0.056, N = 316, *P* = 0.324) or for either PR analysis (Table 4.14).

There is a significant positive association between parasitoid body length and preadult lifespan across species (Pearson, R = 0.385, N = 38, *P* = 0.017) (Figure 4.4). However, there is no association between a) parasitoid body length (response variable) and preadult lifespan (explanatory variable) for either PR analysis (Table 4.14), or for b) preadult lifespan (response

Table 4.13: Results of the PR to detect trade-offs. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Csz – clutch size; Hlt – host adult body length; Plt – parasitoid adult body length; F – fecundity; V – egg volume.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitoid body length (r) and clutch size (e)	119	*0.464** 0.000 -0.103 Csz	**47**	*0.488* 0.000 -0.084 Csz	**67**
Parasitoid body length (r), clutch size (e), host body length (c)	96	*0.513* 0.000 0.335 Hlt -0.093 Csz	**40**	*0.539* 0.000 0.354 Hlt -0.087 Csz	**58**
Clutch size (r) and parasitoid body length (e)	119	*0.334* 0.000 -0.269 Plt	**9**	*0.476* 0.000 -0.233 Plt	**23**
Clutch size (r), parasitoid body length (e), host body length (c)	96	*0.235** 0.000 0.282 Hlt -0.446 Plt	**39**	*0.352* 0.000 0.269 Hlt -0.417 Plt	**57**
Egg volume (r) and fecundity (e)	28	*0.926* 0.000 -0.438 F	**12**	*1.011* 0.000 -0.419 F	**22**
Egg volume (r), fecundity (e), parasitoid body length (c)	27	*0.961* 0.000 1.744 Plt -0.446 F	**10**	*0.848* 0.000 2.271 Plt -0.501 F	**20**
Fecundity (r) and egg volume (e)	28	*0.288** 0.000 -0.282 V	**12**	*0.288** 0.000 -0.243 V	**22**

variable) and parasitoid adult body length (explanatory variable) for either PR analysis (Table 4.14). Parasitoid body length has no significant effect on preadult lifespan, when controlling for parasitoid distribution, for either PR analysis (Table 4.14).

There is a significant positive association between parasitoid adult longevity and parasitoid adult body length across species (Pearson, R = 0.305, N = 78, $P = 0.007$), but not for either PR analysis (Table 4.14). There is no significant association between parasitoid adult longevity and fecundity across species (Pearson, R = -0.085, N = 50, $P = 0.559$) or for either PR analysis (Table 4.14). Parasitoid adult longevity is not significantly associated with solitary / gregarious development across species (t-test, $t = 0.791$, df = 67, $P = 0.432$) or in either PR analysis (Table 4.14).

Egg volume is not significantly associated with parasitoid body length across species (Pearson, R = 0.112, N = 37, $P = 0.510$), however a significant positive association is found for both PR analyses (Table 4.14). Fecundity is not significantly associated with parasitoid body length in either PR analysis (Table 4.14).

No significant association found between preadult lifespan and host body length (Pearson, R = 0.166, N = 29, $P = 0.390$) across species or for either PR analysis, or when parasitoid distribution is controlled for (Table 4.15).

Preadult lifespan is not significantly associated with host stage attacked (15 states) across

Table 4.14: Results of the PR to detect allometric relationships. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Plt – parasitoid adult body length; Hlt – host adult body length; Parasitoid distribution: Te – temperate, Tr – tropical, B –temperate and tropical; F – fecundity; Development: S – solitary, G – gregarious; Plf – preadult lifespan; D – the degree of study.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitoid body length (r) and the degree of study (e)	316	*0.352*	**106**	*0.389*	**140**
		0.000		0.000	
		0.016 D		0.023 D	
Preadult lifespan (r) and parasitoid body length (e)	38	*0.135*	**16**	*0.122*	**30**
		0.000		0.000	
		0.225 Plt		0.201Plt	
Parasitoid body length (r) and preadult lifespan (e)	28	*0.581*	**16**	*0.676*	**30**
		0.000		0.000	
		0.371 Plf		0.311 Plf	
Preadult lifespan (r), parasitoid body length (e), parasitoid distribution (c)	32	*0.082*	**10**	*0.055*	**23**
		0.000 Te		0.000 Te	
		-0.074 Tr		-0.091 Tr	
		-0.136 B		-0.150 B	
		0.175 Plt		0.155 Plt	
Parasitoid longevity (r) and parasitoid adult body length (e)	78	*0.122*	**36**	*0.111*	**53**
		0.000		0.000	
		0.152 Plt		0.128 Plt	
Parasitoid longevity (r) and fecundity (e)	46	*0.082*	**23**	*0.045*	**37**
		0.000		0.000	
		0.010 F		0.005 F	
Parasitoid longevity (r) and solitary / gregarious development (e)	69	*0.150*	**33**	*0.165*	**47**
		0.000 S		0.000 S	
		-0.057 G		-0.090 G	
Egg volume (r) and parasitoid body length (e)	51	*0.581**	**22**	*0.729**	**35**
		0.000		0.000	
		1.334 Plt		1.329 Plt	
Fecundity (r) and parasitoid body length (e)	50	*0.288*	**25**	*0.260*	**40**
		0.000		0.000	
		-0.030 Plt		-0.026 Plt	

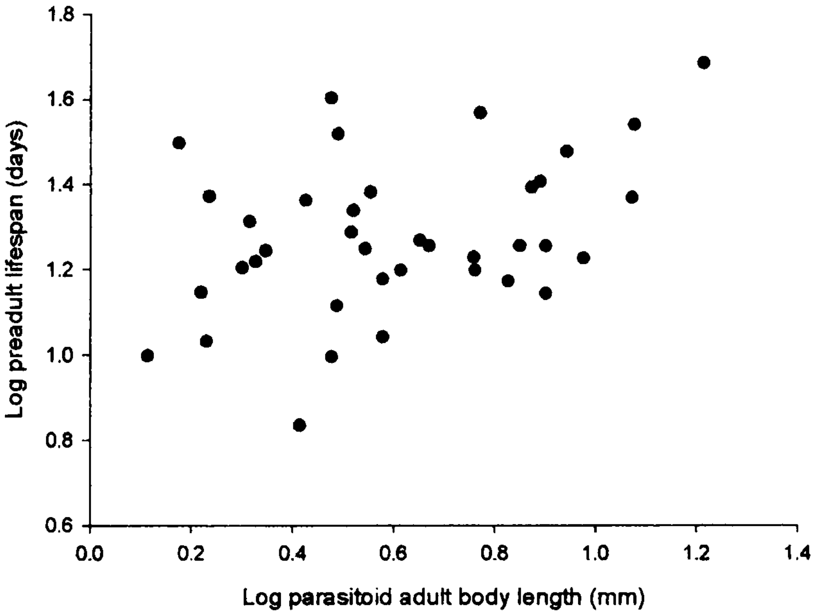


Figure 4.4: Log preadult lifespan against log parasitoid body length across species.

Table 4.15: Results of the PR for host life history variables affecting parasitoid body size. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable. Hlt – host adult body length; : Te – temperate, Tr – tropical, B –temperate and tropical; Host stage attacked: E - egg, N - nymph, L – larva, Pr – prepupa, P – pupa, A – adult, or a combination of the above.

Analyses	Species	Taxonomy		Composite cladogram	
Preadult lifespan (r) and host body length (e)	29	*0.100*	**10**	*0.037*	**20**
		0.000		0.000	
		0.071 Hlt		0.062 Hlt	
Preadult lifespan (r), host body length (e), parasitoid distribution (c)	26	*0.100*	**7**	*0.067*	**16**
		0.000 Te		0.000 Te	
		-0.226 Tr		-0.224 Tr	
		-0.135 B		-0.142 B	
Preadult lifespan (r), and host stage attacked (15 states) (e)	234	*0.334**	**77**	*0.370*	**107**
		0.000 E		0.000 E	
		-0.274 N		-0.257 N	
		-0.450 L		-0.016 L	
		-0.013 Pr		0.001 Pr	
		-0.001 P		0.019 P	
		-0.081 A		-0.055 A	
		-0.206 N/A		-0.188 N/A	
		-0.019 Pr/P		-0.003 Pr/P	
		0.000 E/L/P		0.000 E/L/P	
		-0.151 Any		-0.150 Any	
		-0.261 L/P		-0.235 L/P	
		-0.049 L/Pr		0.235 L/Pr	
		0.203 E/L		0.213 E/L	
		-0.016 L/P/A		-0.027 L/P/A	
		0.303 L/Pr/P		0.377 L/Pr/P	
Parasitoid body length (r) and host stage attacked (15 states) (e)	234	*0.334**	**77**	*0.370*	**108**
		0.000 E		0.000 E	
		-0.274 N		-0.257 N	
		-0.045 L		-0.016 L	
		-0.023 Pr		0.001 Pr	
		-0.001 P		0.019 P	
		-0.081 A		-0.055 A	
		-0.206 N/A		-0.188 N/A	
		-0.019 Pr/P		-0.033 Pr/P	
		0.000 E/L/P		0.000 E/L/P	
		-0.151 Any		-0.115 Any	
		-0.261 L/P		-0.235 L/P	
		-0.049 L/Pr		-0.026 L/Pr	
		0.203 E/L		0.213 E/L	
		-0.016 L/P/A		-0.027 L/P/A	
		0.303 L/Pr/P		0.377 L/Pr/P	
Fecundity (r) and host body length (e)	44	*0.224*	**23**	*0.235*	**36**
		0.000		0.000	
		0.052 Hlt		0.031 Hlt	

species (ANOVA, $F = 1.477$, df = 6, $P = 0.216$). However, there is a significant association in the taxonomic PR analysis (Table 4.15), where parasitoids attacking larval host stages have the shortest preadult lifespans and those attacking egg or pupal host stages have the longest preadult lifespans. There is a significant association between parasitoid body length and host stage attacked

Table 4.16: Results of the PR for host stage attacked and parasitoid fecundity. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable. Host stage attacked: E - egg, N - nymph, L – larva, Pr – prepupa, P – pupa, A – adult, or a combination of the above.

Analyses	Species	Taxonomy		Composite cladogram	
Fecundity (r) and host stage attacked (15 states) (e)	52	*0.202*	**21**	*0.183*	**36**
		0.000 E		0.000 E	
		0.160 N		0.270 N	
		0.002 L		0.002 L	
		0.000 Pr		0.000 Pr	
		0.060 P		-0.067 P	
		-0.700 A		-0.763 A	
		-0.020 N/A		0.093 N/A	
		0.000 Pr/P		0.000 Pr/P	
		0.000 E/L/P		0.000 E/L/P	
		0.000 Any		0.000 Any	
		0.000 L/P		0.000 L/P	
		-0.236 L/Pr		-0.310 L/Pr	
		0.000 E/L		0.000 E/L	
		0.000 L/P/A		0.000 L/P/A	
		0.000 L/Pr/P		0.000 L/Pr/P	
Fecundity (r) and host stage attacked (6 states) (e)	44	*0.260*	**18**	*0.202*	**32**
		0.000 E		0.000 E	
		0.173 N		0.312 N	
		0.031 L		0.013 L	
		0.000 Pr		0.000 Pr	
		0.134 P		-0.062 P	
		-0.668 A		-0.744 A	

(15 states) across species (Kruskal-Wallis test, $\chi^2 = 47.966$, df = 14, $P < 0.001$), which remains significant after sequential Bonferroni correction. This relationship is significant in the taxonomic PR analysis (Table 4.15), where the estimates show that parasitoids attacking nymphal host stages have the smallest body sizes and those attacking egg or pupal host stages have the largest body sizes.

There is no significant association between fecundity and host body length across species (Pearson, R = 0.066, N = 44, $P = 0.672$) or in either PR analysis (Table 4.15). Across species, fecundity is not significantly associated with host stage attacked (15 states) (Kruskal-Wallis test, $\chi^2 = 8.871$, df = 6, $P = 0.181$), or with host stage attacked (6 states) (Kruskal-Wallis test, $\chi^2 = 2.971$, df = 4, $P = 0.563$). In the PR analyses fecundity is not associated with host stage attacked (15 or 6 states) (Table 4.16).

4.4.4 Parasitoid body size and brood size and host body size

There is a significant positive association between parasitoid body length and host body length across species (Pearson, R = 0.507, N = 209, $P < 0.001$) (Figure 4.5), which remains significant after sequential Bonferroni correction. For both PR analysis, a significant positive relationship is also found (Table 4.17). There is a marginally non-significant association between brood size and

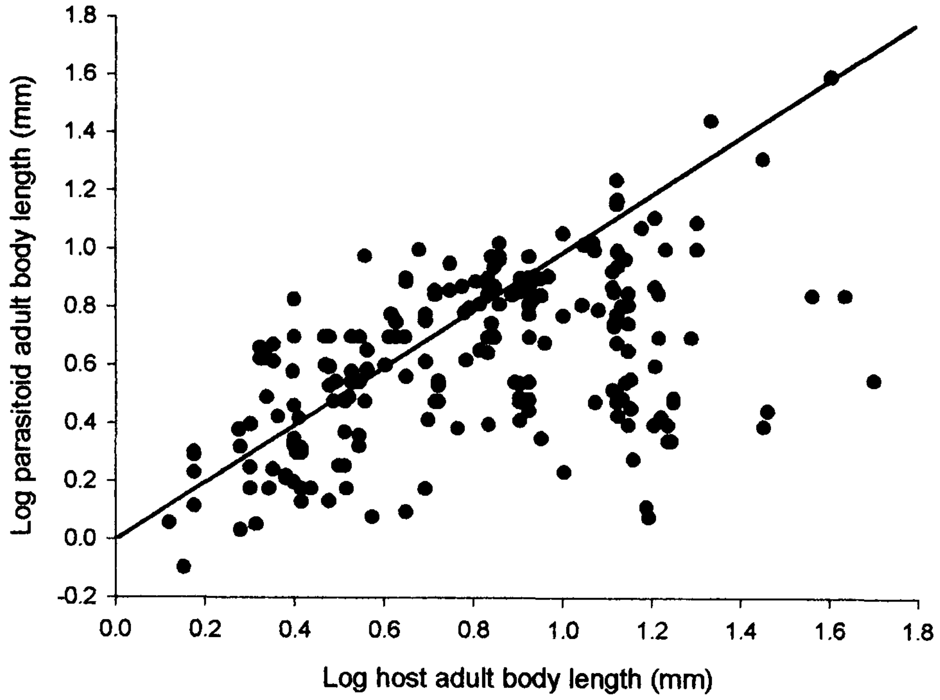


Figure 4.5: Log parasitoid body length against log host body length across species. The line y = x is shown.

Table 4.17: Results of the PR for parasitoid body size, clutch size and host size. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Development: S – solitary, G – gregarious; Plt – parasitoid adult body length; Hlt – host adult body length.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitoid body length (r) and host body length (e)	209	*0.352*$^{**(**)}$ 0.000 0.414 Hlt	**80**	*0.513*$^{**(**)}$ 0.000 0.382 Hlt	**108**
Clutch size (r) and host body length (e)	109	*0.192* 0.000 0.200 Hlt	**12**	*0.288* 0.000 0.218 Hlt	**28**
Clutch size (r) and host body length (e) (gregarious species only)	14	*1.18* 0.000 -0.081 Hlt	**5**	*1.512* 0.000 -0.137 Hlt	**8**
Clutch size (r), host body length (e), parasitoid body length (c)	96	*0.260* 0.000 -0.450 Plt 0.274 Hlt	**40**	*0.389* 0.000 -0.418 Plt 0.260 Hlt	**58**
Parasitoid body length (r) and solitary / gregarious development (e)	159	*0.334* 0.000 S -0.079 G	**55**	*0.488* 0.000 S -0.064 G	**77**
Solitary / gregarious development (r) and parasitoid body length (e)	159	*0.213* 0.000 -0.209 Plt	**16**	*0.247* 0.000 -0.185 Plt	**36**
Solitary / gregarious development (r) and host body length (e)	149	*0.260* 0.000 0.217 Hlt	**16**	*0.318** 0.000 0.247 Hlt	**36**
Solitary / gregarious development (r), parasitoid body length (e), host body length (c)	122	*0.165* 0.000 0.293 Hlt -0.329 Plt	**43**	*0.202* 0.000 0.302 Hlt -0.330 Plt	**64**

Table 4.18: Results of the PR for solitary / gregarious development versus pupation site. (* $P < 0.05$ ** $P < 0.001$). The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Pupation site (4 states): In – inside host's body, Uh – under host's body (mummified aphid), Ext – external to host's body and puparium, Ip – inside host's puparium but outside host's body; Pupation site (2 states): In – inside host's body, Ext – external to host's body.

Analyses	Species	Taxonomy		Composite cladogram	
Solitary / gregarious development (r) and pupation site (4 states) (e)	63	*0.352*	**4**	*0.318*	**15**
		0.000 In		0.000 In	
		0.141 Uh		0.242 Uh	
		0.132 Ext		0.203 Ext	
		-0.123 Ip		-0.082 Ip	
Solitary / gregarious development (r) and pupation site (4 states) (e) (endoparasitoids only)	44	*0.224*	**2**	*0.224*	**7**
		0.000 In		0.000 In	
		0.123 Uh		0.117 Uh	
		0.191 Ext		0.203 Ext	
		-0.151 Ip		-0.075 Ip	
Solitary / gregarious development (r) and pupation site (2 states) (e)	63	*0.352*	**6**	*0.318*	**17**
		0.000 In		0.000 In	
		0.075 Ext		0.153 Ext	
Solitary / gregarious development (r) and pupation site (2 states) (e) (endoparasitoids only)	44	*0.224*	**4**	*0.224*	**9**
		0.000 In		0.000 In	
		0.072 Ext		0.046 Ext	

host body length across species (Spearman R = 0.179, N = 109, $P = 0.063$), neither PR analysis is significant (Table 4.17). These relationships are not significant considering gregarious species alone across species (Pearson, R = 0.298, N = 14, $P = 0.300$) or for either PR analysis (Table 4.17). When studying all parasitoid species and controlling for parasitoid body length, there is a significant positive association between brood size and host body length across species (Partial correlation coefficient = 0.360, df = 93, $P < 0.001$), which remains significant after sequential Bonferroni correction. No relationship is found between brood size and host body length, when controlling for parasitoid body length in either PR analysis (Table 4.17).

There is a significant association between parasitoid body length and solitary / gregarious development across species (Kruskal-Wallis test, $\chi^2 = 6.853$, df = 1, $P = 0.009$), where solitary species are larger than gregarious species. No significant association is found between parasitoid body length (response variable) and solitary / gregarious development (explanatory variable) for either PR analysis (Table 4.17). Solitary / gregarious development (response variable) is not significantly associated with parasitoid body length (explanatory variable) in either PR analysis (Table 4.17).

Across species, solitary / gregarious development is significantly associated with host body length (Kruskal-Wallis test, $\chi^2 = 8.125$, df = 1, $P = 0.004$), where gregarious species are associated with larger hosts than solitary species. In the PR analyses, this relationship is only significant for the composite cladogram (Table 4.17). When controlling for host body length, there is no effect of parasitoid body length on solitary / gregarious development for either PR analysis (Table 4.17).

There is a significant association between solitary / gregarious development and pupation

Table 4.19: The number of solitary and gregarious endoparasitoids pupating in different pupation sites.

Pupation site	Solitary development	Gregarious development	Total
Inside host's body	11	1	12
Under host's body (mummified aphid)	6	3	9
Inside host puparium, but outside host's body	6	4	10
External to host's body and puparium	13	0	13
Total	36	8	44

site (4 states) across species (Pearson, χ^2 = 11.167, df = 3, *P* = 0.001), although this is not the case for the PR analyses (Table 4.18). When taking into account only endoparasitoid species, there is a significant association between solitary / gregarious development and pupation site (4 states) across species (Pearson, χ^2 = 8.260, df = 3, *P* = 0.041) (Table 4.19), although this is not significant for either PR analysis (Table 4.18). Across species, there is a significant association between solitary / gregarious development and pupation site (2 states) (Pearson, χ^2 = 3.925, df = 1, *P* = 0.048), however there is no significant association found in the PR analyses (Table 4.18). For endoparasitoids only, no association is found between solitary / gregarious development and pupation site (2 states) across species (Pearson, χ^2 = 1.076, df = 1, *P* = 0.300) or for either PR analysis (Table 4.18).

4.4.5 Parasitoid geographic range and geographic distribution

Preadult lifespan is associated with parasitoid distribution across species (ANOVA, *F* = 4.095, df = 2, *P* = 0.026) and for the PR composite cladogram analysis (Table 4.20). Temperate parasitoids have longer preadult lifespans than tropical parasitoids. There is no significant relationship between parasitoid body length and parasitoid distribution across species (Kruskal-Wallis test, χ^2 = 2.238, df = 2, *P* = 0.327) or for either PR analysis (Table 4.20). There is no significant association between brood size and parasitoid distribution across species (Kruskal-Wallis test, χ^2 = 0.069, df = 2, *P* = 0.966) or for either PR analysis (Table 4.20). There is no significant relationship between brood size and parasitoid mean latitude across species (Spearman R = -0.048, N = 111, *P* = 0.619) or for the PR analyses (Table 4.20).

Across species, there is a significant positive association between parasitoid geographic range and the degree of study (Spearman R = 0.393, N = 328, *P* < 0.001), which remains significant after sequential Bonferroni correction. This relationship is also significant in both PR analyses (Table 4.20).

There is a significant relationship between parasitoid geographic range and parasitoid distribution across species (Kruskal-Wallis test, χ^2 = 35.475, df = 2, *P* < 0.001), which remains significant after sequential Bonferroni correction, and this association is also significant in both PR analyses (Table 4.20). When controlling for the degree of study, there is a significant effect of parasitoid distribution on parasitoid geographic range across species (*F* = 7.021, df = 2, *P* = 0.001), which is also significant for both PR analyses (Table 4.20). Tropical parasitoids have the smallest geographic

Table 4.20: Results of the PR for parasitoid distribution and latitude. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Parasitoid distribution: Te – temperate, Tr – tropical, B –temperate and tropical; Pml – parasitoid mean latitude; D - the degree of study.

Analyses	Species	Taxonomy		Composite cladogram	
Preadult lifespan (r), and parasitoid distribution (e)	35	*0.192* 0.000 Te -0.040 Tr -0.123 B	**11**	0.122^{*} 0.000 Te -0.058 Tr -0.145 B	**24**
Parasitoid body length (r) and parasitoid distribution (e)	286	*0.318* 0.000 Te 0.050 Tr 0.022 B	**95**	*0.370* 0.000 Te 0.053 Tr 0.029 B	**127**
Clutch size (r) and parasitoid distribution (e)	125	*0.260* 0.000 Te -0.150 Tr -0.056 B	**11**	*0.352* 0.000 Te -0.134 Tr -0.064 B	**26**
Clutch size (r) and parasitoid mean latitude (e)	111	*0.260* 0.000 -0.001 Pml	**12**	*0.370* 0.000 0.001 Pml	**27**
Parasitoid geographic range (r) and the degree of study (e)	328	$0.037^{**(**)}$ 0.000 0.495 D	**107**	$0.037^{**(**)}$ 0.000 0.514 D	**141**
Parasitoid geographic range (r) and parasitoid distribution (e)	328	$0.037^{**(**)}$ 0.000 Te -0.444 Tr 0.641 B	**106**	$0.037^{**(**)}$ 0.000 Te -0.423 Tr 0.657 B	**140**
Parasitoid geographic range (r), parasitoid distribution (e), the degree of study (c)	328	$0.030^{**(**)}$ 0.000 0.405 D -0.488 Tr 0.515 B	**110**	$0.030^{**(**)}$ 0.000 0.421 D -0.430 Tr 0.524 B	**144**

range, whereas those parasitoids found in both temperate and tropical locations have the largest geographic range.

There is a significant positive relationship between parasitoid geographic range and parasitoid body length across species (Spearman R = 0.284, N = 304, $P < 0.001$), which remains significant after sequential Bonferroni correction. However, no significant relationship is found for either PR analysis (Table 4.21). When controlling for the degree of study, there is no significant relationship between parasitoid geographic range and parasitoid body length either across species (Partial correlation coefficient = 0.021, df = 265, $P = 0.728$) or for the PR analyses (Table 4.21).

A significant positive association is found between parasitoid geographic range and host geographic range across species (Spearman R = 0.639, N = 307, $P < 0.001$), which remains significant after sequential Bonferroni correction. A positive association is found in both PR analyses (Table 4.21). When controlling for the degree of study, there is a significant positive association between parasitoid geographic range and host geographic range across species (Partial correlation coefficient = 0.739, df = 304, $P < 0.001$), which remains significant after

Table 4.21: Results of the PR for parasitoid geographic range. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. D – the degree of study; Hgeo – host geographic range; RHge – residual host geographic range; Hsp – the number of host species attacked; Rhsp – the number of host species; Plt – parasitoid adult body length.

Analyses	Species	Taxonomy		Composite cladogram	
Parasitoid geographic range (r) and parasitoid body length (e)	268	*0.045* 0.000 0.522 Plt	**85**	*0.037* 0.000 0.579 Plt	**116**
Parasitoid geographic range (r), parasitoid body length (e), the degree of study (c)	268	*0.030* 0.000 0.533 D 0.369 Plt	**88**	*0.030* 0.000 0.538 D 0.418 Plt	**119**
Parasitoid geographic range (r) and host geographic range (e)	307	*0.037*$^{**(**)}$ 0.000 0.747 Hgeo	**102**	*0.037*$^{**(**)}$ 0.000 0.753 Hgeo	**136**
Parasitoid geographic range (r), host geographic range (e), the degree of study (c)	307	*0.030*$^{**(**)}$ 0.000 -0.037 D 0.714 Rhge	**106**	*0.030*$^{**(**)}$ 0.000 -0.036 D 0.717 Rhge	**140**
Parasitoid geographic range (r) and no. host spp. attacked (e)	304	*0.048*$^{**(**)}$ 0.000 0.471 Hsp	**104**	*0.045*$^{**(**)}$ 0.000 0.497 Hsp	**138**
Parasitoid geographic range (r), no. host spp. attacked (e), the degree of study (c)	304	*0.030* 0.000 -0.001 D 0.262 Rhsp	**108**	*0.030* 0.000 -0.007 D 0.293 Rhsp	**142**

sequential Bonferroni correction and there is a significant positive association found in both PR analyses (Table 4.21, Figure 4.6).

There is a significant positive association between parasitoid geographic range and the number of host species attacked across species (Spearman R = 0.283, N = 304, $P < 0.001$), which remains significant after sequential Bonferroni correction. A significant positive relationship is also found for both PR analyses (Table 4.21). When controlling for the degree of study, there is a significant relationship between parasitoid geographic range and the number of host species attacked in the cross species analysis (Partial correlation coefficient = 0.120, df = 301, $P = 0.038$), which remains significant after sequential Bonferroni correction. There is no relationship found for either PR analysis, when controlling for the degree of study for both the response (parasitoid geographic range) and the explanatory (the number of host species attacked) variables (Table 4.21).

4.4.6 Number of host species attacked

There is a significant positive association between the number of host species attacked and the degree of study across species (Spearman R = 0.366, N = 340, $P < 0.001$), which remains significant after sequential Bonferroni correction. This relationship is also found for both PR

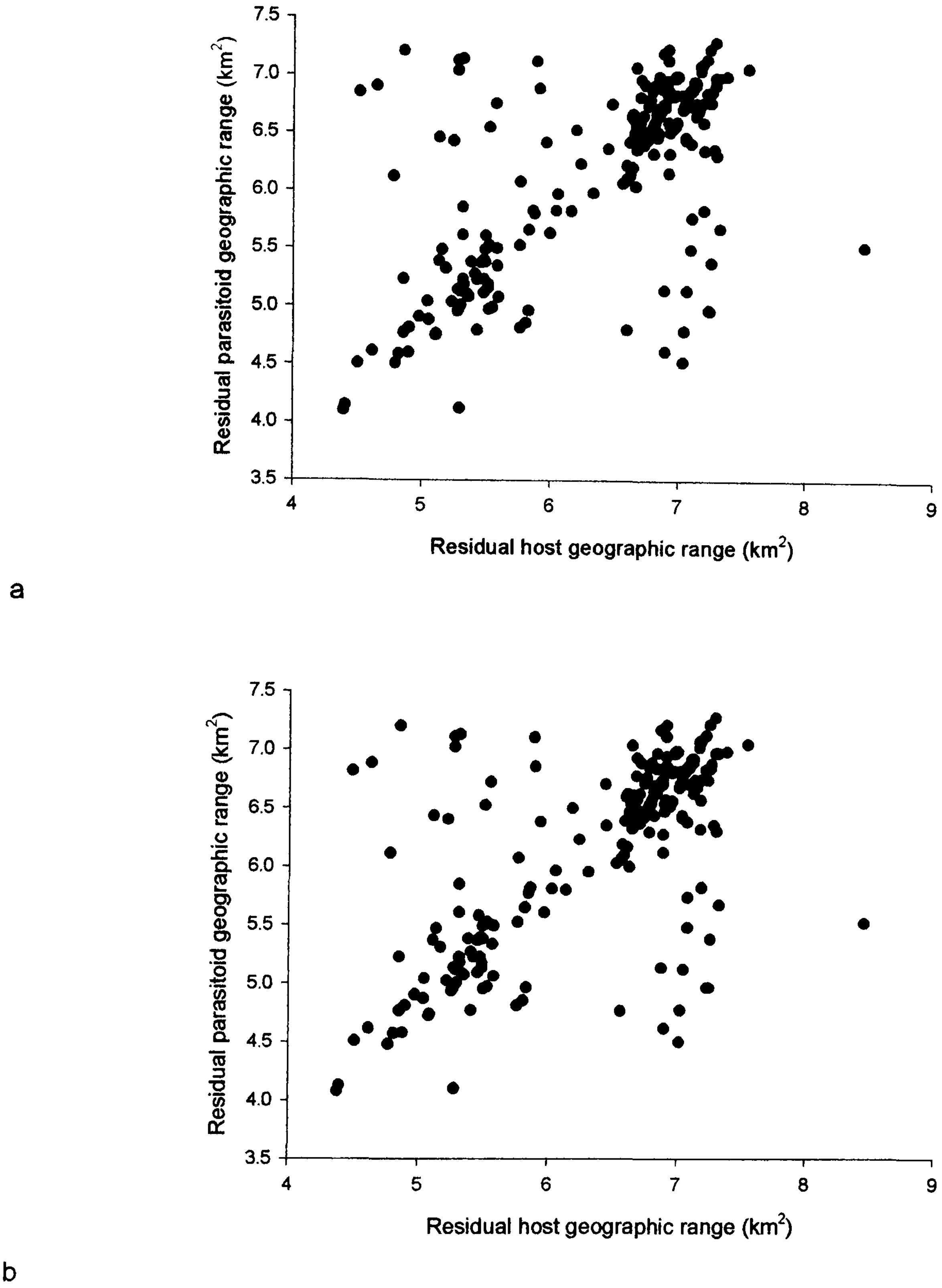


Figure 4.6: Residual parasitoid geographic range (km^2) against residual host geographic range (km^2), controlling for the degree of study for a) the taxonomic and b) the composite cladogram.

analyses (Table 4.22). Therefore the degree of study is used as a control variable, when trying to explain variation in the number of host species attacked.

There is no relationship between the number of host species attacked and host stage attacked (6 states) across species (Kruskal-Wallis test, $\chi^2 = 5.990$, df = 5, $P = 0.307$), but there is a significant association between these variables in the taxonomic PR analysis (Table 4.22), where parasitoids attacking larval host stages have a narrow host range, whilst parasitoids attacking nymphal host stages have a broad host range. When controlling for the degree of study, there is a significant association between the number of host species attacked and host stage attacked for the

Table 4.22: Results of the PR for host stage attacked or fecundity affecting host range. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Host stage attacked (6 states): E - egg, N - nymph, L – larva, Pr – prepupa, P – pupa, A – adult; F – fecundity; D - the degree of study.

Analyses	Species	Taxonomy		Composite cladogram	
No. host spp. attacked (r) and the degree of study (e)	340	*0.055*$^{**(**)}$	**101**	*0.067*$^{**(**)}$	**134**
		0.000		0.000	
		0.313 D		0.306 D	
No. host spp. attacked (r) and host stage attacked (6 states) (e)	230	*0.045**	**75**	*0.045*	**104**
		0.000 E		0.000 E	
		0.400 N		0.388 N	
		-0.065 L		-0.071 L	
		0.305 Pr		0.313 Pr	
		0.042 P		0.033 P	
		0.052 A		0.043 A	
No. host spp. attacked (r), host stage attacked (6 states) (e), the degree of study (c)	230	*0.037**	**83**	*0.037*	**112**
		0.000		0.000	
		0.327 D		0.322 D	
		0.358 N		0.355 N	
		-0.044 L		-0.048 L	
		0.415 Pr		0.425 Pr	
		0.017 P		0.017 P	
		-0.045 A		-0.047 A	
No. host spp. attacked (r) and fecundity (e)	46	*0.003*	**21**	*0.003*	**34**
		0.000		0.000	
		0.113 F		0.114 F	
No. host spp. attacked (r), fecundity (e), the degree of study (c)	46	*0.090*	**22**	*0.135*	**36**
		0.000		0.000	
		0.606 D		0.634 D	
		0.042 F		0.051 F	

taxonomic PR analysis (Table 4.22), parasitoids attacking prepupal host stages have narrow host ranges whereas parasitoids attacking larval host stages have broader host ranges.

There is no significant relationship between the number of host species attacked and fecundity both across species (Spearman R = 0.092, N = 46, P =0.544) and for the PR analyses (Table 4.22). When controlling for the degree of study, there is no significant association between the number of host species attacked and fecundity either cross-species (Partial correlation coefficient = 0.044, df = 43, P = 0.772) or for either PR analysis (Table 4.22).

There is a significant association between the number of host species attacked and parasitoid distribution across species (Kruskal-Wallis test, χ^2 = 28.515, df = 2, P = 0.001) and in both PR analyses (Table 4.23).

When controlling for the degree of study, there is a significant interaction between the degree of study and parasitoid distribution on the number of host species attacked across species (F = 3.785, df = 2, P = 0.024). In the PR analyses, there is a significant relationship between the number of host species attacked and parasitoid distribution, when controlling for the degree of study (Table 4.23). Parasitoids located in tropical areas have narrower host ranges than temperate

Table 4.23: Results of the PR for parasitoid geographic range affecting host range. (* $P < 0.05$ ** $P < 0.001$). Brackets indicate P values that are still significant after sequential Bonferroni correction. The number of species per analysis is given. Numbers denote regression estimates or ρ values (italics) or denominator degrees of freedom (bold). Estimates represent the slopes for continuous variables or the means of each factor level relative to the first factor level, arbitrarily set at zero. r – response variable, e – explanatory variable, c – control variable. Parasitoid distribution: Te – temperate, Tr – tropical, B – temperate and tropical; D - the degree of study; Pml – parasitoid mean latitude; Pgeo – parasitoid geographic range, RPge – residual parasitoid geographic range.

Analyses	Species	Taxonomy		Composite cladogram	
No. host spp. attacked (r) and parasitoid distribution (e)	316	$0.055^{**(**)}$ 0.000 Te -0.180 Tr 0.304 B	**95**	$0.082^{**(**)}$ 0.000 Te -0.196 Tr 0.292 B	**128**
No. host spp. attacked (r), parasitoid distribution (e), the degree of study (c)	316	$0.045^{**(**)}$ 0.000 0.238 D -0.179 Tr 0.215 B	**107**	$0.067^{**(**)}$ 0.000 0.234 D -0.194 Tr 0.208 B	**140**
No. host spp. attacked (r) and parasitoid mean latitude (e)	304	0.055^{*} 0.000 -0.005 Pml	**93**	0.082^{*} 0.000 -0.004 Pml	**126**
No. host spp. attacked (r), parasitoid mean latitude (e), the degree of study (c)	304	0.045^{*} 0.000 0.254 D -0.003 Pml	**106**	0.067^{*} 0.000 0.249 D -0.003 Pml	**139**
No. host spp. attacked (r) and parasitoid geographic range (e)	304	0.055^{**} 0.000 0.097 Pgeo	**93**	$0.082^{**(**)}$ 0.000 0.099 Pgeo	**126**
No. host spp. attacked (r), parasitoid geographic range (e), the degree of study (c)	304	*0.055* 0.000 0.065 D 0.032 RPge	**106**	$0.082^{**(**)}$ 0.000 0.063 D 0.036 Rpge	**139**

species, whereas those parasitoids located in both tropical and temperate areas attack the broadest range of hosts.

There is a significant negative relationship between the number of host species attacked and parasitoid mean latitude across species (Spearman R = -0.148, N = 304, $P = 0.010$) and in both PR analyses (Table 4.23). When controlling for the degree of study, there is a significant negative association between the number of host species attacked and parasitoid mean latitude across species (Partial correlation coefficient = -0.1655, df 301, $P = 0.004$), which is also found in both PR analyses (Table 4.23, Figure 4.7).

A significant positive relationship is found between the number of host species attacked and parasitoid geographic range across species (Spearman R = 0.283, N = 304, $P < 0.001$), which remains significant after sequential Bonferroni correction. This is also found for both PR analyses (Table 4.23). A significant positive relationship is found between the number of host species attacked and parasitoid geographic range, when controlling for the degree of study, across species (Partial correlation coefficient = 0.195, df = 301, $P = 0.038$). When controlling for the degree of study, across both the response (the number of host species attacked) and the explanatory (parasitoid geographic range) variables , a significant positive relationship is found in the composite cladogram PR analysis (Table 4.23, Figure 4.8).

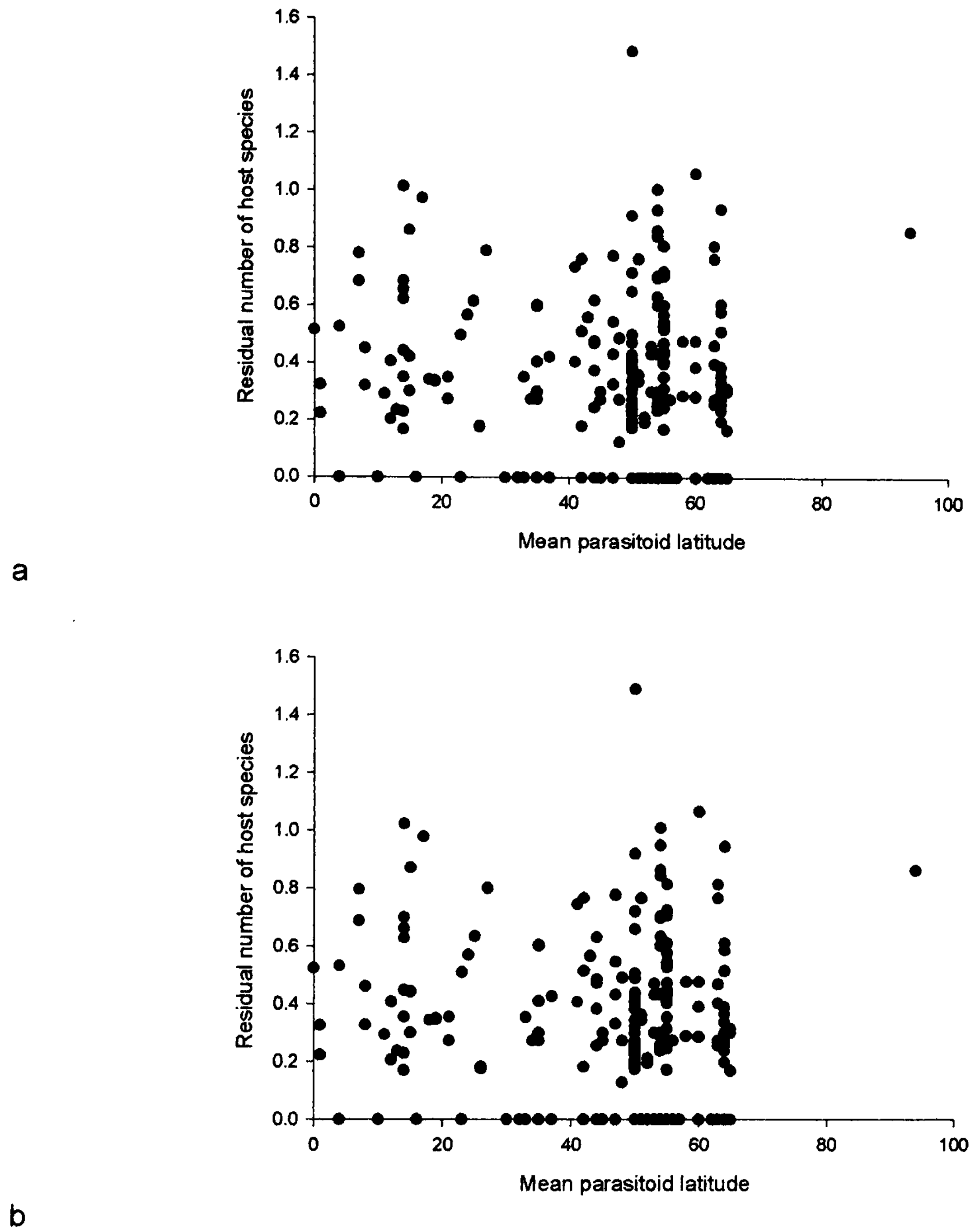


Figure 4.7: Residual number of host species attacked against mean parasitoid latitude for a) the taxonomic and b) the composite cladogram.

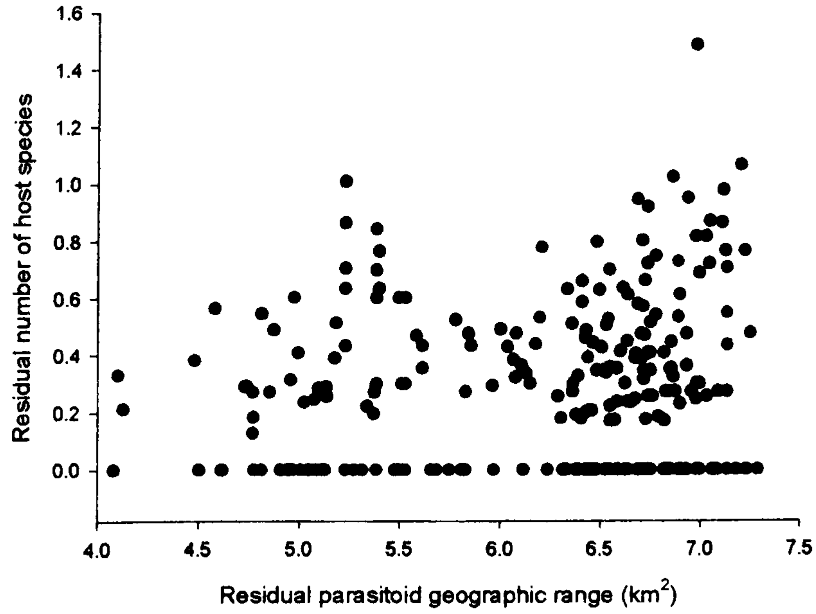


Figure 4.8: Residual number of host species attacked against the residual parasitoid geographic range (km^2).

4.5 Discussion

4.5.1 Main findings

The major findings of this study are as follows:

1. There is some degree of support for the dichotomous hypothesis, both in extant species phenotypes and in terms of evolutionary correlations.
2. There is evidence for trade-offs, both in extant species phenotypes and in terms of evolutionary correlations, and evidence of allometric relationships between some variables in the data set.
3. Parasitoid body size and brood size are associated with host body size.
4. Both host geographic range and the number of host species attacked are associated with parasitoid geographic range.

These will be discussed in turn below.

4.5.2 Dichotomous hypothesis

As expected, we find evidence to support the dichotomous hypothesis; the basis of which is that ectoparasitoids are associated with idiobionts and endoparasitoids are associated with koinobionts. This association is found in the across species and phylogenetic analyses. Parasitoids developing inside their host are more likely to permit their host to continue to develop for a time post-parasitism, whereas parasitoids that develop external to their host are more likely to prevent their host from developing post-parasitism, or to attack those host stages which are non-active (Askew & Shaw 1986). Gauld (1988) discussed possible reasons why this association would occur, with reference to the Ichneumonoidea. The primitive state for this superfamily is hypothesized to be an idiobiont ectoparasite, attacking hosts concealed in plant tissue. The evolution of koinobiosis is thought to have allowed parasitoids to attack exposed hosts, with the parasitoids developing after the hosts concealed themselves. However, this strategy is risky as there is a high probability of egg mortality due to factors like egg desiccation, host moulting and host movement. The evolution of endoparasitism would mean that those risks would not be problematic. However in some instances, endoparasitism may have evolved prior to koinobiosis to overcome the problem of increased exposure on host pupae. An alternative hypothesis is that endoparasitism was ancestral to the braconids (Dowton *et al.* 1998). However, some parasitoids are known to exhibit koinobiont ectoparasitism, for example in the Adelognathinae (Ichneumonidae), whereas idiobiont endoparasitism is relatively rare (Gauld 1988).

Previous studies have suggested that koinobiont endoparasitoids have more restricted host ranges, due to the intimate relationship between the parasitoid and the host than idiobiont ectoparasitoids (see Askew & Shaw 1974 & 1986, Godfray 1994, Mills 1992, Müller *et al.* 1999, Sato 1990, Sheehan & Hawkins 1991). Koinobiont endoparasitoids have to overcome the host's internal defences to successfully develop to adulthood, which may require the parasitoid to evolve specialist adaptations to overcome this. There may be fitness trade-offs involved for those parasitoids adapting this more specialized strategy. We failed to find a relationship, either across species or within the PR analyses, between the number of host species attacked and ecto- / endoparasitism or idio- / koinobiosis. There may be several confounding variables that mask the affect of this relationship, for example the degree of study, latitude, or geographic range. In contrast to the above studies, our data are taken from species attacking many different types of host and many different geographical locations.

The relationships between ecto- / endoparasitism, idio- / koinobiosis, host exposure and host niche are thought to have come about due to the life history switch from idiobiont ectoparasitism to koinobiont endoparasitism, that has been influenced by shared host taxonomy and ecology (Gauld 1988). Cross-species analysis revealed a relationship between idio- / koinobiosis and host exposure (Table 4.6). Koinobionts were found to attack mostly hosts in exposed locations and concealed locations rather than semi-concealed locations. Ichneumonoid koinobiont species are commonly found to utilise hosts feeding in exposed locations (Gauld 1988, Shaw 1983), although they are also known to attack hosts concealed in plant tissue (Belshaw & Quicke 2002). Informal Ichneumonoidea comparisons have also found this relationship (Belshaw *et al.* 1998, Gauld 1988). As we find host exposure a crude measurement of host ecology, we also used the variable of host niche, which provided a more detailed categorisation of host concealment (see Mayhew & Blackburn 1999). We found a significant phenotypic association between host niche and a) ecto– / endoparasitism, and b) idio- / koinobiosis. Approximately two thirds of the species that we had data for were endoparasitoids / koinobionts, the majority of which were associated with hosts found in exposed locations, endoparasitoids were the least prevalent on hosts found in concealed niches. However, some koinobionts were prevalent on hosts found in concealed niches, for example borers, although it was not clear whether these parasitoids attacked the host before it had begun to 'bore'. On the other hand, ectoparasitoids were more associated with hosts found in those niches that could be classed as concealed and semi-concealed. Idiobionts were more associated with hosts found in semi-concealed niches (for example casebearers) and concealed niches (for example frugivores). Those species associated with casebearer host niches all belong to the Agriotypinae (Ichneumonidae) and are all idiobiont ectoparasitoids. Although we found associations across species, none of the PR analyses were significant. A likely reason is that transitions to different hosts have occurred relatively rarely (Table 4.6 & 4.9). This shows the value of phylogenetically based analyses.

Previous studies have found koinobionts to have longer preadult lifespans than idiobionts (see Blackburn 1991a, Mayhew & Blackburn 1999), which may ultimately be due to idiobionts suffering higher mortality rates than koinobionts, as their hosts may be more vulnerable to attack (Askew & Shaw 1986, Blackburn 1991a/b). Alternatively it may also be because koinobionts delay their development until the host has reached a suitable size (Godfray 1994). However, we failed to find any support for this relationship, which may be because we did not have sufficient information available for preadult lifespan, resulting in low sample sizes. The majority of species, for which preadult lifespan information was available, were mostly larval parasitoids and may develop quickly regardless of whether they are koinobionts or idiobionts. Idiobionts are expected to grow quickly as the resources provided by the host degrade quickly. Koinobionts may also develop quickly as the larval host stage is an active one, itself growing quickly, resulting in the parasitoid also having to develop rapidly. Alternatively, there may be many confounding variables that need to be controlled for (for example host size and latitude). With regards adult longevity, we found that ectoparasitoids / idiobionts live longer than endoparasitoids or koinobionts (see Mayhew & Blackburn 1999). Adult longevity has been hypothesized to reflect trade-offs between fecundity and survival (see Ellers 1996, Ellers & van Alphen 1997), and factors such as predation risks (see Gauld 1987).

Mayhew and Blackburn (1999) found that ectoparasitoids and / or idiobionts had larger eggs than endoparasitoids and / or koinobionts. This may be due to the developing ectoparasitoids / idiobionts requiring a greater amount of resources prior to larval feeding than the latter parasitoids, which can instead absorb nutrients from the host prior to hatching (Godfray 1994, Shaw & Huddleston 1991). Alternatively, it may be because endoparasitoids have to inject their eggs into a host's body and it may be more adaptive for the parasitoid eggs to be small in size. In this study, we find that ectoparasitoids have larger eggs than endoparasitoids, but only when controlling for fecundity. In the taxonomic PR analysis, idiobionts had larger eggs than koinobionts, although the opposite and unexpected trend was apparent in the cross-species analysis. This may be due to a bias in the data set; there may be a few large koinobiont species laying large eggs that nonetheless have smaller eggs than related idiobionts. Endoparasitoids were found to be more fecund than ectoparasitoids, both across species and in the taxonomic analysis, although no relationship was found between fecundity and idio- / koinobiosis. Mayhew and Blackburn (1999) suggested reasons why endoparasitoids / koinobionts might have a higher fecundity than ectoparasitoids / idiobionts. Endoparasitoids / koinobionts might experience a higher rate of juvenile mortality because they attack more exposed hosts, which experience a high mortality rate themselves, also endoparasitoids might be out-competed by ectoparasitoids (Price 1974). There may be a trade-off between fecundity and survival. Endoparasitoids may not live as long as ectoparasitoids, however they are more fecund, which may result in them attacking a greater proportion of hosts than ectoparasitoids (Ellers *et al.* 1998).

4.5.3 Trade-offs and allometries

Studies like that of Mayhew (1998) suggest that body size and brood size are negatively evolutionarily correlated, which was found in the taxonomic PR analysis. Body size and brood size are expected to have a negative association if they trade-off for a given host size, and this found in the cross-species and taxonomic PR analyses. The comparative analysis carried out in chapter 3 failed to find a significant evolutionary correlation between these variables, although the cross-species result was significant. It was then suggested that any association between these variables may be dependent upon a number of confounding variables (for example host size, host stage attacked, or development mode) remaining constant. In this study host stage attacked is more constant as is parasitoid body size, and this may be one explanation. A trade-off between egg volume and fecundity was found for the PR analyses only; parasitoids with high lifetime fecundities lay smaller eggs. This trade-off has been demonstrated previously in the ichneumonids (Price 1974) and the parasitoid Hymenoptera (Blackburn 1991b). Thus suggesting that those parasitoids with high lifetime fecundities, that lay smaller eggs, have allocated more resources to reproduction than survival. This, in turn, suggests that resources allocated to reproduction are relatively fixed such that greater fecundity can only be achieved at the cost of smaller eggs.

We identify a positive phenotypic association between parasitoid adult body length and a) preadult lifespan and b) adult longevity, however no evolutionary correlations were identified. Larger parasitoids take longer to grow presumably because of limits on growth rate. A positive evolutionary correlation is found between egg volume and parasitoid adult body length. Larger parasitoids produce larger eggs and larger eggs provide developing offspring with a greater amount of resources. This may be a result of physiological constraints, or of a selection advantage to produce larger offspring if they must grow to a larger final size.

Although host size was not found to be associated with preadult lifespan, there was an evolutionary association, for the taxonomic analysis, between preadult lifespan and host stage attacked. Parasitoids attacking larval host stages have the shortest preadult lifespans whereas those attacking pupal host stages have the longest preadult lifespans. This may be due to the degradation of host resources over time. Pupal host stages are quiescent, whereas larval host stages are active. Larvae are soft bodied and therefore perishable in comparison to pupae. Those parasitoids developing within larval host stages may have to develop rapidly in order to exploit the host resources before they degrade. Host stage attacked was also associated with parasitoid body length, both across species and in the taxonomic PR analysis. Parasitoids attacking nymphal host stages have the smallest body sizes and those attacking egg or pupal host stages have the largest body sizes. Nymph hosts are aphids, known to have a very small body size and hence limited resources for parasitoid development, even if they continue to develop to adulthood. Although egg host stages are the smallest host stage available for attack, they are producing the largest bodied parasitoids. This is probably a result of koinobionts attacking these host stages and allowing them to grow considerably post-parasitism. It is expected that pupal host stages, being one of the largest host stages available for a parasitoid to attack, produce the largest bodied parasitoids also.

4.5.4 Parasitoid body size, brood size and host body size

Parasitoids attack hosts differing in a) body size, b) development stage, c) ecological niche and d) taxonomic group. Host size is predicted by theoretical models to be a critical factor influencing parasitoid body size and brood size across species (see Mayhew & Glaziot 2001). Here we find a positive evolutionary and phenotypic relationship between parasitoid body size and host body size, and a phenotypic association between brood size and host body size, when parasitoid body size was controlled for. Other comparative analyses have provided evidence for these relationships (see Le Masurier 1987, Mayhew & Hardy 1998). Some previous studies have used host stage attacked as a crude measurement of host size (see Mayhew & Blackburn 1999, chapter 3). Instead, we measured the adult body length of the host, which we believe to be a more suitable variable than host stage attacked, as some host stages can vary enormously in size with different host species.

The cross-species analysis revealed that solitary parasitoid species are larger than gregarious species. This result is expected as juvenile parasitoids, which develop gregariously, have to share the host resource, whereas solitary species do not. A cross-species and evolutionary correlation (composite cladogram only) were found between solitary / gregarious development and host body length, with gregarious species being associated with larger hosts than solitary species. Indeed, Godfray (1987b) suggested that a gregarious strategy might evolve when parasitoids attack hosts that can support many parasitoids.

A phenotypic relationship was found between solitary / gregarious development and pupation site. All ectoparasitoid species are, by definition, found to develop externally to the host. Therefore we were more interested in the pupation sites of endoparasitoid species, where we found a phenotypic association. Gregarious parasitoids have already been shown to attack larger bodied hosts than solitary parasitoids. This may be facilitated by an increase in clutch size, which would allow the developing parasitoids to completely consume their host and develop inside its puparium. With regards solitary parasitoids, there are approximately equal numbers pupating inside the host's body and pupating externally to the host's body and puparium. It may be the case that those with the former pupation site are attacking smaller hosts, which are completely consumed therefore allowing parasitoid pupation to occur inside the hosts' body. On the other hand, those with the latter type of pupation site may be attacking larger hosts, which they are unable to fully consume. Excess host tissues may prevent the parasitoid from successfully pupating, leading to the need for an external pupation site. It has been suggested that an external pupation site can reduce the risk of being unable to consume larger host species, and might be more favourable to the evolution of gregariousness (see Harvey *et al.* 2000). Within this data set, there are no gregarious species with pupation sites 'external to the host's body and puparium' (Table 4.19). However, if one is to class pupation sites as either inside or outside the host's body, then 18 out of the 19 gregarious species pupate outside of the host's body.

4.5.5 Parasitoid geographic range and geographic distribution

Phenotypically, temperate parasitoids had longer preadult lifespans than tropical parasitoids. This is an expected result as development takes longer at lower temperatures (Blackburn 1991a). An increase in geographic range with an increase in latitude was hypothesised (Rapoport's rule) (see Stevens 1989). A relationship was found between residual parasitoid geographic range and distribution, where tropical species had smaller geographic ranges than temperate ones and species found in both tropical and temperate locations had the largest geographic ranges. Cardillo (2002) also found this to be the case for Holarctic birds.

An increase in parasitoid body length corresponded with an increase in geographic range, but only phenotypically, although this relationship did not remain significant when the degree of study was controlled for. Parasitoid and host geographic ranges are positively correlated, even when the degree of study was controlled for. This intuitively makes sense, as parasitoids should only be found in those locations where suitable hosts are found. Studies of the Glanville fritillary butterfly (*Melitaea conxia*) have shown that the population size of the butterfly has a significant positive effect on the presence of local populations of the parasitoid species attacking it (*Cotesia melitaearum* and *Hyposoter horticola*) (Lei & Hanski 1998). It may be that larger bodied species have the ability to disperse further and hence expand their ranges more than smaller bodied individuals. Lei & Hanski (1998) found that the larger bodied *Hyposoter horticola* (12mm) had a greater dispersal rate than the smaller bodied *Cotesia melitaearum* (4mm). Alternatively, if parasitoid species have been much studied and have a greater than expected geographic range, they may have been studied more because of apparency, for example if they are found in exposed locations, or are larger bodied. Therefore not all bias in the degree of study may be controlled for the degree of study.

4.5.6 Number of host species attacked

Parasitoid host range is evolutionary correlated to host stage attacked in the taxonomic analysis, even when controlling for the degree of study. Parasitoids attacking larval host stages had the smallest number of hosts, whereas those attacking nymphal host stages had the greatest host numbers. The majority of parasitoids in this study attack larval host stages and are mostly endoparasitoid / koinobionts. These parasitoids have had to adapt to utilise their hosts, due to the intimate way in which they interact with them, therefore they are more likely to be specialised on a few hosts. With regards parasitoids attacking nymphal host stages, they may be shown to have a wide host range as many of these parasitoids have been used as biological control agents. They have been introduced into new environments where they have successfully exploited novel hosts (see Gonzalez *et al.* 1995, Hufbauer 2002, Huffaker & Messenger 1976).

Tropical parasitoids are found to attack fewer host species than temperate species. There is a negative relationship between parasitoid mean latitude and the number of host species attacked, and a positive relationship between parasitoid geographic range and the number of host species attacked. The resource fragmentation hypothesis states that as host diversity increases towards the tropics, each host population density decreases, until the host population density is too low to support specialist parasitoids (see Janzen 1981, Janzen & Pond 1975). In other words, more generalist parasitoids are expected towards the tropics. An alternative explanation is that of the nasty host hypothesis (Gauld *et al.* 1992). Tropical woody plants have on average more chemical toxins than temperate plants. Therefore any herbivores feeding on these trees will also contain more toxins. Due to these high toxin levels, parasitoids would have to evolve specialist adaptations to overcome these potentially fatal toxins. Therefore tropical species may experience more severe fitness trade-offs if they are generalists because of these nasty hosts. The data in this study are consistent with the nasty host hypothesis, but not of the resource fragmentation hypothesis.

4.5.7 Analytical issues

Several analytical issues arise from our work. Firstly, we compiled a composite cladogram, which provided us with a higher degree of resolution (a greater number of nodes) than the taxonomy. The composite cladogram was constructed from a number of molecular studies, some of which combined morphological data, and were carried out at different taxonomic levels. However, the composite cladogram only provided significant results on a few occasions. This may be due to; a) the taxonomic analysis producing false positive results (Type I errors) or b) because the taxonomy provides a better representation of the true phylogeny than the composite cladogram, due to the method and / or studies used to construct the cladogram. Benton (1998) gathered 206 mammalian cladograms and found that those trees based on morphological, rather than molecular data, seemed to match the known fossil record better. This suggests that molecular phylogenetic studies are not always more reliable than morphological studies and consequently, that the taxonomic analyses may be more reliable. To overcome this problem a better, more substantial, working phylogeny for the Ichneumonoidea is required. The comparative analysis carried out in chapter 3 also used taxonomy as well as two cladograms constructed from a number of phylogenetic studies. Unlike this current study, the cladograms used in chapter 3 improved the power of the analyses in comparison to the taxonomic analysis more significantly than those used here. This resulted in several relationships being much more significant when phylogenetic evidence was taken into account.

Secondly, we lacked substantial information for several variables (for example pupation site, egg volume, fecundity, preadult lifespan) which meant that certain analyses lacked power due to a poor representation of species and fewer contrasts between nodes. More detailed information needs to be gathered to correct this, although the information for some variables is either scarce and / or of poor quality in the literature.

Thirdly, body length (mm) data was gathered for both parasitoid and host. Body length has been criticised as a suitable life history variable. It has been argued that body dry mass is a more accurate and comparable measurement (see Blackburn 1991a). Sexual dimorphism, for either parasitoids or their hosts, was not accounted for either, due to the time frame, availability of specimens and information in the literature (Gauld & Fitton 1987). Nonetheless body size does appear to be a useful variable here because it associates significantly with other traits in the direction predicted.

Fourthly, there are many problems associated with determining the geographic range of a species (see Gaston 1990, Udvardy 1969). The data required to accurately map geographic range is not always available, as distribution maps may be inaccurate, the number of species for which there is detailed information available is small, as well as species misidentifications in the literature. Bigger geographic regions may give larger apparent geographic ranges (for example Russia or Canada) as the area taken up by bodies of water are not accounted for. We assumed that presence in a country meant presence over the whole country, which is unlikely to be true and is a potential source of bias.

Finally, it is assumed that, by controlling for the degree of study per parasitoid species, there is an underlying biological reason why some residual values are larger than others. For example, high residual numbers of host species attacked is taken to indicate that the parasitoid is a relative generalist. However, it may merely indicate more apparent hosts. In addition, we have assumed that the degree of study causes apparent geographic range, host range etc. to increase, rather than vice-versa. These are all untested assumptions.

4.5.8 Conclusions

Blackburn (1990) compiled a large comparative data set on the parasitic Hymenoptera, and several previous analyses have used this data set (see Blackburn 1991a/b, Mayhew & Blackburn 1999, see also chapter 3). In comparison to Blackburn's data, the current data set only concerns the Ichneumonoidea, which means that certain life history traits apparent in Blackburn's data set are not as relevant here. For example, Blackburn included many species of microhymenoptera (the Chalcidoidea). Many of those species have very small body sizes, attack the egg host stage, and often attack Hemiptera hosts. In comparison, within the Ichneumonoidea there are few a) very small bodied parasitoids, b) egg parasitoids and c) species attacking Hemiptera hosts. Therefore some results highlighted from Blackburn's data set may not be shown within the Ichneumonoidea. Also we compare close relatives, have included more relevant variables and have used cladistically based phylogenetic estimates.

Our data suggest that across the Ichneumonoidea (Hymenoptera) several biological transitions (such as endoparasitism / ectoparasitism and koinobiosis / idiobiosis) regulate life history variation, such as adult longevity, preadult lifespan and fecundity. Aspects of the host's ecological niche (such as degree of host exposure, and distribution) and life history (such as body size) also influence parasitoid life history variation.

Comprehensive mathematical theories of parasitoid life history variation, like those for mammals (see Charnov 1993, 2001, Kozlowski & Weiner 1997), are still required and are the next important and essential step forward. Some limited theories are known for example Mayhew & Glaziot (2001), which address three traits simultaneously (body size, clutch size and solitary / gregarious development). Although the dichotomous hypothesis explains some parasitoid life history traits, not all parasitoid life history traits are determined exclusively by this dichotomy. Theories explaining clutch size variation are already available (for review see Godfray 1994, pp. 99-106). However, theories to explain the dichotomous hypothesis and various life history transitions are still required. Aspects of the dichotomous hypothesis will need to be incorporated into a model explaining parasitoid life history variation, but this model should also include details of trade-offs, and importantly aspects of the host as a resource. In order to achieve this, more detailed and good quality data is required, which should fill in any gaps in parasitoid life history knowledge.

Chapter 5: The evolutionary lability of life history traits in the Ichneumonoidea (Hymenoptera)

Ruth E. Traynor & Peter J. Mayhew

5.1 Abstract

Assessing the evolutionary lability of traits can help to formulate evolutionary hypotheses about life history evolution. Several metrics (ρ in phylogenetic regression, the retention index and the proportion of variance due to different taxonomic levels) are used to assess the evolutionary lability of life history traits within the Ichneumonoidea. Values of ρ indicate that life history traits are less labile than ecological traits. However, there was no difference in lability between traits defined as a) categorical and continuous or b) morphological and behavioural. Several constrained traits are identified, including ecto- / endoparasitism, idio- / koinobiosis, solitary / gregarious development, pupation site, brood size and fecundity. Both parasitoid body size and host body size are conserved, as is host order attacked. However, parasitoid longevity and preadult lifespan are not conserved. Labile traits include parasitoid and host geographic ranges and mean latitudes, host niche, host stage attacked and killed, parasite window and the number of host species attacked. For the majority of traits studied, the most variance is observed at family or subfamily level. These results suggest that much trait evolution occurred early in the history of the Ichneumonoidea.

5.2 Introduction

Evolutionary lability describes the ease and speed with which a trait evolves over time. Knowledge of the evolutionary lability of a trait can aid the formulation of appropriate hypotheses. For example, traits that have evolved rapidly in the recent past are likely to be associated with recent events that provide a source of directional selection. In contrast, traits that are constrained in their evolution or diversified only in the distant past are likely to be associated with events long past, or may require more mechanistic types of explanation.

The neo-darwinian synthesis set out the general framework for understanding different rates of evolution. Rapid evolution is promoted by directional selection pressures, or circumstances that favour stochastic processes, such as drift and founder effects. It also requires an absence of constraints, such as lack of genetic variation or interdependence between the different traits that make up a phenotype, which manifest themselves as physiological or developmental constraints. Traits that evolve only slowly however, may be subject to stabilising selection, or may be constrained by low genetic variation or physiological and developmental links with other traits.

These ultimate variables may themselves vary systematically over the lifetime of a clade, or between traits of different type. During an adaptive radiation species may rapidly diversify in form, for example by competitive release giving rise to strong directional selection. Later on when the species richness of the clade rises, diversity of form (disparity) may slow due to stabilising selection caused by competition. Such processes have been advocated to explain some of the prominent patterns over the history of life, such as the Cambrian explosion and the Tertiary radiation of mammals. However, it is possible that other processes may also contribute to such patterns. For example Gavrilets (1999) described a model for the diversification of binary characters which showed an early peak in disparity. This is simply due to geometric constraints on character evolution. In such characters there is a limit to the number of forms that can evolve and therefore evolutionary rates must inevitably slow. In contrast, similar models for continuous characters show a more gradual diversification of form (Foote 1996).

Traits of different type may also vary in their evolutionary rates. Many authors have suggested that behavioural traits are more malleable and can respond to immediate ecological, environmental, or social situations affecting a species (see Gittleman *et al.* 1996a, Lorenz 1965, Mayr 1963). Behavioural change is said to precede morphological change in many instances (see Arnold 1992, Wcislo 1989) and has also been shown to affect morphology (see Basolo 1990). Behavioural traits appear to have a lack of constraints affecting their evolution. Several factors can aid behavioural evolution, including offspring copying parental behaviour and species learning to exploit novel environments due to inherited capacities. It can also be aided by an increase in genetic variability of offspring, due to behavioural invasion of a novel environment, structural or physiological constraints being compensated for by behavioural plasticity and behavioural traits developing later than structural traits in ontogeny (Gittleman *et al.* 1996a).

Morphological traits in contrast can be highly constrained by physiological factors that prevent rapid evolution taking place. For example, a change in body size may necessitate changes in many different life history characters, such as metabolic rate, development rate and structural characteristics. Ecological traits have also been suggested to be more flexible than many morphological traits (Gittleman 1993) and can be affected by strong selection pressures, such as competition, predation and parasitism, or dispersal ability, as well as physical or chemical environmental factors. Alternatively, some morphological traits do change both rapidly and significantly with environmental change, in a similar way to behavioural characters (James 1983).

It is generally appreciated, amongst comparative biologists, that categorical characters will generally show less evolution than continuous variables when mapped onto a phylogenetic tree (see Mayhew & Pen 2002). There are many possible contributing causes, for example continuous variables are more susceptible to measurement error, such that two individuals that do not in fact vary are likely to produce more variable continuous rather than categorical data. However there are more interesting evolutionary possibilities: multiple genes may code for quantitative characters and hence show greater genetic variation. Categorical characters may also be associated with major transitions in biology and hence more subject to developmental constraints.

Many studies on evolutionary rates have focused on morphological traits, as they are easily preserved in the fossil record and therefore relatively easy to study (see Fenster & Sorhannus 1991). However other traits, for example behavioural and ecological traits, are poorly preserved in the fossil record and therefore other methods, like comparative studies, are required to analyse evolutionary change (Gittleman & Decker 1994). Phylogenies can provide information about changes among taxa with areas of divergence (nodes) and branch lengths (time) being used to estimate rates of trait evolution (Maddison & Maddison 1992). In this chapter, both phylogenetic and taxonomic information is used to address the lability of trait evolution in Ichneumonoidea parasitoids.

Parasitoids are insects that, whilst free living as adults, develop to maturity by feeding on and killing an arthropod host. They are a very diverse group and exhibit much greater developmental variation than any other arthropod group (Strand & Grbic 1997). They have long been known as good study subjects for addressing life history evolution (see Godfray 1994, Harvey & Strand 2002, Harvey *et al.* 2000), as they normally obtain their resources for development from a single source, the host. The Ichneumonoidea is the largest superfamily within the Hymenoptera, with an estimated 150,000 species within the two extant families: the Braconidae and the Ichneumonidae (Belshaw *et al.* 1998, Gauld & Shaw 1995). Due to the wealth of information, as well as the numerous phylogenetic hypotheses (see Belshaw *et al.* 1998, Belshaw *et al.* 2003, Dowton 1999, Dowton & Austin 1998, Dowton *et al.* 2002, Quicke *et al.* 2000) available for this superfamily, they are a useful group to use to study trait lability.

Although parasitoids display many traits that are common to all organisms (such as size at maturity or body size), others are unique to the group. Idiobionts are parasitoids that permanently paralyse their hosts by using lethal or paralysing venom at the time of oviposition, then the developing parasitoid larva rapidly consumes the host. Koinobionts temporarily paralyse their host, allowing it to resume development for a time post-parasitism, the parasitoid larva remains inactive until the host reaches a suitable stage for final consumption to take place. Ectoparasitoids oviposit on or near their host and parasitoid larvae complete development outside the host's body. Endoparasitoids oviposit into their host's body, where the developing larvae consume the host's haemolymph and / or tissues internally. Endoparasitoids normally complete their development internally to the host, but sometimes they complete development externally. Solitary development is when only a single parasitoid offspring successfully completes development per host, here larvae display contest competition or siblicidal behaviour (Godfray 1994). Gregarious development is when several offspring can successfully complete development per host and larvae display scramble competition (Quicke 1997).

Some authors have speculated on the lability of various parasitoid life history traits. Both Shaw (1983) and Gauld (1988) addressed the evolution of different host utilisation patterns, such as ecto- / endoparasitism and idio- / koinobiosis, within the Ichneumonoidea. Changes in behavioural and ecological traits have been suggested to precede the evolution of koinobiont endoparasitoids from idiobiont ectoparasitoids. Several adaptations may also be required to adopt these strategies: koinobionts need to produce venom that will temporarily paralyse their hosts and endoparasitoids have to avoid or overcome internal host defences. Overall then, one should expect idio- / koinobiosis and endo- / ectoparasitism to be relatively constrained and slowly evolving traits.

Godfray (1987b) addressed the evolution of solitary and gregarious larval development, using a genetic model. His work suggested that solitary development is an evolutionary trap or 'black hole' (Harvey & Partridge 1987), in that gregarious development should not be able to readily evolve from solitary behaviour. This is because in mixed broods of solitary and gregarious parasitoids, such as those formed from a gregarious mutant female of a solitary species, those that are solitary will kill those displaying gregarious behaviour and the trait will not spread. Some empirical work supports the Godfray model (Le Masurier 1987), but other work is less supportive and suggests that the trait is less constrained than Godfray's model might predict (see Boivin & van Baaren 2000, Mayhew 1998, Mayhew & Hardy 1998, Rosenheim 1993).

Mayhew and Hardy (1998) addressed the evolution of clutch size and body size in bethylid wasps. They found that body size changed mainly with host size at deep nodes in the phylogeny, but less within genera. It was postulated that this was due to weak selection pressures acting on body size, or that a change in parasitoid body size requires other physiological or morphological changes that slow the selection response. On the other hand, they found that parasitoid clutch size was more labile, in that it changed with host size within genera, as well as within species. This trait may be more labile as wasps can vary their clutch sizes across individual hosts.

Phylogenetic lability can be analysed using several different metrics (see section 1.5.3). In this study three metrics are used to address the evolution of parasitoid life history traits: a) ρ in phylogenetic regression, b) the retention index and c) the proportion of trait variance due to different taxonomic levels (a nested analysis of variance). These were chosen because they do not require a bifurcating phylogeny or branch length estimates and can be applied to both continuous and categorical data.

We hypothesize that:

1. Continuous, behavioural and ecological variables are more labile than categorical, morphological and life history variables respectively, due to the greater physiological constraints affecting the latter variables (see Arnold 1992, Gittleman *et al.* 1996a, Lorenz 1965, Mayr 1963, Wcislo 1989).
2. Most trait variation occurs at the higher taxonomic levels (i.e. family or subfamily levels) (see Clutton-Brook & Harvey 1977, Harvey & Mace 1982, Read & Harvey 1989).
3. Transitions from ectoparasitism or idiobiosis to endoparasitism or koinobiosis are constrained due to the specialist adaptations required to adopt the latter strategies (see Gauld 1988, Shaw 1983).
4. Solitary larval development is a slowly evolving trait (see Godfray 1987, Harvey & Partridge 1987).

5.3 Methods

5.3.1 Data

The data comprise information on 382 Ichneumonoidea parasitoid species, derived from the published literature (Appendix 5, see chapter 4).

The variables investigated are as follows:

Egg volume (mm^3): Calculated from the equation

$$\text{Egg volume} = 4/3\pi \times a \times b^2$$

Where a = half the egg length, and b = half the maximum egg width, which assumes an ovoid egg shape (see Blackburn 1991b).

Larval feeding strategy: Haemocoel or tissue feeders.

Preadult lifespan (days): Total number of days for egg, larval and pupal development.

Parasitoid adult body length (mm): Excluding antennae (and ovipositor where necessary).

Adult longevity (days): The mean longevity per parasitoid species.

Brood size: The mean number of parasitoid offspring completing development per individual host.

Fecundity: The maximum number of eggs reported to be laid by an individual of the species.

Parasitism: Ectoparasitoids oviposit on or near their host and the parasitoid larvae complete development outside the host's body. Endoparasitoids oviposit into their host's body, where the developing larvae consume the host's haemolymph and or tissues internally. Endoparasitoids normally complete their development internally to the host, but can sometimes complete development externally to the host.

Solitary or gregarious development: Solitary wasps are those whereby only a single individual successfully completes development per host. Gregarious development is when several offspring can successfully complete development on each host.

Development mode: Idiobionts permanently paralyse their hosts, using lethal or paralysing venom at the time of oviposition, with the parasitoid larva rapidly consuming the host. Koinobionts temporarily paralyse their host but allow it to resume development for a time post-parasitism. The parasitoid larva remains inactive until the host reaches a suitable stage for final consumption to take place.

Pupation site (4 states): Inside the host's body, under the host's body (for example mummified aphid), inside the host's puparium but outside it's body, external to the host's body and puparium; it was also recorded as 2 states either inside the host's body or external to the host's body.

Parasitoid geographic range (km^2): A list of countries that each species was recorded from in the literature. The area (km^2) for each country was obtained from the national geographic society at http://plasma.nationalgeographic.com/mapmachine/countryprofiles.html and the total area of the list of countries that each parasitoid was recorded from was calculated.

Parasitoid geographic distribution: Temperate species are located in countries that are found north of 23.5^{0}N or south of 23.5^{0}S. Tropical species are located in countries that are found between 23.5^{0}S and 23.5^{0}N. Species found in both temperate and tropical countries were recorded as such.

Parasitoid mean latitude: Calculated by dividing the maximum plus the minimum absolute latitude, of the countries where the parasitoid is found, by two.

Host stage attacked (6 states): Egg, nymph, larva, prepupa, pupa, adult; it was also recorded as 15 states which included combinations of the above host stages (see Appendix 5).

Host stage killed (4 states): larva, prepupa, pupa, adult; it was also recorded as 9 states which included combinations of the above host stages (Appendix 5).

Parasite window (days): length of time an individual host can be successfully parasitized.

Host exposure: Exposed hosts are fully exposed and occupy no structural refuges, semi-concealed hosts are those that have a slight refuge within their shelter but remain susceptible to parasitoid attack (for example leaf-miners), and concealed hosts are those that are physically protected and generally well concealed (for example borers).

Host niche: external, leaf-miner, leaf-roller, web-spinner, casebearer, galler, borer, root feeder, predator, nest, in vegetation or leaf litter, pollen feeder, in stored grain, decaying plant material, frugivore, saprotroph.

Host adult body length (mm): excluding antennae (and ovipositor where necessary).

Host geographic range (km^2): Compiled per host species from the parasitoid literature, as defined in parasitoid geographic range.

Host geographic distribution: Compiled per host species as defined in parasitoid geographic distribution.

Host mean latitude: Compiled per host species as defined in parasitoid mean latitude.

Parasitoid host range: The total number of host species recorded per parasitoid species. Taken from the literature used in this study.

Degree of study: The total number of pages recorded per parasitoid species. Taken from the literature used in this study, a page is counted if it mentions the parasitoid species of interest. Some parasitoid species have been studied more frequently than other species, for example those used for biological control, or those with a wider geographic range. This variable is used as a control variable.

5.3.2 Analysis

All continuous variables (except mean latitude) were $\log_{10}$ transformed prior to analysis. This ensures that lability is not biased by a few large values that have changed greatly an absolute amount, but not proportionately so. Some parasitoid species have been studied more frequently than others, for example those used for biological control. The degree of study per parasitoid species can be a confounding variable affecting the value of certain traits, such as geographic range and the number of host species attacked. To control for degree of study, residual values were taken by plotting the trait in question against the degree of study and subtracting the raw species values from those predicted by the slope of the regression equation. The regression equations were taken from the phylogenetic regression analyses rather than the raw species analyses as they are less biased by the particular species sampled by the data. The residual values are calculated as follows:

Taxonomic PR analysis: log parasitoid geographic range – (log parasitoid geographic range (0.495) x log degree of study); log host geographic range – (log host geographic range (0.217) x log degree of study); log host range – (log host range (0.313) x log degree of study). Composite cladogram PR analysis: log parasitoid geographic range – (log parasitoid geographic range (0.514) x log degree of study); log host geographic range – (log host geographic range (0.239) x log degree of study); log hosts range – (log host range (0.306) x log degree of study).

The variables were classified in three ways, in order to test the differences between the trait types (independent t-test):

1. Continuous or categorical traits - continuous traits have quantitative values, categorical traits are those that can only take a finite number of states (Harvey & Pagel 1991).
2. Life history or ecological traits – life history traits are those that affect survival and reproduction of a species (Stearns 1992), ecological traits are those that reflect a species spatial relations and how they interact with their environment (Martin and Bateson 1993).
3. Morphological or behavioural traits - morphological traits are those that represent aspects of a species morphology or form, behavioural traits are those that define how a species acts, reacts or functions (Plotkin 1988).

The variables were listed as having the following trait classifications: Parasitism, biosis, solitary / gregarious development, feeding site, and pupation site are categorical, behavioural, life history variables. Preadult lifespan, longevity, fecundity, parasitoid size, and egg volume are continuous, morphological, life history variables. Brood size is a continuous, behavioural, life history variable. Parasitoid and host geographic distribution, host exposure, host stage attacked, host stage killed, host niche, and host order are categorical, behavioural, ecological variables. Parasitoid and host mean latitude, residual parasitoid and host geographic range, host size, the number of host species attacked, parasite window, and the degree of study are continuous, behavioural, ecological variables.

Sequential Bonferroni correction (Rice 1989) was carried out for the t-test analyses. This method assumes that the same null hypothesis (that there are no significant results as a whole) is being tested in all tests. The correction reduces the critical level of significance when multiple comparisons are carried out because of the increased chance of a Type I error (a false positive). As 17 tests were carried out, one would expect 0.85 tests to be significant at $P < 0.05$ by chance alone, but only two were found.

Three alternative metrics of evolutionary lability were used (ρ, the retention index and a nested analysis of variance) and each will be discussed in turn below.

Phylogenetic Regression (ρ value)

Phylogenetic Regression (PR) is an independent contrast method (Grafen 1989). From the raw species data it calculates sets of contrasts, which represent the differences between sister-taxa in the phylogeny, and are evolutionarily independent. PR scales branch lengths of the phylogeny, in order to adopt an appropriate evolutionary model, which is important if evolutionary correlations are to be detected (see Freckleton *et al.* 2002, Harvey & Rambaut 2000, Price 1997). This it does by using a parameter, ρ, which is estimated from the data and the phylogenetic topology.

The ρ value reflects the degree of phylogenetic independence of the data. If there is a high degree of phylogenetic dependence in the data then the ρ value is high (it approaches 1), whereas if there is no phylogenetic dependence in the data then ρ is low (it approaches zero). Freckleton *et al.* (2002) illustrated that ρ is a relatively good estimator of phylogenetic dependence when the number of species analysed is quite large, although it is not so reliable when there are few species included in an analysis. In particular ρ is biased such that small sample sizes tend to produce large values of ρ.

Phylogenetic analyses were performed on those variables that were continuous or binary categorical (as the response variable can only be either continuous or binary) using both the taxonomy (Appendix 6) and the composite cladogram (Appendix 7) (see section 4.3.2).

Retention index

The retention index (RI) is a measure of character fit to a given tree, or a measure of evolutionary lability (how readily characters inverse their states) (Archie 1989a/b, Farris 1989). RI is calculated using the formula:

$$\text{Character RI} = (M_i - s_i) / (M_i - m_i)$$

Here m_i is the minimum possible treelength or the minimum conceivable number of steps for character i on any tree; s_i is the observed treelength or the reconstructed number of steps for character i on the given tree; M_i is the maximum number of conceivable steps for character i on any tree. When RI equals 1, then the character has not changed much relative to how it might have, but when RI equals 0 the character has changed much (Farris 1989). This analysis was implemented in MacClade 4 (Maddison & Maddison 2001).

Nested analysis of variance (ANOVA)

Sokal and Rohlf (1969) originally developed the nested analysis of variance (ANOVA) method, which was later adapted for use with phylogenies (Clutton-Brock & Harvey 1977, Harvey & Clutton-Brock 1985, Harvey & Mace 1982). It is used here to describe how the total variation among species, for a continuous (or in a binary categorical) variable, is distributed among different taxonomic levels. The variance is partitioned into components that represent each nested taxonomic level. The variance distribution, by taxonomic level, is often used to suggest which taxonomic level to use as the unit of analysis, or a taxonomic level at which phylogenetic independence can more or less be assumed.

The formula for this method is:

$$\sigma^2_{tot} = \sigma^2_{s(g)} + \sigma^2_{g(t)} + \sigma^2_{t(sf)} + \sigma^2_{sf(f)} + \sigma^2_{f(spf)}$$

Where σ^2_{tot} is the total amount of variance among species for the trait of interest; $\sigma^2_{s(g)}$ is the total amount of variance among species nested within genera; $\sigma^2_{g(t)}$ is the total amount of variance among genera nested within tribes; $\sigma^2_{t(sf)}$ is the total amount of variance among tribes nested within subfamilies; $\sigma^2_{sf(f)}$ is the total amount of variance among subfamilies nested within families; $\sigma^2_{f(spf)}$ is the total amount of variance among families nested within superfamilies. Then

$$(\sigma^2_{tot} / \sigma^2_{tot}) \text{ x } 100 = [(\sigma^2_{s(g)} + \sigma^2_{g(t)} + \sigma^2_{f(sb)} + \sigma^2_{o(f)}) / \sigma^2_{tot}] \text{ x } 100$$

The left-hand side of the equation equals 100, and the terms on the right hand side become the percentage of variance found at each taxonomic level. The right hand term can be used to compare percentages of different characters variance with the different total variances. Alternatively one can use the terms can be used as cumulative proportions of variance moving from the highest to the lowest taxonomic level (known as intra-cumulative correlations). These are interpreted as the correlation expected between any two data points, selected at random from the same group (Harvey & Pagel 1991).

This analysis was carried out using SPSS® 10.1; univariate analysis of variance; for continuous and binary categorical variables; the dependent variable was the trait of interest, and the random factors were the various taxonomic levels. The syntax line, defining the nesting, read as follows:

Family subfamily(family) tribe(subfamily(family)) genus(tribe(subfamily(family))).

5.4 Results

5.4.1 Comparing metrics

There is a significant positive relationship across all traits, between the taxonomic ρ values and proportion of variance due to family plus subfamily level (Pearson R = 0.439, N = 19, P = 0.043) (Figure 5.1). There is also a significant positive relationship between the taxonomic RI values and the proportion of variance due to family plus subfamily level (Pearson R = 0.882, N = 5, P = 0.048) (Figure 5.2). However, there is no significant relationship between a) the taxonomic ρ and RI values

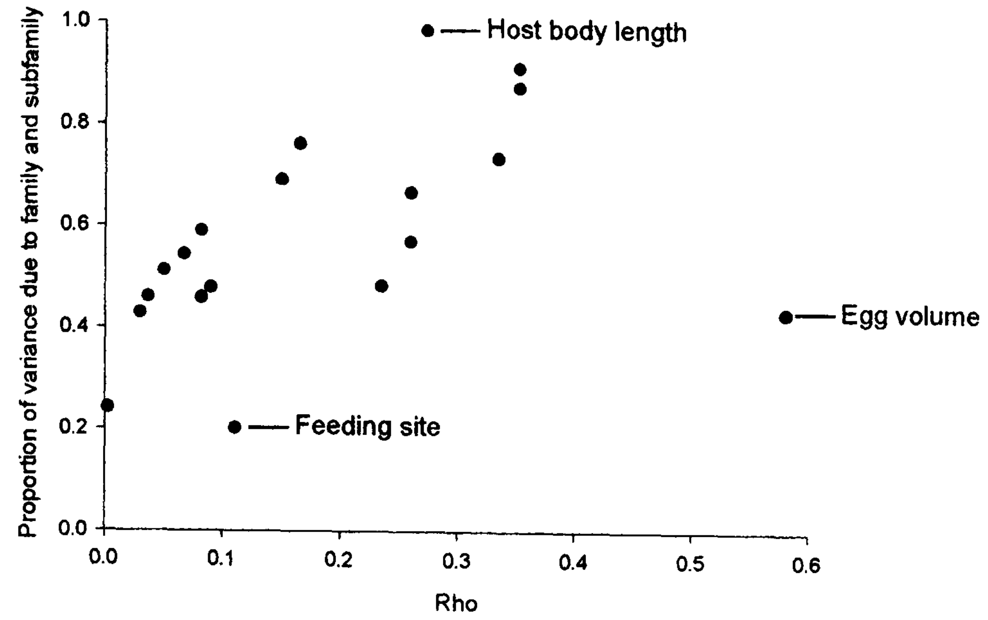


Figure 5.1: Taxonomic ρ values (PR) against the total proportion of variance due to family plus subfamily taxonomic levels (nested ANOVA).

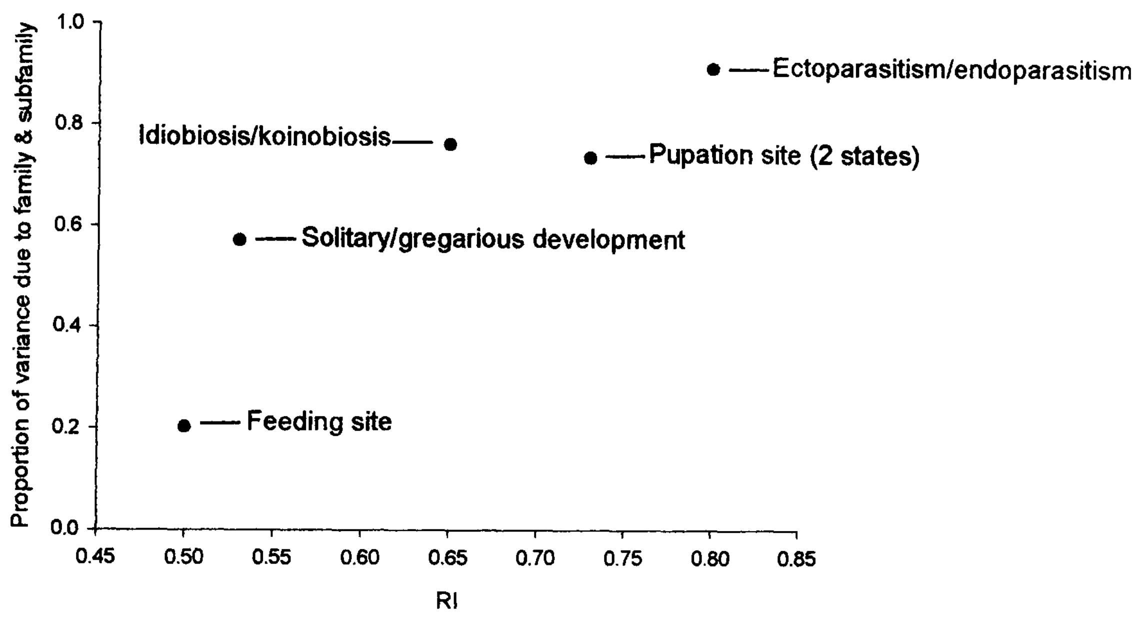


Figure 5.2: Taxonomic RI values against the total proportion of variance due to family plus subfamily taxonomic levels (nested ANOVA).

(Pearson R = 0.773, N = 5, P = 0.126) (Figure 5.3) or b) the composite cladogram ρ and RI values (Pearson R = 0.810, N = 5, P = 0.097). However in both cases power is low, since only a few characters can be compared, and the correlation coefficients are high.

There is no relationship between the number of species for which we have data for and a) the taxonomic RI values (Pearson R = -0.272, N = 17, P = 0.291) (Figure 5.4), b) the composite cladogram RI values (Pearson R = -0.343, N = 17, P = 0.177), c) the taxonomic ρ values (Pearson R = -0.288, N = 19, P = 0.232), and d) the composite cladogram ρ values (Pearson R = -0.278, N = 19, P = 0.249) (Figure 5.5). This suggests that there is no severe problem of bias due to sample size across all traits.

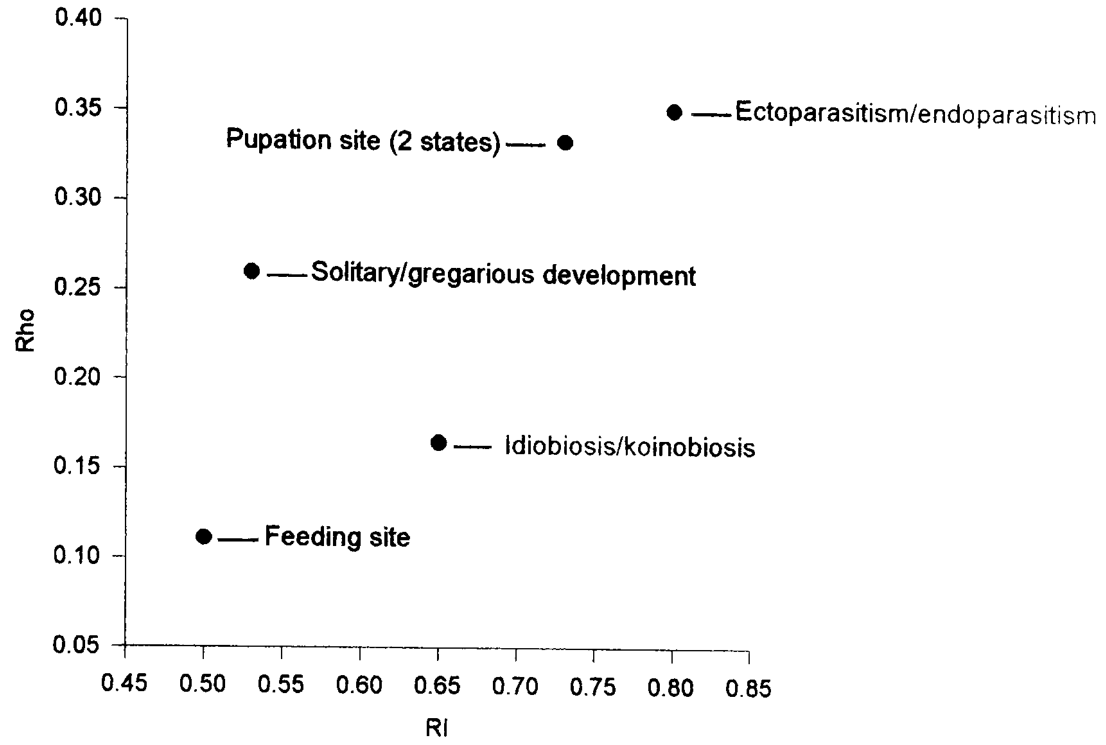


Figure 5.3: Taxonomic ρ values (PR) against taxonomic RI values.

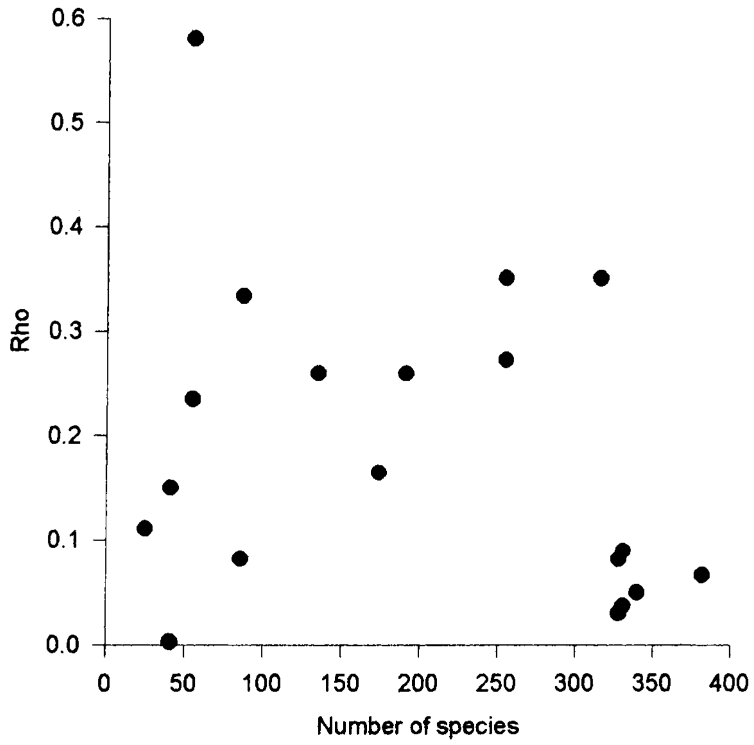


Figure 5.4: Taxonomic ρ values (PR) against the number of species included in the analyses.

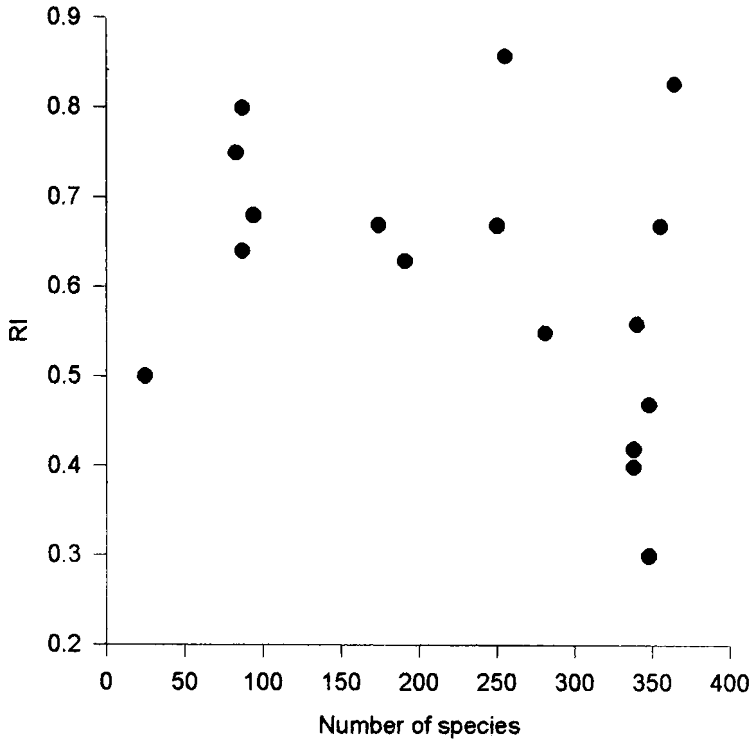


Figure 5.5: Composite cladogram RI against the number of species included in the analyses.

5.4.2 Trait lability

A significant difference is found between life history and ecological trait ρ values for both the taxonomic and composite cladogram analyses, however these results fail to remain significant after sequential Bonferroni correction (Table 5.1). No significant differences are found for the remainder life history versus ecological analyses, or between the categorical and continuous traits, or the behavioural and morphological traits (Table 5.1). However, nearly all the mean values for ρ, RI and the proportion of variance due to different taxonomic levels, were in the predicted direction (continuous, behavioural and ecological variables are less conserved than the categorical, morphological and life history traits) (Table 5.1).

The ρ values for each trait are shown in Table 5.2, RI values are in Table 5.3, and the total proportion of variance due to each taxonomic level is given in Table 5.4. Egg volume has very high ρ values (Table 5.2), where the most variance is found at the subfamily level (Table 5.4). Ecto- / endoparasitism has the highest RI value for any trait both for the taxonomic and composite cladogram (Table 5.3) and has the highest ρ values for any categorical traits (Table 5.2). The greatest proportion of variance in this trait is due to family and subfamily levels of which the latter is highly significant (Table 5.4). Pupation site (both 2 and 4 states) displays high ρ and RI values, where much variance takes place at the family and subfamily level (Table 5.4). Parasitoid and host body lengths display high ρ values (Table 5.2), with the most variance for both traits observed at the family level (Table 5.4). Host order displays very high RI values (Table 5.3).

Solitary / gregarious larval development displays moderate ρ values (Table 5.2) and high RI values (Table 5.3), the greatest proportion of variance is shown at the subfamily level (Table 5.4).

Table 5.1: Differences in lability of categorical and continuous characters, morphological and behavioural characters, and ecological versus life history characters. *P* * values denote the results that do not remain significant after sequential Bonferroni correction.

Response variable	t	df	*P*	Explanatory variable	N	Mean±SE
ρ (Taxonomy)	1.032	17	0.317	Categorical	5	0.244±0.047
				Continuous	14	0.164±0.043
ρ (Composite cladogram)	0.897	17	0.382	Categorical	5	0.284±0.058
				Continuous	14	0.196±0.054
Nested ANOVA (Family)	-0.243	17	0.811	Categorical	5	0.275±0.101
				Continuous	14	0.310±0.078
Nested ANOVA (Subfamily)	1.636	17	0.120	Categorical	5	0.364±0.70
				Continuous	14	0.252±0.033
Nested ANOVA (Family+Subfamily)	0.636	17	0.502	Categorical	5	0.639±0.122
				Continuous	14	0.562±0.052
ρ (Taxonomy)	1.742	17	0.100	Morphological	5	0.280±0.088
				Behavioural	14	0.151±0.032
ρ (Composite cladogram)	1.374	17	0.187	Morphological	5	0.315±0.116
				Behavioural	14	0.185±0.040
Nested ANOVA (Family)	0.044	17	0.965	Morphological	5	0.305±0.150
				Behavioural	14	0.299±0.069
Nested ANOVA (Subfamily)	0.062	17	0.951	Morphological	5	0.285±0.071
				Behavioural	14	0.280±0.036
Nested ANOVA (Family+Subfamily)	0.096	17	0.924	Morphological	5	0.590±0.085
				Behavioural	14	0.579±0.060
ρ (Taxonomy)	3.249	17	0.005*	Life history	11	0.262±0.043
				Ecological	8	0.079±0.030
ρ (Composite cladogram)	2.872	17	0.011*	Life history	11	0.306±0.056
				Ecological	8	0.094±0.039
RI (Taxonomy)	1.156	15	0.266	Life history	6	0.620±0.052
				Ecological	11	0.542±0.041
RI (Composite cladogram)	1.426	15	0.174	Life history	6	0.683±0.053
				Ecological	11	0.573±0.049
Nested ANOVA (Family)	0.187	17	0.854	Life history	11	0.311±0.080
				Ecological	8	0.287±0.103
Nested ANOVA (Subfamily)	1.013	17	0.325	Life history	11	0.309±0.047
				Ecological	8	0.245±0.037
Nested ANOVA (Family+Subfamily)	0.895	17	0.383	Life history	11	0.619±0.064
				Ecological	8	0.531±0.075

Brood size and fecundity display moderate ρ values (Table 5.2) and the greatest proportion of brood size variance is shown at the family level, whereas it is at the subfamily level for fecundity (Table 5.4). Idio- / koinobiosis has moderate ρ (Table 5.2) and RI values (Table 5.3), and again family and subfamily levels explain the greatest proportion of variance (Table 5.4).

Preadult lifespan displays low ρ values (Table 5.2), where variance is mostly observed at the family level (Table 5.4). Larval feeding site has low ρ (Table 5.2) and RI values (Table 5.3), and most trait variance is observed at species level (Table 5.4). Adult longevity displays very low ρ values (Table 5.2), trait variance is mostly observed at the subfamily and tribal levels (Table 5.4).

Table 5.2: Phylogenetic regression results, including the total number of species per analysis and ρ values for the taxonomic and composite cladogram analysis.

Variables	Species	Taxonomy	Composite cladogram
Parasitism (ecto/endoparasitism)	255	0.352	0.370
Biosis (idio/koinobiosis)	174	0.165	0.165
Solitary / gregarious development	191	0.260	0.318
Feeding site (haemolymph / tissue)	25	0.111	0.135
Pupation site (internal / external to the host's body)	87	0.334	0.430
Preadult lifespan	41	0.150	0.165
Longevity	86	0.082	0.067
Brood size	135	0.260	0.370
Fecundity	55	0.235	0.224
'Residual' parasitoid geographic range	328	0.030	0.030
Parasitoid mean latitude	328	0.082	0.122
Parasitoid body length	316	0.352	0.389
Egg volume	55	0.581	0.729
Host body length	255	0.273	0.352
Parasite window	41	0.003	0.003
'Residual' host geographic range	331	0.037	0.037
Host mean latitude	331	0.090	0.111
'Residual' number of host species attacked	340	0.050	0.063
Degree of study	382	0.067	0.082

Table 5.3: Retention index (RI) values.

Variables	Taxonomy	Composite cladogram
Parasitism (ecto/endoparasitism)	0.80	0.86
Development mode (idio/koinobiosis)	0.65	0.67
Solitary / gregarious development	0.53	0.63
Feeding site (haemolymph / tissue)	0.50	0.50
Pupation site (4 states)	0.51	0.64
Pupation site (2 states)	0.73	0.80
Parasitoid geographic distribution (3 states)	0.45	0.47
Parasitoid geographic distribution (combination)	0.30	0.30
Host exposure	0.62	0.67
Host stage killed (9 states)	0.62	0.68
Host stage killed (4 states)	0.66	0.75
Host stage attacked (15 states)	0.54	0.55
Host stage attacked (6 states)	0.66	0.67
Host niche (16 states)	0.51	0.56
Host geographic distribution (3 states)	0.44	0.42
Host geographic distribution	0.40	0.40
Host order	0.76	0.83

Parasite window has the lowest ρ values out of all the traits studied (Table 5.2). Most variance is observed at the genus level (Table 5.4). Residual number of host species attacked displays very low ρ values (Table 5.2), with most variation observed at the subfamily and family taxonomic levels (Table 5.4). Host exposure, host niche, host stage attacked and killed all display low RI values (Table 5.3).

Table 5.4: Nested ANOVA results, numbers indicate the proportion of the total variance that each taxonomic level represents for each trait studied (* $P < 0.05$ ** $P < 0.001$). (Species level is never significant as species proportion value is obtained from the genus error).

Variables	Proportion of total variance				
	Family	Subfamily	Tribe	Genus	Species
Parasitism (ecto/endo-parasitism)	0.520	0.396**	0.034	0.036**	0.014
Biosis (idio/koinobiosis)	0.388	0.376**	0.116	0.065	0.056
Solitary / gregarious development	0.002	0.570**	0.126	0.144	0.159
Feeding site (haemolymph / tissue)	0.071	0.132	N/A	0.000	0.796
Pupation site (internal / external to host's body)	0.393	0.345*	0.132	0.108*	0.033
Preadult lifespan	0.546	0.147*	0.022	0.178	0.107
Longevity	0.177	0.282	0.235	0.194	0.112
Brood size	0.517	0.152	0.139*	0.049	0.143
Fecundity	0.007	0.478	0.181	0.259*	0.075
'Residual' parasitoid geographic range	0.196	0.233	0.176	0.239	0.157
Parasitoid mean latitude	0.306	0.285**	0.163	0.134	0.112
Parasitoid body length	0.764*	0.114*	0.088	0.041**	0.018
Egg volume	0.032	0.404	0.157	0.310*	0.096
Host body length	0.970**	0.020**	0.004	0.005**	0.001
Parasite window	0.010	0.231	0.127	0.549*	0.085
'Residual' host geographic range	0.179	0.282*	0.143	0.236*	0.160
Host mean latitude	0.123	0.356*	0.173	0.219*	0.129
'Residual' number of host species attacked	0.309	0.204	0.179	0.180	0.129
Degree of study	0.200	0.344*	0.174	0.150	0.132

All traits relating to geographic range (parasitoid and host residual geographic ranges, mean latitudes and distributions) have very low ρ values (Table 5.2) and low RI values (Table 5.3). Both residual host geographic range and host mean latitude show the greatest variance at the subfamily level, whereas the greatest variance for parasitoid 'residual' geographic range is at the genus level, and for parasitoid mean latitude is at family and subfamily levels (Table 5.4).

5.5 Discussion

5.5.1 General findings

Several metrics are used to analyse trait lability amongst the Ichneumonoidea. After sequential Bonferroni correction, there is no significant difference between the lability of categorical and continuous traits, behavioural and morphological traits, or life history and ecological traits. However, mean values are nearly always in the predicted directions (with categorical, behavioural and ecological traits tending to be more labile). The majority of trait variation is found at the family and subfamily taxonomic levels. Both ecto- / endoparasitism and idio- / koinobiosis appear to be constrained traits, as does solitary / gregarious development. We discuss these findings in turn.

We find weak evidence that ecological traits are more labile than life history traits, where the mean ρ and RI values were consistently lower for the ecological traits. This is expected if ecological traits have more selection pressures influencing them, yet are not as constrained by morphological or physiological adaptations as life history traits are. The number of host species attacked is a relatively labile ecological trait. Although most variance still occurs at the family level, half the trait variance is attributable to tribal level or below. The two families do not differ significantly in overall in the number of host species attacked (Table 5.4). Two species of Pimplinae (Ichneumonidae) (*Itoplectis conquisitor* and *Pimpla turionellae*) are known to attack 80 and 91 host species respectively, whereas the greatest number of host species attacked by braconid species is 30, for both *Diaeretiella rapae* and *Lysiphlebus testaceipes* (Aphidiinae). Other ecological traits that are very labile are parasitoid and host geographic ranges. This is expected as many species studied have been used as biological control agents and have therefore been introduced into new areas, where they have subsequently increased their geographic ranges further. However, may be a bias in this variable as we assumed presence in a country meant that the parasitoid was present over the entire country. This is unlikely to be true due to the likely abundance of unsuitable habitat. Host order, on the other hand, is a very constrained trait. Parasitoids may attack taxonomically similar hosts as they share similar defense mechanisms and physiological properties (see Godfray 1994). This is more likely to affect endoparasitoids / koinobionts, which require specialist adaptations due to the close association they have with their hosts, in comparison to ectoparasitoids / idiobionts who are less restricted by host taxonomy. Within this data set the majority of parasitoids are either endoparasitoids and / or koinobionts, therefore this close association with host taxonomy seems plausible. In relation to host taxonomy, closely related host species will more likely have similar biologies and / or ecologies, which can also influence what hosts a parasitoid will attack.

Although there is no significant difference between the trait categories, we do find that mean ρ and RI values are higher for the categorical variables than for the continuous traits. This is expected due to the biological transitions required to evolve from one categorical trait state to another. For example, the transition from ectoparasitism to endoparasitism requires a parasitoid to adapt to successfully develop within the host's body, which includes the ability to breathe, and avoid or overcome the host's immune system. A transition from idiobiosis to koinobiosis again requires specialist adaptations, for example the production of venom that will only temporarily paralyse a host. There may be a higher degree of measurement error for the continuous variables. Alternatively it may be because continuous variables show a greater degree of genetic variation because multiple genes code them.

Morphological traits tend to have greater ρ and RI values than the behavioural traits, which may be due to a greater level of physiological constraints on morphological rather than on behavioural evolution. Other studies have found such a difference, for example Edwards and Kot (1995) carried out a comparative study, at the species level, on grey-crowned babblers (*Pomatostomus temporalis*). They found that group size, which was deemed a behavioural trait, was more labile than the morphological traits studied (for example wing size, body weight, and tarsus length). Similar results were found by Gittleman *et al.* (1996a/b) who studied mammalian traits. We find that parasitoid body size is a constrained trait within the Ichneumonoidea, which may be due to physiological or morphological constraints (see Mayhew and Hardy 1998), as well as brood size and other traits associated with reproduction (egg volume and fecundity). This is also reflected by the greatest amount of variation in these traits occurring at the family level.

It is likely that some traits affect other traits evolutionary rates. For example, in both parasitoid body length and host body length, the vast majority of trait variation is found at family level. This is expected given the strong functional links between the two, which suggest that they should evolve in concert. Parasitoid longevity and fecundity in contrast, are both relatively labile, and are likely to be related through resource-based trade-offs (Ellers & van Alphen 1997, Pexton & Mayhew 2002). Egg volume and fecundity are also remarkably similar in the trait variance attributable to different taxonomic levels, as expected again from a resource-based trade-off (Blackburn 1991b). Using taxonomy, we found that the greatest proportion of variation was found to occur at the higher taxonomic levels (family and subfamily). This suggests that ancient evolutionary events have shaped most of the variation observed today across species. A rapid diversification of forms may have occurred during the adaptive radiation of species, but since then the evolution of the traits in question has slowed down due to competition causing stabilising selection pressures. Alternatively it may be that, for binary characters, there was an early peak in disparity and because there are a limited number of forms that can evolve, the rate of evolution inevitably slows down. Similar results have also been recorded for angiosperm niches (see Prinzing *et al.* 2001), and bird life histories (see Owens & Bennett 1995). However in cichlid fish colour patterns, most variation is between closely related species (Seehausen *et al.* 1999). The latter result is likely to be because cichlids are a young radiation and coloration is under strong directional selection from both ecological forces and sexual selection. Most variation in parasitoid body size is observed at the family level, which is expected as braconids are on average smaller bodied than ichneumonids (see Table 4.3).

A relationship between ecto- / endoparasitism and idio- / koinobiosis has been identified (see chapter 4). Idiobiont ectoparasitism has been suggested to be the plesiomorphic state for most parasitoid groups, due to this strategy requiring the least specialization, whereas koinobiont endoparasitism is the most specialized form of parasitism (see Godfray 1994). Endoparasitism may have evolved to overcome problems, such as the risk of desiccation or predation, associated with ectoparasitism. Endoparasitism is generally considered a more specialized life history strategy than ectoparasitism due to the intimate relationship the endoparasitoid has with its host. Endoparasitoid eggs are injected into the host's body and develop internally, because of this the developing parasitoid may have to overcome the host's immune defenses. We find that variation in ecto- / endoparasitism is generally more ancient than variation in idio- / koinobiosis. Therefore it is possible that idio- / koinobiosis is responding to the evolution of ecto- / endoparasitism. Koinobiosis has been hypothesized to have evolved from the primitive life history strategy of idiobiont ectoparasitism, so that parasitoids could attack exposed hosts rather than those concealed in plant tissues (Gauld 1988), and that parasitoid development could take place after the exposed hosts had concealed themselves. Yet this strategy is risky, due to the increased risks of egg mortality from desiccation, host moulting and host movement. The evolution of endoparasitism would therefore overcome these problems. Alternatively endoparasitism may have, in some instances, evolved prior to koinobiosis (Gauld 1988) to overcome the problem of increased exposure on host pupae. Our data, in general, tend to support this latter strategy.

Solitary larval development is thought to be the ancestral state in the parasitic Hymenoptera (see Mayhew 1998, Rosenheim 1993). As previously mentioned, solitary larval development may be considered an evolutionary dead end, such that only under stringent conditions, can gregarious development evolve. However despite this, transitions to gregarious development have occurred a minimum of 43 times in several lineages of parasitic wasps (see Mayhew 1998). For the Ichneumonidae, 7 out of the 34 subfamilies include both solitary and gregarious species, and for the Braconidae, there are 4 gregarious subfamilies and 9 subfamilies including solitary and gregarious species, out of the 46 subfamilies (see Mayhew 1998). The greatest variation for solitary / gregarious development is found at the subfamily level, which is expected as several subfamilies of both braconids and ichneumonids (for example the Macrocentrinae and the Adelognathinae respectively) contain a large proportion of gregarious species whereas other subfamilies do not. Therefore although the evolution of gregarious development is not expected to readily evolve from solitary behaviour, it has nonetheless occurred several times amongst the Ichneumonoidea. The evolution of gregarious development is probably closely tied to several other traits, namely idio- / koinobiosis, parasitoid body size, host size, feeding site, and pupation site (see Godfray 1987, Harvey *et al.* 2000, Mayhew 1998). In chapter 4, we found that solitary parasitoids are larger than gregarious parasitoids and that gregarious species rather than solitary parasitoids are associated with larger hosts. We also identified that most gregarious endoparasitoids pupate externally to the host, a strategy which has been suggested to favour the evolution of gregariousness, by reducing the fitness disadvantages of attacking larger hosts (see Harvey *et al.* 2000). Godfray (1987b) has suggested that a gregarious strategy might evolve when parasitoids attack hosts that can support a larger number of parasitoids. The evolution of gregarious development may also have arisen in conjunction with host range expansion (utilising larger bodied hosts) due to the pre-existing traits, such as haemolymph feeding and external pupation sites (see Godfray 1987, Strand 2000). If gregarious development requires several other traits to evolve simultaneously then that would also constrain its evolution.

5.5.2 Analytical issues

Several analytical issues have arisen from this study. Firstly, as both the taxonomy and composite cladogram were not completely resolved, this limited the type of analyses that could be carried out. For example, we could not carry out analyses using Pagel's (1997 & 1999a) generalised least squares model, as this method requires a resolved bifurcating tree. Secondly, ρ values calculated by PR may be biased for some variables. The greater the number of species included in any one analysis the smaller the ρ value, whereas the smaller the number of species in an analysis the greater the ρ value (Freckleton *et al.* 2002). Small sample sizes tend to inflate the estimated value of ρ above the true value. Therefore we are not confident about the value of ρ for those analyses where species numbers were low (for example feeding site, preadult lifespan, fecundity, egg volume and parasite window). However, the potential bias is not a severe problem overall as the nested ANOVA values do correlate quite well with the ρ values. Thirdly, only analyses based on taxonomy could be carried out using the nested analysis of variance method. Fourthly, it is up to the researcher to define life history from ecological traits, and behavioural from morphological traits. However, in some instances defining each trait can be open to interpretation. For example parasitoid feeding site can be interpreted as being an ecological trait (referring to the environment in which the parasitoid develops) or as a life history trait, because the amount of resources available for parasitoid consumption can affect the survival of the parasitoid. Ecto- / endoparasitism can equally be deemed as behavioural or morphological traits, behavioural as they represent how a species functions or acts, but also morphological as specialist adaptations are required for the latter life strategy (for example the development of breathing tubes).

5.5.3 Conclusions

Using several metrics (ρ in phylogenetic regression, the retention index and the proportion of variance due to different taxonomic levels) has allowed us to determine the evolutionary lability of Ichneumonoidea traits. We find that several traits are very conserved, such as ecto- / endoparasitism, idio- / koinobiosis, and solitary / gregarious larval development, which have previously been identified as important traits that regulate parasitoid life history variation (see chapter 4). As most trait variation occurs at the higher taxonomic levels (family and subfamily), it is suggested that ancient adaptive radiation evolutionary events have shaped the variation observed today within the Ichneumonoidea. This information can now be used to infer future hypotheses about the evolution of the Ichneumonoidea and the parasitic Hymenoptera in general.

Chapter 6: Conclusions and future prospects

6.1 Introduction

This chapter recaps the central thesis chapters, highlighting how each study has contributed knowledge to parasitoid research. Profitable future research directions will be mentioned. Finally, I discuss the broader implications of this work for a) parasitoid biologists and b) evolutionary ecologists.

6.2 Host use in solitary versus gregarious parasitoids

Chapter 2 investigated host range of a solitary (*Aphaereta genevensis*) versus a gregarious (*Aphaereta pallipes*) parasitoid species (Braconidae: Alysiinae). Previous theoretical and empirical work suggests that the host range of solitary species may be narrower than that of gregarious species. The study does not reject the null hypothesis that there is no difference in fundamental host range between species. However, several factors that affect the host range of these species were highlighted.

Previous research has brought to light differences between solitary and gregarious species host ranges. Studies on *Cotesia rubecula* (solitary) and *C. glomerata* (gregarious) have demonstrated that the former species has a narrower host range than the latter species (Brodeur *et al.* 1996, 1998). *C. rubecula* is a specialist on *Pieris rapae*, whereas *C. glomerata* is a generalist using several *Pieris* species as hosts. Bruchid beetles, which are known to have a parasitoid-like biology, also have solitary and gregarious developing larvae. The gregariously developing larvae have decreased oviposition specificity, implying a larger host range (Smith 1991). These two studies represent just two independent contrasts in favour of the hypothesis that gregarious species are more generalist. Our study has now contributed a contrast that does not support this hypothesis. The hypothesis should therefore be treated with increased scepticism. Obviously, however, a full assessment of the hypothesis must wait until more contrasts are available, something that this research should stimulate.

The most important factor to affect host range was host species or strain. Differences in the host species' or strains' ability to physiologically defend itself from parasitoid attack is a likely contributing influence. A host strain selected for its known high encapsulation rates was less suitable in comparison to those selected for their reduced ability to encapsulate. Fly strains with high encapsulating abilities were hypothesized to be more suitable hosts for gregarious species rather than for solitary species, as an abundance of gregarious offspring may overwhelm the hosts' immune response. However, both the solitary and gregarious species were similarly affected by the hosts' ability to encapsulate. This finding was unexpected and suggests that being solitary or gregarious *per se* is not sufficient to overwhelm host immune responses. It may be that the solitary species was depositing several eggs in each host, a phenomenon known from other solitary species (Rosenheim & Honkham 1996). However, given the poor performance of both species on the high-encapsulating host, it seems clear that increased clutch size is not always sufficient to make immunologically challenging hosts suitable. In short, this work suggests that gregarious development does not always affect host suitability via immunological effects and as a result does not always increase host range.

The performance of both species of wasp was unrelated to either host size or host taxonomy. The latter result is contrary to the dogma that host taxonomy is a major influence on host use in parasitoids. It may be that host taxonomy is important in this system only at higher levels (for example host order). This work should now stimulate further research on the extent to which host taxonomy matters, for example by investigating the issue at different parasitoid and host taxonomic scales. The fact that host size was not influential on wasp performance merely indicates that other factors were more important here. For the majority of species used, we do not yet know what those other factors might be. Possibilities include small-scale differences in host apparency, or physiological differences that affect growth and development. These possibilities might be investigated further by dissection treatments that count the actual number of eggs laid.

Larger wasps, in both species, parasitized a greater proportion of fly pupae than smaller wasps. This may be due to larger wasps containing more eggs than smaller ones, or because larger wasps have longer ovipositors and as a result can reach, subdue and / or oviposit into hosts. Larger wasps may also be better able to overcome a host's behavioural defenses. Although there has been much work on the relationship between body size and fitness in parasitoids (Godfray 1994), the effects of body size on host availability and parasitization ability have been poorly studied. These different possibilities provide useful avenues for further investigation.

As the gregarious species used in these experiments is generally smaller than the solitary species, this may result in the former having a lower performance than the latter. Thus the realized host range of the gregarious species in the field may be smaller than that of the solitary species. Oviposition rate also appears to peak earlier in the gregarious species than in the solitary species. This may be a result of a lower life expectancy in the gregarious species, due to a trade-off between reproduction and longevity. Alternatively, it may be because the gregarious species has a higher egg load than the solitary species, which may increase the gregarious species tendency to oviposit. Therefore these factors may in fact counterbalance the affect of body size mentioned above. These findings should motivate two research directions; first, host use in the field needs to be investigated in the light of these findings. Second, although the influence of life history traits such as egg load and longevity has seldom been the focus of host range studies, the work presented here suggests that such traits may be more influential than is generally appreciated.

The study presented was laboratory based and therefore more closely addressed fundamental than realized host range, something that field studies of host range cannot so easily address. Species can be challenged under identical conditions and therefore be fairly compared, again something that field studies cannot easily achieve. In addition, this study was able to identify intra-specific differences that are rarely the focus of field studies. Clearly, laboratory studies have much to offer in the study of parasitoid host ranges. However, a full picture must be complemented with field studies, including rearing records, which define the realized niche. Laboratory studies are also limited in the extent to which different hosts can be tested under controlled conditions; clearly, not all possible hosts can be reared under laboratory conditions, nor will practical considerations ever allow a large number to be tested. The published literature records are potentially problematic from a comparative perspective because of the high incidence of errors. In addition, there is the problem of species differing in the extent to which they have been studied, which is difficult to control for. Finally, literature based comparative studies may be forced to compare quite distant relatives, which differ in many biological traits that might influence host range. Thus, it is expected that these relative advantages and disadvantages, well illustrated in this thesis, will continue to argue for a two-pronged approach to host range studies.

The main interest of this work, for evolutionary ecologists in general, is in investigating the potential effects of social evolution on life history and other traits. This study has provided some encouragement for such researchers. Although the general hypothesis tested is not supported, other factors that might themselves be the result of social evolution were important and may influence the realized niche.

6.3 The evolution of body size and clutch size across the parasitoid Hymenoptera

Interspecific life history studies of the parasitoid Hymenoptera have focused on the dichotomy of endoparasitic koinobiosis and ectoparasitic idiobiosis, showing it to be a major axis of parasitoid life history variation. Yet, differences in parasitoid body size and clutch size have not been readily associated with this trait axis. From theories available on other organisms of interest, body size and clutch or brood size have been identified, with a suite of associated life history traits, that are used to determine life history evolution in, for example mammals or birds. Parasitoid theory predicts that parasitoid life history traits such as host size will greatly affect both parasitoid body size and clutch size.

In chapter 3, a data set originally compiled in 1990 by Blackburn, in conjunction with recent phylogenetic estimates for the parasitic Hymenoptera, were used to address those factors associated with body size and clutch size evolution. Hypotheses were tested in two ways. The raw data across species was used to identify significant phenotypic associations between traits. Phylogenetic regression (PR) was used to identify significant evolutionary correlations between traits. We also carried out additional analyses when the cross-species PR results were in disagreement, in order to identify any historically influential events and / or how some contrasts in the PR were in the opposite direction to that expected from the cross-species analysis.

It was hypothesized that parasitoid body size and clutch size are associated with host stage attacked. Theoretical models of interspecific variation have suggested that both body and clutch size have the potential to increase with an increase in host size, as previously demonstrated in the genus *Apanteles* (Le Masurier 1987) and in the family Bethylidae (Mayhew & Hardy 1988). Host size ultimately limits the amount of resource available to the developing offspring hence it influences body size and in turn, influences clutch size allocation. Our study differs from those previously mentioned, in that they only address close relatives and parasitoids attacking a single host stage (larva). Our main finding is that both body size and clutch size are associated with host stage attacked (used as a crude measurement of host size). This suggests that evolutionary theories or models that address the evolution of clutch size and body size across species should include host size information. This finding may also stimulate studies to address the fitness costs of parasitoid body and clutch size when attacking different host stages. For example, parasitoids may alter their clutch sizes in response to the host's immune system, which is known to vary depending on the stage of development. Larval host stages can elicit an immune response whereas egg or pupal host stages cannot.

We expected to find a negative relationship between body and clutch size, if they trade-off for a given host size. The larger the clutch size, the smaller the amount of resources per developing parasitoid offspring, therefore the smaller their adult body size upon emergence (Hardy *et al.* 1992). Gregarious parasitoid families have been shown to be smaller than their solitary sister taxa (Mayhew 1998). This relationship was apparent across species, but no evolutionary correlation was found, when we controlled for host stage attacked. This relationship may be dependent on other confounding variables (such as host size, or whether a parasitoid is an idiobiont or a koinobiont) remaining constant.

As koinobionts allow the host to continue to grow for a time post-parasitism, we expect to find that koinobionts either have larger body or clutch sizes than idiobionts. Previous studies (see Mayhew & Blackburn 1999) failed to find a relationship between idio- / koinobiosis and body size, which may be because they failed to control for host size. When controlling for host stage attacked, we found a phenotypic relationship here. Further analyses suggested that differences in host body size might confound these results such that we do not find an evolutionary correlation between these traits. This illustrates the need to use a more precise trait for host size (for example measuring adult host size, see chapter 4) instead of host stage attacked. Koinobionts were not found to lay larger clutches than idiobionts and this suggests that the fitness advantage of koinobiosis seems to be gained through an increase in parasitoid body size rather than through an increase in clutch size. This finding should help to formulate hypotheses on how transitions between idiobiosis and koinobiosis came about.

We also tested some novel hypotheses, whether parasitoid latitude (temperate or tropical) influenced body size and clutch size. We hypothesized that there would be a positive correlation between latitude and both body size (Bergmann's rule) and clutch size, as demonstrated in birds (see Cardillo 1999, 2002). Cross-species analysis revealed temperate species to have larger bodies than tropical species, although this was not mirrored evolutionarily. Again confounding variables, such as host size, may affect the phylogenetic analyses. No relationship was found between clutch size and latitude when considering all parasitoid species. This is probably due to the great number of solitary species in the data set, which do not have labile clutch sizes by definition. Analysis of only the gregarious species revealed an evolutionary correlation between clutch size and latitude. However, this correlation was in the opposite direction to that expected, tropical gregarious species having larger clutches than temperate species, but can be attributed to a trade-off between body size and clutch size. These findings should interest macroecologists studying large-scale patterns in ecological traits when searching for general trends across taxa. Exceptions are often interesting from a macroecological perspective as they can indicate crucial underlying mechanisms that differ between organisms. When searching for explanations for Bergmann's rule, parasitoids may be useful study organisms, as body size is relatively simply connected to other life history traits. In this case, it may simply reflect differences in host size, but there may also be more subtle underlying mechanisms common to other taxa. Finally, these trends may help explain a long-standing mystery in macro-ecology, why ichneumonid diversity peaks at intermediate latitudes. If speciation or extinction rates depend on life history traits such as body size and clutch size, as seems possible, this might explain why ichneumonids are relatively exceptional amongst the parasitoids in this trend.

Several times a discrepancy was found between the cross-species and PR results, and this indicates that there is not an overall significant evolutionary association between the traits of interest. This may arise due to confounding variables, which cannot be easily controlled for, because a) we do not know what they are, or b) we do not have relevant information for them. Furthermore, the more control variables that are necessary in a comparative analysis, the less likely a biological signal is to be detected, because of the increased associated error. However, some non-significant evolutionary correlations may be real and represent historical evolutionary events that are in the same direction in both the cross-species and PR analyses. These events have been influential in that the differences have been inherited by their descendants, resulting in the traits being correlated across species but not evolutionarily. This highlights the problem with cross-species analyses in that they do not always accurately reflect evolutionary correlations, due to trait inheritance by decent. In several cases, non-significant evolutionary correlations are associated with low phylogenetic lability of the trait, suggesting a genuine lack of evolutionary independent replicates. Such cases do not mean that the causative hypotheses under investigation are incorrect, but merely that evolutionary history cannot provide sufficient data to confirm them. Experimental or other such functional studies must then provide the way forward.

Relying only on taxonomy may have the effect of lowering the power of the analysis, and / or introducing bias if the taxonomy is not an accurate reflection of phylogeny. Therefore this study has built on the previous ones that have used the same data set (see Blackburn 1990, 1991a/b, Mayhew & Blackburn 1999) in that several different phylogenies, as well as taxonomic information, were used to analyse the data. The use of phylogenetic information allowed us to increase the power of the analyses in comparison to that taking into account the taxonomy. In fact, this increase in power results in several evolutionary correlations being more significant when using phylogenetic information in comparison to using taxonomic information, for example body size and host stage attacked are highly correlated using phylogenetic information, but only marginally significant using taxonomic information. This provides encouragement to the vast number of researchers currently investigating phylogenetic relations of organisms in the hope that it will increase our understanding of evolutionary questions.

Hopefully, complete genus-level phylogenies, or at the very least phylogenies that include all relevant subfamilies, will in the not-too-distant future, be available for the parasitoid Hymenoptera, and that using these phylogenies will help to reveal novel life history trait associations. They may also identify evolutionary correlations where we have only found phenotypic correlations. In concert, there is an obvious need for a greater abundance of accurate data on most of the traits in question, and data on new potentially influential traits such as host size.

The principle interest of this study for evolutionary ecologists in general lies in how body size is related to other traits, and hence is potentially controlled. Unlike the vast majority of organisms, which harvest replaceable resources from their environment and decide when to mature, parasitoid body size is determined by parental allocation of eggs to hosts. It is likely therefore that a general parasitoid life history model will be very different from those of other organisms. Because of the influence of the host on parasitoid life history evolution in general however, some evolutionary patterns, such as Bergmann's rule, may still be common to other organisms.

6.4 Associations between life history traits across the Ichneumonoidea

The aim of chapter 4 was to carry out a multi-species analysis on the Ichneumonoidea, to improve on Blackburn's data set such that more detailed and relevant variables were studied. We also used up-to-date phylogenetic information in order to find out what life history variables are important regulators of life history variation within this group of parasitoids. Several life history trait associations are found for this group, and help to identify several biological transitions that potentially regulate Ichneumonoidea life history variation.

Support is found for the dichotomous hypothesis (idiobionts / ectoparasitoids have an opposite suite of traits in comparison to koinobionts / endoparasitoids) as expected from previous studies (see Mayhew & Blackburn 1999). Cross-species analyses found koinobionts are associated more with hosts in exposed locations in comparison to idiobionts, which mostly attack hosts in semi-concealed locations, as is expected by the switch from idiobiosis to koinobiosis (see Gauld 1988). However, there is no evidence for a significant evolutionary correlation here and one potential reason is a lack of evolutionary replication. Both idio- / koinobiosis and host exposure are relatively conserved traits, and as such do not provide powerful tests. This is a shame, as comparative studies provide the only possible historical tests of why transitions between koinobiosis and idiobiosis might have occurred. It is also an illustration of the necessity of using phylogenetic information. The hypothesis of Gauld (1988) is not strongly supported, but it is also not rejected.

Further analyses, using host niche as a more refined measurement of host exposure, revealed cross-species relationships between host niche and a) idio- / koinobiosis and b) ecto- / endoparasitism. Due to the intimate relationship koinobiont endoparasitoids are said to have with their hosts, they are said to have a more restricted host range than idiobiont ectoparasitoids (see Askew & Shaw 1974 & 1986, Godfray 1994, Mills 1992, Müller *et al.* 1999, Sato 1990, Sheehan & Hawkins 1991). This is because of the specialist adaptations koinobiont endoparasitoids require to develop inside their hosts, which continue to develop for a time post-parasitism. We did not find such a relationship either across species or for the phylogenetic analyses, and may not be apparent due to confounding variables masking it (for example the degree of study, latitude, or geographic range).

Idiobionts are expected to have longer preadult lifespans than koinobionts (see Blackburn 1991a, Mayhew & Blackburn 1999). Surprisingly, we did not find any evidence for this. This may be because we had low sample sizes, due to a lack of sufficient data for preadult lifespan. Also the majority of species we did have preadult lifespan information for were larval parasitoids, which may develop quickly regardless of whether they are idiobionts or koinobionts. Alternatively we may need to control for confounding variables, such as host size or latitude. In any case, we can conclude that the difference in development time between koinobiosis and idiobiosis may not always be great. This fact means that one of the potential costs of koinobiosis may be low in ichneumonoids, which may account for its prevalence in this group.

Adult idiobionts / ectoparasitoids live longer than koinobionts / endoparasitoids, a relationship which has previously been found in the parasitic Hymenoptera (Mayhew & Blackburn 1999). This association may be due to trade-offs between survival and fecundity. In fact, we find that endoparasitoids are more fecund than ectoparasitoids, although this result is not found for idio- / koinobionts. Endoparasitoids may have a reduced longevity because they invest more resources in reproduction in comparison to ectoparasitoids, which show the opposite trend. We expected to find that ectoparasitoids / idiobionts had larger eggs than endoparasitoids / koinobionts, because the former life history strategy requires a greater amount of resources before larval feeding begins, in comparison to the latter strategy. Alternatively it may be physically impossible for endoparasitoids to inject large eggs into the host's body. Only when controlling for fecundity did we find this result, and this is an interesting result which may suggest that selection pressures on egg size *per se* are not strong, but that it varies more as a consequence of fecundity. This may provide a useful guide for future modelling of parasitoid life history evolution.

Another evolutionary correlation was found between preadult lifespan and host stage attacked, and the latter trait is also associated with parasitoid body size. Parasitoids attacking larval host stages develop quickly in comparison to those attacking pupal host stages. Larvae are active, soft bodied and perishable in comparison to non-active pupal host stages, which means that larval resources may degrade quickly in comparison to pupal resources. Parasitoids of nymphs have the smallest body sizes, whereas those attacking egg or pupal host stages have the largest body sizes. Nymphal hosts include aphids, which are very small, and hence have limited resources available for developing parasitoids. Pupal host stages are large and therefore contain a large amount of resources available for developing parasitoids. However egg host stages are very small, here the parasitoids are koinobionts, allowing their hosts to develop for a time post-parasitism until they have reached a bigger size so that they provide adequate resources for the parasitoid's development.

Larger bodied hosts provide more resources for parasitoids and this increase in resources appears to be exploited in two ways; parasitoid body size can or female parasitoids can increase their brood size to exploit this increase in resources. A very strong association was found between host size and parasitoid size. This trend may reflect the fact that most of the species in our data are solitary. We also find that, across-species, solitary parasitoids are larger than gregarious ones, this is expected as solitary offspring do not share the host resource like gregarious ones do. An evolutionary association between solitary / gregarious development and host body size was also found. Solitary species are associated with smaller hosts than gregarious species, and this may be due to the evolution of the gregarious strategy when larger hosts are attacked (see Godfray 1987). A phenotypic association is found between solitary / gregarious development and pupation site. As ectoparasitoids, by definition, develop and therefore pupate externally to their host, we focused on their pupation sites. We found that gregarious species are more associated with external rather than internal pupation sites, which has previously been suggested to favour the successful parasitization of larger hosts and therefore be more favourable to the evolution of gregarious development (see Godfray 1987 Harvey *et al.* 2000).

We took a more detailed look at how parasitoid geographic range and distribution may affect various life history traits than previous studies have (Blackburn 1991a/b, Mayhew & Blackburn 1999, see chapter 3). The more a parasitoid species has been studied in the literature the greater its geographic range, therefore the degree of study was used as a control variable. As expected, we find a relationship between parasitoid and host geographic range, where a host is found, its parasitoid is also found. We also find many relationships between parasitoid life history traits and host a) ecological niche traits and b) life history traits. Host stage attacked is associated with the number of host species attacked, where larval parasitoids attack the smallest number of hosts. This is most likely because the majority of larval parasitoids are endoparasitic koinobionts, which have had to evolve specialist adaptations to successfully exploit their hosts, therefore limiting their host range. Nymphal parasitoids attack the greatest number of host species, here it is possible that this is a result of many nymphal parasitoids being used as biological control agents, introduced to novel areas where many not only attack the host they were introduced to control, but also attack novel hosts. Tropical rather than temperate parasitoids attack the smallest number of host species, which also corresponds to the negative relationship between parasitoid mean latitude and the number of host species attacked, and the positive relationship between parasitoid geographic range and the number of host species attacked. Our data seem to support the nasty host hypothesis (Gauld *et al.* 1992), such that tropical parasitoids attack herbivores that feed on plants that contain a higher level of toxins than temperate species do. Therefore generalist tropical parasitoids may experience more severe trade-offs because of these chemicals than specialist parasitoids would, resulting in tropical parasitoids having a narrower host range than temperate parasitoids.

Although we compiled a composite cladogram from recent phylogenetic studies, providing a higher degree of resolution than the taxonomy, it only provided a few significant results. This suggests that either a) the composite cladogram is a poor representation of the true phylogeny whereas the taxonomy is a better representation or b) the taxonomy produced many Type I errors. As mentioned in section 6.3, future phylogenetic work should hopefully provide more resolved and complete phylogenies to the finer taxonomic levels of, for example, genus level. When these phylogenies become available it may be worthwhile re-testing some of the hypotheses, which we expected to be significant evolutionarily, but were either not significant at all or were only significant phenotypically. Also more data could be collected for those variables for which we had insufficient data.

This study has revealed several important traits that need to be taken into account when developing parasitoid life history models. The biological transitions of ectoparasitism / endoparasitism and idiobiosis / koinobiosis regulate other life history traits such as preadult lifespan, adult longevity, and fecundity, which is already known from previous studies (see Mayhew & Blackburn 1999). The study also indicates that some traits are under more direct selection than others, for example fecundity over egg size. Furthermore, the development time costs of koinobiosis may not be great. We have also revealed aspects of the host's life history that affect parasitoid life history traits, for example its body size. Furthermore, we have evidence for important resource-based trade-offs and allometric relationships. The study therefore provides important evidence of both assumptions for theory to make, and predictions it should aim for. In addition, experimental studies can now address some of the underlying reasons for the patterns shown here. For evolutionary ecologists in general, this study reinforces many of relationships found in chapter 3; the importance of host body size for parasitoid body size evolution; the differences between parasitoid life history evolution and that of other organisms; the value of phylogenetically based comparative work. The attempt here, to address host range correlates must be seen as a first attempt, and should encourage future parasitoid researchers to revisit the questions posed here. One possible statistical avenue would be to only analyse data on those species that have been very well studied. That would however require a much more complete data set. Ultimately, the diversity of parasitoids, both in terms of species richness and life history traits, may be controlled by the degree of host specificity they show.

6.5 The lability and rate of evolution of traits in the Ichneumonoidea

The aim of chapter 5 was to assess the evolutionary lability or Ichneumonoidea traits, which may provide information that can help to form hypotheses about life history evolution.

The vast majority of trait variation is ancient, being found at family of subfamily level. This is consistent with hypotheses of adaptive radiation, whereby strong directional selection occurs early in a group's history followed by stabilising selection as niches fill. The niches in this case are likely to represent the diversification of holometabolous host species that occurred in the Cretaceous period, coincident with the diversification of angiosperms. It would be interesting to have a dated phylogeny to investigate particular events in more detail. The fact that most variation is ancient is bad news for our understanding of life history evolution because a) understanding ancient events is inherently more difficult than understanding recent events and b) most traits do not present many evolutionary replicates. Our data confirm other studies on life history variation in birds and flowering plants.

Although we found no statistically significant differences (after sequential Bonferroni correction) in the labilities of continuous versus categorical, behavioural versus morphological, and life history versus ecological traits, all the mean effects were in the predicted direction. This should encourage other researchers to re-examine these differences.

Traits that intuitively represent a significant biological transition (for example ectoparasitism / endoparasitism, idiobiosis / koinobiosis, solitary / gregarious development) are constrained, have evolved a long time ago and may have influenced or shaped other life history traits within the Ichneumonoidea. Other constrained traits include pupation site, brood size, fecundity, both parasitoid and host size, and host order attacked. Many of these traits may be interdependent. Both parasitoid body and brood size are affected by host size (see chapter 4) and as such are all relatively constrained traits at the family level. Mayhew and Hardy (1998) found that, within the Bethylidae, changes in parasitoid body size correlated with changes in host size, at deep phylogenetic nodes. Alternatively, physiological or morphological constraints, as well as traits associated with reproduction (brood size, egg volume and fecundity), may constrain parasitoid body size evolution. A parasitoid's pupation site is influenced by whether it is an ecto- / endoparasitoid, or solitary / gregarious (see chapter 4). Host order is constrained and may be due to endoparasitoids and / or koinobionts attacking taxonomically similar hosts, due to the hosts having similar defense mechanisms and physiological properties (see Godfray 1994). Closely related hosts may have similar biologies and / or ecologies, which can also influence what hosts a parasitoid attacks. Thus, these data have suggested underlying evolutionary mechanisms that can now be addressed by further studies.

Future studies might advance this work in several ways. New information on phylogenetic topology might allow Pagel's (1997) method to be applied. Pagel's method allows one to easily test whether the maximum likelihood values of λ are better than alternative values. Pagel's λ is also a less biased estimate of lability than Grafen's ρ. Nonetheless, the correlations between the different measures used here, and lack of apparent bias, suggests that our results are reasonably robust. A dated phylogeny might allow rates to be scaled in units of time, and thus linked to historical events. The most challenging area for future research will be to address the reasons for constraint, and also for change, when it has occurred. One area of parasitoid research has already shown a possible way forward: our understanding of the evolution of gregarious development has been advanced by small-scale comparative and experimental studies that aim to test specific hypotheses (see Boivin & van Baaren 2001, Pexton & Mayhew 2004, Ode & Rosenheim 1998, Rosenheim 1993). It is perhaps time that the approach was applied to other traits.

6.6 General conclusions

This thesis highlights several general issues for comparative biologists and evolutionary ecologists. Two-species studies have been shown to be useful, under conditions, where a multi-species comparative study may not be able to successfully identify the influencing factors of the trait of interest, due to a lack of relevant information in the literature. Alternatively, there may be confounding variables present, due to the complex relationship between morphology, behaviour, and / or ecology that may confuse or obscure the interpretation of cross-species results (Price 1997). This can, to some degree, be controlled for in two-species studies through the use of closely related species. These studies are also useful in that they allow the experimenter, to manipulate at least one variable, to test for a relationship between the variables of interest.

Godfray (1994, p. 320) criticised Blackburn's (1991a/b) data set and results as he used a rather poorly resolved taxonomy. We used the most up-to-date phylogenetic information available, which improved the power of the phylogenetic regression analyses, and provided many significant evolutionary correlations. In this case phylogenetic developments were of sufficient quality to improve the worth of this data set. Another criticism was that the data set contained a sparse representation of the Hymenoptera that are an extremely diverse group. Although there is a great body of literature available for this group, it is of varying quality and relevance, and there is a lack of basic biological information available for many parasitoid groups. Concentrating on one superfamily, the Ichneumonoidea, allowed us to gather a more detailed data set with more relevant variables, some of which had not previously been studied, providing more useful information on life history evolution. Evolutionary theories need to be tested on working phylogenies, yet within the parasitoid Hymenoptera certain groups have been studied in more detail than others. For example, although many species of chalcid are used as biological control agents, there is a lack of phylogenetic studies on this group.

Using up-to-date phylogenetic information provides more power, by an increase in the number of nodes that contrasts can be made from, for phylogenetic regression analyses.

However, it is important to state that it does not always provide more significant results in comparison to a taxonomic based analysis, as shown in chapter 4. As more phylogenetic studies become available, and are carried out at the more detailed taxonomic levels, such as genus level, this may provide more robust phylogenies that we feel more confident about, in that they represent more accurately a true phylogeny. Therefore addressing the evolution of life histories, through the use of phylogeny based methods, has been worthwhile and should continue to be so. Phylogenetic studies are only as good as the information used to construct them.

Overall this thesis cautions against a universal application of dogma, or hypotheses based on previous research, when the evidence underlying them is either sparse, or based on different taxa. In chapter 2, several, admittedly speculative, assumptions about host range in gregarious versus solitary species were not supported. In chapters 3 and 4, several associations between traits were found that are relatively unique to parasitoids, and other hypothesized associations were found across species but not when using phylogenetically based methods. In chapter 5, no significant differences in the labilities of different types of characters were found. Parasitoids are a biologically unique yet prominent part of the natural world, and show us some of the full extent of biological diversity. They can provide challenging but interesting tests of the generality of our assumptions.

Appendix 1: Parasitic Hymenoptera life history data set

Variables

1. Body length (mm)
2. Clutch size
3. Solitary / gregarious development – solitary (1); gregarious (2)
4. Development mode – idiobiont (1); koinobiont (2)
5. Geographic distribution – temperate (1); tropical (2)
6. Host stage attacked - egg (1); nymph (2); larva (3); prepupa (4); pupa (5); adult (6); nymph or adult (7); larva or prepupa (8); larva or pupa (9); prepupa or pupa (10); egg, larva or pupa (11); all (12); larva, pupa or adult (13)
7. Host stage attacked - egg (1); nymph (2); larva (3); prepupa (4); pupa (5); adult (6)

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Division Apocrita							
Superfamily Chrysidoidea							
Family Bethylidae							
Subfamily Bethylinae							
Tribe Sierolini							
Goniozus columbianus	2.5			1	1		
Goniozus emigratus				1	1	3	3
Goniozus gallicola				1	1	3	3
Goniozus indicus	2.75	7	2	1	2	3	3
Goniozus legneri		14	2	1	2	3	3
Goniozus nephantidis	3.58	9	2	1	2	3	3
Parasierola cellularis					1	3	3
Parasierola species				1	2	3	3
Prorops nasuta	2.3	1	1	1	2	3	3
Subfamily Epyrinae							
Tribe Cephalonomiini							
Cephalonomia tarsalis	1.33	2	2	1	1	9	
Cephalonomia utahensis		4	2	1	1	9	
Cephalonomia waterstoni	1.56					3	3
Tribe Epyrini							
Laelius anthrenivorus	3.5	2	2		1	3	3
Laelius pedatus	3.2	3	2	1	1	3	3
Laelius utilis	2.29			1	1	3	3
Subfamily Pristocerinae							
Pristocera rufa	6.05			1	2	3	3
Family Dryinidae							
Subfamily Dryininae							
Dryinus pyrillae						2	2
Subfamily Gonatopodinae							
Gonatopus sepsoides	3.27	1	1	2	1	6	
Pseudogonatopus distinctus	3.08			2	1	6	
Division Parasitica							
Superfamily Ceraphronoidea							
Family Ceraphronidae							
Subfamily Ceraphroninae							
Aphanogmus ?fijiensis	1.16	4	2		2	4	5
Subfamily Megaspliniae	3.2			1	1	9	
Lygocerus testaceiannus	0.91				1	6	
Superfamily Chalcidoidea							
Family Aphelinidae							
Subfamily Aphelininae							
Tribe Aphelinini							
Aphelinus asychis	1	1	1		1	2	2
Aphelinus flavus		1	1	2	1	12	
Aphelinus jucundus				1	1	6	
Aphelinus nigra	0.8	1	1	1	1	2	2
Aphelinus semiflavus	0.9				1	12	
Aphelinus chilensis	0.8			1	2	6	
Aphelinus chrysomphali	1.04				1	2	2
Aphelinus coheni	1.1	1	1		1	2	2
Aphelinus diaspidis	1			2	2	6	
Aphelinus maculicornis	1				2	6	
Aphelinus melinus	0.8	7	2	1	1	4	5
Centrodora speciosissima		1	1		2	6	
Coccobius ?debachi	0.71	1	1	1	2	9	
Tribe Coccophagini							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Coccophagus basalis	1				1	2	2
Encarsia formosa	0.6	1	1		2	2	2
Encarsia pergandiella	0.45	1	1	1	1	2	2
Encarsia quaintancei	0.59	1	1	1	1	2	2
Tribe Pteroptricini							
Pteroptrix parvipennis	0.39	1	1		2	2	2
Pteroptrix smithi				1	1	5	6
Family Chalcididae							
Subfamily Brachymeriinae							
Brachymeria lasus					2		
Brachymeria nephantidis		1	1		2	4	5
Brachymeria nosatoi	4.57	1	1	1	2	4	5
Brachymeria podagrica	4.5	1	1	2	1	3	3
Brachymeria species		1	1	1		4	5
Subfamily Chalcidinae							
Spilochalcis albifrons	3.8			1	1	4	5
Spilochalcis hirtifemora					1	3	3
Spilochalcis side					1	3	3
Subfamily Dirhininae							
Dirhinus pachycerus		1	1	1	2	4	5
Family Encyrtidae							
Subfamily Encyrtinae							
Tribe Aphycini							
Metaphycus helvolus	1	1	1	1	1	6	
Metaphycus insidiosus				2	1		
Metaphycus luteolus		19	2		1	12	
Tribe Cheiloneurini							
Cheilonerus noxius	1.52	1	1	1	1	9	
Cheilonerus paralia	1.57	1	1		2	3	3
Diversinervus elegans	2	4	2	2	1	12	
Diversinervus cervantesi	1.38	4	2		1	12	
Tribe Comperiini							
Comperia merceri	1.87	15	2	1	1	1	1
Tribe Copidosomatini							
Copidosoma species (1)	1.9	9	2	2	1		
Copidosoma species (2)		347	2	2	2	1	1
Parablastothrix species		1	1	1	1		
Tribe Encyrtini							
Encyrtus infidus	2.97	6.4	2	2	1	2	2
Tribe Habrolepidini							
Comperiella bifasciata	0.61	1	1	2	1	2	2
Comperiella unifasciata	1.3	1	1	1	2	5	6
Plagomeris diaspidis	0.88	1	1		1	6	
Spaniopterus crucifer	0.49	1	1		2	2	2
Tribe Microteryini							
Microterys flavus	0.95	12	2	2	1	5	6
Ooencyrtus pyrillae	0.85			1		1	1
Ooencyrtus trinidadensis					2	1	1
Ooencyrtus utethesiae	0.91	1.68	2	1		1	1
Syrphophagus inquisitor		1	1	1	1	3	3
Tachinaephagus zealandicus	3.2	6	2		1	9	
Tribe Thomsoniscini							
Thomsonisca pakistanensis					2	6	
Subfamily Tetracneminae							
Tribe Anagyrini							
Anagyrus pseudococci	1.8	1	1		1		
Epidinocarsis lopezi	1.58	1	1		2	6	

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Leptomastidea abnormis	1	1	1		1	2	2
Tribe Ericydini							
Clausenia josephi	1.29			1	1	5	6
Tribe Tetracnemini							
Paraleurocerus bicoloripes	0.88	25	2	2	1	1	1
Family Eucharitidae							
Stilbula tenuicornis				2	1	4	5
Family Eulophidae							
Subfamily Entedontinae							
Tribe Entedontini							
Chrysocharis bipunctatus	1.16	6	2	1	1		
Chrysocharis albipes	2.92				1	3	3
Chrysocharis gemma	2.08	1	1		1	3	3
Chrysocharis laomedon	1.54	1	1	2	1		
Chrysocharis laricinellae	1.85	1	1	1	1	3	3
Chrysocharis lepelleyi	1.51	1	1		2	3	3
Chrysocharis milleri	1.14	1	1	1	1		
Chrysocharis pentheus	1.26			1	1	3	3
Chrysocharis phryne	1.49			1	1	4	5
Chrysocharis pubens	1.89			1	1	4	5
Chyrsocharis pubicornis	1.62				1	4	5
Chrysocharis sunosei				2	1	9	
Chrysonotomyia formosa				1	1	1	1
Chrysonotomyia ritchiei	1.3				2	3	3
Chrysonotomyia ruforum	1.06			1	1	1	1
Chrysonotymia species		2	2	2	1		
Chrysonotymia violaceus	0.66				2	3	3
Closterocerus africanus	1.39			2	2		
Closterocerus trifasciatus	1.3	1	1	1	1	3	3
Cotterellia japonica	2.04				1	4	5
Entedon ergias		1	1	2	1	1	1
Goetheana shakespearei		1	1	2	2	3	3
Horismenus fraternus	2.14	1	1	1	1		
Pediobius acantha	1.62			2	1	4	5
Pediobius coffeicola	1.63			1	2	3	3
Pediobius foveolatus	1.6	15	2		2	3	3
Pediobius furvus	1.5	100	2		2	4	5
Pediobius nr-facialis	1.5	54	2			7	4
Platocharis ?coffeae	2.1				2	3	3
Psephenivorus mexicanus	1.55	39	2	1	2	10	
Teleopterus erxias	0.83				1	3	3
Thripobius species		4	2	1	1		
Tribe Elachertini							
Trichospilus pupivora	1.1	94	2	1	2	9	
Subfamily Euderinae							
Tribe Euderini							
Euderus agromyzae				1	2	9	
Euderus lividus	2.75	1	1	1	2	3	3
Subfamily Eulophinae							
Tribe Cirrospilini							
Cirrospilus cinctiventris	0.82				2	3	3
Cirrospilus diallus	2				1	3	3
Cirrospilus inimicus	2.1			1	1	9	
Cirrospilus pictus	1.89	2	2	1	1	3	3
Cirrospilus species	2	1	1	1	1		
Cirrospilus variegatum	1.17	3	2		2	3	3
Cirrosplius vittatus	1.7	2	2	1	1	3	3

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Diglyphus intermedius		1	1	1	1	3	3
Diglyphus minoeus	1.39				1	3	3
Zagrammosoma americanum		5	2	1	1		
Zagrammosoma multilineatum	1.44	1	1		1		
Tribe Elasmini							
Elasmus albicoxa		1	1	1	1		
Elasmus bellicaput	2.77			1		3	3
Elasmus broomensis	2.43	1	1			3	3
Elasmus leucopteras	1.7				2	3	3
Tribe Eulophini							
Dhalbominus fuscipennis	2.86	72.5	2	1	1	7	4
Eulophus larvarum	2.5					3	3
Hemiptarsenus fulvicollis	2.6	6	2		1	3	3
Hyssopus thymus	1.76			1	1	3	3
Necremnus brevisamulus		9	2	1	1	7	4
Notanisomorphella borboricus	1.7			1	2	4	4
Pnigalio argraules				1	1	3	3
Pnigalio longulus	2.65	1	1		1		
Pnigalio maculipes		1	1		1		
Pnigalio minio	1.9	1	1		1		
Pnigalio pallipes		1	1		1		
Pnigalio species				1	1	9	
Stenomesius rufescens	2.04	2	2		1	9	
Sympiesis marylandensis		1	1	1	1		
Sympiesis sericercornis		1	1		1		
Sympiesis viridulus		16.5	2	1	1	3	3
Euplectrus parvulua	1.21			1	2	3	3
Euplectrus puttleri	2.16			1	2	3	3
Euplectrus species		3.5	2		1	3	3
Euplectrus spodopterae						3	3
Subfamily Tetrastichinae							
Tribe Tetrastichini							
Aceratoneuromyia evanescens				1		9	
Aprostocetus ceroplastae		1	1	2	1	9	
Aprostocetus hagenowii	2	37.5	2	1	2	1	1
Aprostocetus leucopterae	0.83	2	2		2	9	
Citrostichus phyllocnistoides		1	1	1	2	3	3
Melittobia australica	1.3					10	
Minotetrastichus ecus		2	2		1	3	3
Nesolynx albiclavus	1.56	34	2	1	2	9	
Oomyzus incertus	1.4	5	2	2	1	3	3
Oomyzus scaposus	1.4			2	2	9	
Parachrysocharis pyrillae	0.84			1		1	1
Tetrastichus coeruleus	1.75	5	2	2	1	1	1
Tetrastichus howardi				1	2	9	
Tetrastichus julis					1	3	3
Tetrastichus krishneri	2.5			2	2	9	
Tetrastichus species					2	4	5
Family Eupelmidae							
Subfamily Calosotinae							
Anastatus albitarsis				1	1	1	1
Anastatus amarus				1	2	1	1
Anastatus colemani	3.41	1	1	1	2	1	1
Anastatus floridanus	3.19	306	2	1	1	1	1
Anastatus japonicus				1	1	1	1
Anastatus ramakrishnai				1	2	1	1
Euplemus australiensis		1	1	1	1	3	3

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Family Eurytomidae							
Subfamily Eurytominae							
Eurytoma nesiotes		1	1	2		3	3
Family Mymaridae							
Subfamily Alaptinae							
Tribe Anagrini							
Anagrus epos		1	1	1	1	1	1
Subfamily Mymarinae							
Tribe Anaphini							
Anaphes behmani		1	1	1	1	1	1
Anaphes calendrae	0.95	1	1	1	1	1	1
Anaphes nitens	0.73	1	1	1	2	1	1
Anaphes ovijentatus	0.6	1	1	1	1	1	1
Anaphes sordidatus		1	1	1	1	1	1
Tribe Mymarini							
Polynema striaticorne	1.6	1	1	1	1	1	1
Family Perilampidae							
Subfamily Perilampinae							
Perilampus tristis	3			2	1	4	5
Family Pteromalidae							
Subfamily Asaphinae							
Asaphes lucens					1	3	3
Asaphes vulgaris	3.3			2	1	9	
Subfamily Cerocephalinae							
Theocolax formicoformis	2.55				1		
Subfamily Miscogasterinae							
Tribe Miscogasterini							
Sphaeripalpus species				1	1	3	3
Tribe Sphegigasterini							
Cyrtogaster species		1	1	1	1	4	5
Sphegigaster flavicornis	2.41	1	1	1	1	4	5
Subfamily Pteromalinae							
Tribe Pachyneurini							
Pachycrepoideus vindemmiae		1	1	1	1	4	5
Pachyneuron albutius		18	2	1	1	4	5
Pachyneuron muscarum	1.22	1	1	1	2	9	
Tribe Pteromalini							
Anisopteromalus schwenkei	1.8	1	1		1	3	3
Callitula bicolor	1.7	1	1		1	4	5
Catolaccus aeneoviridis					1	3	3
Dibrachoides druso	3	3.7	2	1	1	10	
Dibrachys boarmiae	2.9	51.7	2	1		10	
Dibrachys cavus	1.3	2.4	2		1	3	3
Dinarmus acutus	2.75				1	9	
Hypopteromalus tabacum	2.26	1	1	1	1	3	3
Mesopolobus bruchophagi		1	1	1	1	3	3
Mesopolobus subfumatus	1.75	9.5	2	1	1	3	3
Nasonia vitripennis	2.35	20	2	1		4	5
Pteromalus cerealellae		1	1	1	1	3	3
Peteromalus veneris	3.3	17	2	1	1	7	4
Sisyridivora cav igena	2.85	1	1	1	1	9	
Spaniopus japonicus					1	3	3
Spaniopus species				2		9	
Trichomalopsis americanus				1	1	10	
Trichomalus fasciatus		1	1	1	1	3	3
Subfamily Spalangiinae							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Spalangia cameroni	2.63	1	1	1	1	4	5
Spalangia drosophilae	1.16	1	1		1	4	5
Family Tetracampidae							
Subfamily Tetracampinae							
Dipriocampe diprioni	1.2	1	1	1	1	1	1
Family Torymidae							
Subfamily Monodontomerinae							
Monodontomerus aereus	2.9	3	2		1	9	
Monodontomerus dentipes	3.13	4.5	2	1	1	7	4
Roptrocerus xylophagorum	3.14	1	1		1	3	3
Family Trichogrammatidae							
Subfamily Lathromerinae							
Lathromeroides species	1			1	2	1	1
Oligositoides semicinctium	0.83	1	1	1	2	1	1
Subfamily Trichogrammatinae							
Trichogramma ?australicum	0.63	3	2	1	2	1	1
Trichogramma brevicapillum		1	1	1	1	1	1
Trichogramma evenescens	0.56			1	1	1	1
Trichogramma minutum	0.45	1	1	1		1	1
Trichogramma platneri		1	1	1		1	1
Trichogramma semifumatum	0.45	2	2	1		1	1
Trichogrammatoidea armigera	0.48	1	1	1	1	1	1
Trichogrammatoidea bactrae	0.34			1	2	1	1
Superfamily Cynipoidea							
Family Figitidae							
Subfamily Charipinae							
Alloxysta megourae		1	1	2	1	3	3
Subfamily Eucoilinae							
Cothanaspis species (*?boulardi*)		1	1		1	3	3
Hexacola species					1	3	3
Hexacola websteri				1	2	9	
Family Ibalidae							
Ibalia drewensi	12.5	1	1		1	3	3
Superfamily Evanoidea							
Family Evanidae							
Evania appendigaster	6.87	1	1	1		1	1
Prosevanis fuscipes		1	1	1	2	1	1
Superfamily Ichneumonoidea							
Family Braconidae							
Subfamily Agathidinae							
Agathis calcarta	5.6	1	1	2	1	3	3
Agathis gibbosa	3.8	1	1	2	1	3	3
Agathis laticincta	4.4	1	1	2	1	3	3
Agathis unicolorata	4.7	1	1	2	1	3	3
Bassus dimidiator	5.25			2		3	3
Microdus acrobasidis	3.14	1	1		1	3	3
Microdus pumilus	2	1	1	2	1	3	3
Subfamily Alysiinae							
Tribe Alysiini							
Alysia manducator	6.25	1	1		1	3	3
Aphaereta pallipes	2.13	11.2	2	2	1	3	3
Dapsilarthra species				1	1	3	3
Tribe Dacnusini							
Dacnusa nipponica	1.62			2	1	3	3
Subfamily Aphidiinae							
Tribe Aphidiini							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Aphidius avenae	2.7	1	1		1	5	6
Aphidius matricariae	1.95			1	1		
Aphidius sonchi	2.09	1	1	2	1	6	
Aphidius species				2	2	6	
Tribe Ephredrini							
Ephredrus plagiator	1.63	1	1	1	1	6	
Tribe Praini							
Praon exsoletum	1.7	1	1	2	1	12	
Praon volucre	2.07	1	1	2	1	5	6
Tribe Trioxini							
Monoctonus paulensis		1	1	1	1	6	
Trioxys complanatus	1.3	1	1	2	1	12	
Subfamily Blacinae							
Tribe Blacini							
Pygostolus falcatus	3.59	1	1		1	5	6
Tribe Orgilini							
Orgilus jenniae					1	3	3
Orgilus lepidus	4.5	1	1	2	1	3	3
Orgilus obscurator	4.02	1	1	2	1	3	3
Orgilus parcus	3.76				1	3	3
Subfamily Braconinae							
Aphrastobracon flavipennis		1	1	1	2	3	3
Bracon ?hancocki	3.44				2	3	3
Bracon cajani	3.27			1	2	3	3
Bracon greeni					2	3	3
Bracon lissogaster	3.5			1		3	3
Bracon mellitor	3.8	1	1		1	3	3
Bracon thurberiphagae		6.5	2	2	2	3	3
Bracon vulgaris	8	1	1		1	3	3
Campyloneurus mutator	6.7	1	1	1	2	3	3
Coeloides dendroctoni	5.17	1	1	1	1	3	3
Habrobracon hebetor	2.74			1		3	3
Habrobracon instabilis	2.29	2	2	1	2	3	3
Habrobracon lineatellae		7	2	1	1	3	3
Habrobracon politiventris		28	2	1	1	3	3
Habrobracon stabilis	2.81	8	2	1	1	3	3
Hybogaster varipalpis	10.68	4	2	2	2	3	3
Iphiaulax kimballi						3	3
Microbracon chilonis					2	3	3
Microbracon pygmaeus		1	1	1	1	3	3
Microbracon variabilis					1	3	3
Ophthalmobracon kirkpatricki	4	3	2	1	1	3	3
Stenobracon deesae	11.87	1	1	1	2	3	3
Stenobracon nicevillei	12.99			2	2	3	3
Subfamily Cardiochilinae							
Cardiochiles hymeniae	4.07	1	1	2	2	3	3
Cardiochiles nigricollis	5.81				1	3	3
Toxoneuron nigriceps	7.15	1	1	2	1	3	3
Subfamily Cheloninae							
Ascogaster quadridentatus	4.42	1	1	2	1	1	1
Ascogaster reticulatus	4.17	1	1			1	1
Chelonus annulipes	6.5	1	1	2	1	1	1
Chelonus curvimaculata	3.32	1	1	2	1	3	3
Chelonus heliopae	3.29	1	1	2	2	1	1
Chelonus inanitus	5.2	1	1	2	2	1	1
Chelonus kellieae	3	1	1	2	1	1	1
Chelonus phthorimaeae	2.95	1	1	2	1	1	1

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Chelonus texanus	5	1	1	2	1	1	1
Phanerotoma bennetti		1	1	2	2	1	1
Phaenerotoma phyllotomae	3.73			1	1		
Phaenerotoma toreutae	4.5	1	1	2	1	1	1
Subfamily Doryctinae							
Dendrosoter protuberans	3	1	1	2	1	3	3
Heterospilus coffeicola	2.5	1	1	1	2	11	
Rhaconotus roslinensis	3.69	15	2	1	2	3	3
Spathius vulnificus	4.05			1	2	3	3
Subfamily Euphorinae							
Tribe Euphorini							
Aridelus cameroni		1	1		2	3	3
Aridelus rufus		1	1		2	3	3
Microctomus hyperodae	2.1	1	1	2	1	5	6
Microtonus sitonae				1	1	5	6
Microtonus stelleri	2.75	1	1		1	3	3
Perilitus dubius	2.86	3	2	1	1	5	6
Tribe Meteorini							
Meteorus campestris				2	1	3	3
Meterous pallipes		1	1	2	1	2	2
Meteorus ruficeps	4.44	1	1		1	3	3
Meterous unicolor	5.23	1	1	1	2	3	3
Subfamily Macrocentrinae							
Macrocentrus gifuensis	4.5	21	2	2		3	3
Macrocentrus instabilis		1	1		1		
Macrocentrus linearis	4.74	13	2	2	1	3	3
Subfamily Microgasterinae							
Apanteles ater	2.25			2	1	3	3
Apanteles bordagei	1.81			2	2	3	3
Apanteles dignus	2.23	1	1	2	1	3	3
Apanteles dilectus	2.71			2		3	3
Apanteles epinotaie	1.23	1	1	2	1	3	3
Apanteles etiellae	2.57	1	1	2	2	3	3
Apanteles forbesi	3.63			2	1	3	3
Apanteles fumiferanae	3.5			2	1	3	3
Apanteles maculitarsis	3.29			2	1	3	3
Apanteles murinanae	2.86			2	1	3	3
Apanteles obliquae	2.09			2	2	3	3
Apanteles solitarius	2.67	1	1		1	3	3
Apanteles subandinus	3.86	1	1		1	3	3
Apanteles syleptae	3	1	1	2	1	3	3
Apanteles targamae	3.5	1	1		2	3	3
Apanteles thompsoni	3	23	2		1	3	3
Cotesia congregatus	2.47				1	3	3
Cotesia flavipes	1.72	42.6	2		2	3	3
Cotesia marginiventris		1	1			3	3
Cotesia sesamiae	2.4	33	2	2	2	3	3
Cotesia xanthostigma	2.75	1	1	1	1	3	3
Hypomicrogaster tiro					1	3	3
Microgaster tibialis	3.5	1	1		1	3	3
Microplitis croceipes	4.4	1	1	1	1	3	3
Microplitis feltiae				1	1	3	3
Microplitis mediator	2.86			2	1	3	3
Microplitis plutellae		1	1		1	3	3
Microplitis rufiventris	3.08	1	1		2	3	3
Microplitis species		1	1		2	3	3
Subfamily Miracinae							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Mirax minuta		1	1	2	1		
Subfamily Opiinae							
Tribe Opiini							
Opius species				2	1	3	3
Subfamily Rogadinae							
Aleiodes tristis					1	3	3
Chremylus elaphus	2			1	1	3	3
Pelecystoma harrisinae	5.55				1	3	3
Rogas nolophanae		1	1	2	1	3	3
Rogas species		1	1	1	2	3	3
Rogas terminalis	6.71			2	1	3	3
Rogas testaceus	4.6	1	1	2	2	3	3
Family Ichneumonidae							
Subfamily Agriotypinae							
Agriotypus armatus	6.76	1	1	1	1	10	
Subfamily Banchinae							
Tribe Banchini							
Banchus flavescens	10.71	1	1		1	3	3
Tribe Glyptini							
Australoglypta latrobei	9.06	1	1	2	1	3	3
Cephaloglypta murinanae				2	1	3	3
Glypta fumiferanae	8			2	1	3	3
Glypta haesitator	5.5	1	1	2	1	3	3
Glypta fufiscutellaris	5.7	1	1		1	3	3
Tribe Lissonotini							
Lissonota complicator	5.5	6	2		1	3	3
Subfamily Campopleginae							
Bathyplectes anurus	3.41	1	1		1	3	3
Bathyplectes stenostigma		1	1	2	1		
Bathyplectes tristis	5	1	1		1	3	3
Campoletis flavicincta	5.79	1	1		2	3	3
Campoplex haywardi	4.84	1	1	2	1	3	3
Campoples mutabilis	7.82					3	3
Diadegma fenestrale		1	1	2	2	3	3
Diadegma insulare		1	1		1	3	3
Diadegma mollipla					1	3	3
Diadegma rufipes	6.14					3	3
Diadegma semiclausen	4.12			2	1	3	3
Diadegma species				2	1	3	3
Dolophron pedella	4.58			2	1	3	3
Hyposoter didymator	6.49	1	1		2	3	3
Hyposoter exiguae		1	1	2	1	3	3
Hyposoter rivalis				2	1	3	3
Lathrostizus euurae	4.9			2	1	3	3
Lemophagus curtus	4.73	1	1		1	3	3
Olesicampe benefactor	7	1	1	2	1	3	3
Olesicampe monticola	8.16	1	1	2	1	3	3
Olesicampe ratzeburgi	11.5			1	1	3	3
Sinophorus crassifemur	10.67	1	1		1	3	3
Tranosema rostrale	6	1	1	1	1	3	3
Subfamily Cremastinae							
Eiphosoma dentator	10.2	1	1	1	2	3	3
Pristomerus species				1	1	3	3
Temelucha (*platensis* group)	6	1	1		1	3	3
Subfamily Cryptinae							
Tribe Aptesini							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Pleolophus basizonius	7.5	1	1	2	1	4	5
Pleolophus indistinctus		1	1	2	1	9	
Tribe Cryptini							
Agrothereutes abbreviator					1	3	3
Agrothereutes adustus	8.25	1	1	1	1	4	5
Agrothereutes extremalis		33	2	1	1	3	3
Agrothereutes tunetanus	9.5				1	13	
Gambroides javensis	13.5	1	1	1	2	7	4
Glabridorsum stokesii				1	1	4	5
Goryphus nursei	7.15	1	1	1	2	3	3
Itamoplex australis	11.83			1	2	7	4
Itamoplex inornatus		1	1	1	1	3	3
Trathala flavoorbitalis	7.8	1	1	2	1	3	3
Tribe Hemitelini							
Aclastus gracilis		1	1	1	1	10	
Hemiteles ridibundus				2	1		
Phygadeuon trichops	4.25	1	1	2	1	4	5
Sozites kerichoensis	3.26	1.6	2	2	2	1	1
Subfamily Ctenopelmatinae							
Tribe Mesoleiini							
Lamachus eques	9.52			2	1	3	3
Tribe Perilissini							
Lophyroplectus oblongopunctatus	10.57	1	1	2	1	3	3
Subfamily Diplazontinae							
Diplazon laetatorius	5.94			2	1	3	3
Syrphoctonus maculipennis	6.05	1	1	2	1	3	3
Subfamily Ichneumoninae							
Tribe Gyrodontini							
Afromelanichneumon transvaalensis	12.75			1	2	7	4
Cratichneumon sublatus	11.55			1		4	5
Dentichasmias busseolae	10.44			2	2	4	5
Melanichneumon rubicundus	7.5	1	1	1	1	4	5
Pterocormus suspiciosus	20				1	3	3
Stenichneumon scutellator	11.72	1	1		1	4	5
Tribe Phaeogenini							
Centeterus alternecoloratus	8.8	1	1		2	4	5
Phaeogenes maculicornis	8.03			1	1	4	5
Phaeogenes nigridens	8	1	1	1	1	4	5
Phaeogenes semivulpinus	7.34	1	1	1		4	5
Tribe Platylabini							
Peoecilostictus cothurnatus	10.71	1	1	2	1	3	3
Subfamily Mesochorinae							
Mesochorus agilis	1.5	1	1	2	1	3	3
Mesochorus nigripes		1	1	2	1	3	3
Subfamily Metopiinae							
Macromalon species	4.07	1	1		1	3	3
Metopius discolor	13.43			1	1	3	3
Subfamily Ophioninae							
Enicospilus species		1	1	2	2	3	3
Subfamily Pimplinae							
Tribe Delomeristini							
Pseudorhyssa maculicoxis	18.46	1	1	1	1	3	3
Tribe Phytodietini							
Phytodietus (*polysonias* group)	7.15	1	1		1	3	3
Tribe Pimplini							
Acropimpla pictipes	7.77			1		3	3
Apecthis quadridentata	11.33			1	1	4	5

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Calliephialtes grapholithae	10.34				1	3	3
Gregopimpla inquisitor				2	1	3	3
Itoplectis cristatae	7.15	1	1		1	4	5
Itoplectis maculator	8.01			2	1	9	
Liotryphon species				1	2	3	3
Pimpla turionellae	8.81			1	1	4	5
Scambus brevicornis	6.73	1	1	1	1	7	4
Scambus foliae	6.38			1	1	3	3
Sericopimpla sericata	12	1	1	1	1	3	3
Xanthopimpla citrina	10.13	1	1	1	2	4	5
Xanthopimpla stemmator	11.29	1	1		2	4	5
Tribe Polysphinctini							
Acrodactyla degener	3.94				1		
Acrodactyla quadrisculpta	4.73				1	2	2
Polysphincta tuberosa	6.08				1	2	2
Schizopyga frigida	7.46			1	1	6	
Zatypota albicoxa	5			2	1		
Zatypota bohemani	4.12				1	2	2
Zatypota percontatoria	4.71			1	1	6	
Subfamily Rhyssinae							
Tribe Rhyssini							
Rhyssa persuasoria	28.15	1	1	1	1	3	3
Subfamily Tersilochinae							
Diaparsus carinifer	3.88	1	1	2	1	3	3
Subfamily Tryphoninae							
Tribe Exenterini							
Exenterus abruptorius	9.25	1	1	2	1	3	3
Exenterus adspersus	7.7				1	3	3
Exenterus amictorius	9.02	4	2		1	3	3
Exenterus canadensis	9.5	1	1	2	1	3	3
Exenterus tricolor	6.8			2	1	8	
Tribe Tryphonini							
Grypocentrus albipes	3.1				1	3	3
Subfamily Xoridinae							
Xorides corcyrensis	16.5	1	1	1	1	13	
Superfamily Platygasteroidea							
Family Platygasteridae							
Subfamily Platygasteriinae							
Platygaster foersteri	1.64	4	2		2	1	1
Platygaster oryzae	0.95	60	2	1	2	1	1
Family Scelionidae							
Gryon ajax	1.4	1	1	1	1	1	1
Gryon antestiae	1.08	1	1	1	2	1	1
Gryon gnidus	1.21	1	1	1	2	1	1
Scelio aegypticus		1	1	1	2	1	1
Scelio hieroglyphi		1	1	1	2	1	1
Scelio species		1	1	1	2	1	1
Superfamily Prototrupoidea							
Family Diapriidae							
Subfamily Diapriinae							
Basalys tritoma	1.86				1	4	5
Trichopria atrichomelinae		5.7	2	1	1	4	5
Trichopria popei		10	2	1	1	4	5
Family Proctotrupidae							
Subfamily Proctotrupinae							
Codrus carolinensis		4	2		1	3	3
Subfamily Telenominae							

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Ascolus seychellensis				1	2	1	1
Eumicrosoma beneficum	0.75	1	1	1	1	1	1
Platytelenomus busseolae	0.77	1	1	1	2	1	1
Telenomus alsophilae		1	1	1	1	1	1
Telenomus calvus		1	1	1	1	1	1
Telenomus chloropus		1	1	1	1	1	1
Telenomus coelodasidis		1	1	1	1	1	1
Telenomus cosmopeplae	0.85	1	1	1	1	1	1
Telenomus costa-lima		1	1		2	1	1
Telenomus remus	0.54	1	1	1	2	1	1
Telenomus seychellensis	1.19	1	1		2	1	1
Telenomus ulyetti	0.45	1	1	1	1	1	1

Appendix 2: Traditional taxonomy for the parasitoid Hymenoptera (adapted from Blackburn 1990)

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
Apocrita	Chrysidoidea	Bethylidae	Bethylinae	Sierolini	*Goniozus*	*columbianus*
						emigratus
						gallicola
						indicus
						legneri
						nephantidis
					Parasierola	*cellularis*
						species
					Prorops	*nasuta*
			Epyrinae	Cephalonomiini	*Cephalonomia*	*tarsalis*
						utahensis
						waterstoni
				Epyrini	*Laelius*	*anthrenivorus*
						pedatus
						utilis
			Pristocerinae		*Pristocera*	*rufa*
		Dryinidae	Dryininae		*Dryinus*	*pyrillae*
			Gonatopodinae		*Gonatopus*	*sepsoides*
					Pseudogonatopus	*distinctus*
Parasitica	Ceraphronoidea	Ceraphronidae	Ceraphroninae		*Aphanogmus*	*?fijiensis*
			Megasplinae		*Lygocerus*	*testaceiannus*
	Chalcidoidea	Aphelinidae	Aphelininae	Aphelinini	*Aphelinus*	*asychis*
						flavus
						jucundus
						nigra
						semiflavus
						chilensis
						chrysomphali
						coheni
						diaspidis

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
						maculicornis
						melinus
					Centrodora	*speciosissima*
					Coccobius	*?debachi*
				Coccophagini	*Coccophagus*	*basalis*
					Encarsia	*formosa*
						pergandiella
						quaintancei
				Pteroptricini	*Pteroptrix*	*parvipennis*
					Pteroptrix	*smithi*
		Chalcididae	Brachymeriinae		*Brachymeria*	*lasus*
						nephantidis
						nosatoi
						podagrica
						species
			Chalcidinae		*Spilochalcis*	*albifrons*
						hirtifemora
						side
			Dirhininae		*Dirhinus*	*pachycerus*
		Encyrtidae	Encyrtinae	Aphycini	*Metaphycus*	*helvolus*
						insidiosus
						luteolus
				Cheiloneurini	*Cheilonerus*	*noxius*
						paralia
					Diversinervus	*elegans*
						cervantesi
				Comperiini	*Comperia*	*merceri*
				Copidosomatini	*Copidosoma*	species (1)
						species (2)
					Parablastothrix	species
				Encyrtini	*Encyrtus*	*infidus*
				Habrolepidini	*Comperiella*	*bifasciata*

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
						unifasciata
					Plagomeris	*diaspidis*
					Spaniopterus	*crucifer*
				Microteryini	*Microterys*	*flavus*
					Ooencyrtus	*pyrillae*
						trinidadensis
						utethesiae
					Syrphophagus	*inquisitor*
					Tachinaephagus	*zealandicus*
				Thomsoniscini	*Thomsonisca*	*pakistanensis*
			Tetracneminae	Anagyrini	*Anagyrus*	*pseudococci*
					Epidinocarsis	*lopezi*
					Leptomastidea	*abnormis*
				Ericydini	*Clausenia*	*josephi*
				Tetracnemini	*Paraleurocerus*	*bicoloripes*
		Eucharitidae			*Stilbula*	*tenuicornis*
		Eulophidae	Entedontinae	Entedontini	*Chrysocharis*	*bipunctatus*
						albipes
						gemma
						laomedon
						laricinellae
						lepelleyi
						milleri
						pentheus
						phryne
						pubens
						pubicornis
						sunosei
					Chrysonotomyia	*formosa*
						ritchiei
						ruforum
						species

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
					Chrysonotomyia	*violaceus*
					Closterocerus	*africanus*
						trifasciatus
					Cotterellia	*japonica*
					Entedon	*ergias*
					Goetheana	*shakespearei*
					Horismenus	*fraternus*
					Pediobius	*acantha*
						coffeicola
						foveolatus
						furvus
						nr-*facialis*
					Platocharis	*?coffeae*
					Psephenivorus	*mexicanus*
					Teleopterus	*erxias*
					Thripobius	species
				Elachertini	*Trichospilus*	*pupivora*
			Euderinae	Euderini	*Euderus*	*agromyzae*
						lividus
			Eulophinae	Cirrospilini	*Cirrospilus*	*cinctiventris*
						diallus
						inimicus
						pictus
						species
						variegatum
						vittatus
					Diglyphus	*intermedius*
						minoeus
					Zagrammosoma	*americanum*
						multilineatum
				Elasmini	*Elasmus*	*albicoxa*
						bellicaput

Division	Superfamily	Family	Subfamily	Tribe	Genus	Species
					Elasmus	*broomensis*
						leucopteras
				Eulophini	*Dhalbominus*	*fuscipennis*
					Eulophus	*larvarum*
					Hemiptarsenus	*fulvicollis*
					Hyssopus	*thymus*
					Necremnus	*brevisamulus*
					Notanisomorphella	*borboricus*
					Pnigalio	*argraules*
						longulus
						maculipes
						minio
						pallipes
						species
					Stenomesius	*rufescens*
					Sympiesis	*marylandensis*
						sericercornis
						viridulus
					Euplectrus	*parvulua*
						puttleri
						species
						spodopterae
			Tetrastichinae	Tetrastichini	*Aceratoneuromyia*	*evanescens*
					Aprostocetus	*ceroplastae*
						hagenowii
						leucopterae
					Citrostichus	*phyllocnistoides*
					Melittobia	*australica*
					Minotetrastichus	*ecus*
					Nesolynx	*albiclavus*
					Oomyzus	*incertus*
						scaposus

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
					Parachrysocharis	*pyrillae*
					Tetrastichus	*coeruleus*
						howardi
						julis
						krishneri
						species
		Eupelmidae	Calosotinae		*Anastatus*	*albitarsis*
						amarus
						colemani
						floridanus
						japonicus
						ramakrishnai
					Euplemus	*australiensis*
		Eurytomidae	Eurytominae		*Eurytoma*	*nesiotes*
		Mymaridae	Alaptinae	Anagrini	*Anagrus*	*epos*
			Mymarinae	Anaphini	*Anaphes*	*behmani*
						calendrae
						nitens
						ovijentatus
						sordidatus
				Mymarini	*Polynema*	*striaticorne*
		Perilampidae	Perilampinae		*Perilampus*	*tristis*
		Pteromalidae	Asaphinae		*Asaphes*	*lucens*
						vulgaris
			Cerocephalinae		*Theocolax*	*formicoformis*
			Miscogasterinae	Miscogasterini	*Sphaeripalpus*	species
				Sphegigasterini	*Cyrtogaster*	species
					Sphegigaster	*flavicornis*
			Pteromalinae	Pachyneurini	*Pachycrepoideus*	*vindemmiae*
					Pachyneuron	*albutius*
						muscarum
				Pteromalini	*Anisopteromalus*	*schwenkei*

Division	Superfamily	Family	Subfamily	Tribe	Genus	Species
					Callitula	*bicolor*
					Catolaccus	*aeneoviridis*
					Dibrachoides	*druso*
					Dibrachys	*boarmiae*
						cavus
					Dinarmus	*acutus*
					Hypopteromalus	*tabacum*
					Mesopolobus	*bruchophagi*
						subfumatus
					Nasonia	*vitripennis*
					Pteromalus	*cerealellae*
						veneris
					Sisyridivora	*cavigena*
					Spaniopus	*japonicus*
						species
					Trichomalopsis	*americanus*
					Trichomalus	*fasciatus*
			Spalangiinae		*Spalangia*	*cameroni*
						drosophilae
		Tetracampidae	Tetracampinae		*Dipriocampe*	*diprioni*
		Torymidae	Monodontomerinae		*Monodontomerus*	*aereus*
						dentipes
					Roptrocerus	*xylophagorum*
		Trichogrammatidae	Lathromerinae		*Lathromeroides*	species
					Oligositoides	*semicinctium*
			Trichogrammatinae		*Trichogramma*	*?australicum*
						brevicapillum
						evenescens
						minutum
						platneri
						semifumatum
					Trichogrammatoidea	*armigera*

Division	Superfamily	Family	Subfamily	Tribe	Genus	Species
					Trichogrammatoidea	*bactrae*
	Cynipoidea	Figitidae	Charipinae		*Alloxysta*	*megourae*
			Eucoilinae		*Cothanaspis*	species (?*boulardi*)
					Hexacola	species
						websteri
		Ibalidae			*Ibalia*	*drewensi*
	Evanoidea	Evanidae			*Evania*	*appendigaster*
					Prosevanis	*fuscipes*
	Ichneumonoidea	Braconidae	Agathidinae		*Agathis*	*calcarta*
						gibbosa
						laticincta
						unicolorata
					Bassus	*dimidiator*
					Microdus	*acrobasidis*
						pumilus
			Alysiinae	Alysiini	*Alysia*	*manducator*
					Aphaereta	*pallipes*
					Dapsilarthra	species
				Dacnusini	*Dacnusa*	*nipponica*
			Aphidiinae	Aphidiini	*Aphidius*	*avenae*
						matricariae
						sonchi
						species
				Ephredrini	*Ephredrus*	*plagiator*
				Praini	*Praon*	*exsoletum*
						volucre
				Trioxini	*Monoctonus*	*paulensis*
					Trioxys	*complanatus*
			Blacinae	Blacini	*Pygostolus*	*falcatus*
				Orgilini	*Orgilus*	*jenniae*
						lepidus

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
					Orgilus	*obscurator*
						parcus
			Braconinae		*Aphrastobracon*	*flavipennis*
					Bracon	*?hancocki*
						cajani
						greeni
						lissogaster
						mellitor
						thurberiphagae
						vulgaris
					Campyloneurus	*mutator*
					Coeloides	*dendroctoni*
					Habrobracon	*hebetor*
						instabilis
						lineatellae
						politiventris
						stabilis
					Hybogaster	*varipalpis*
					Iphiaulax	*kimballi*
					Microbracon	*chilonis*
						pygmaeus
						variabilis
					Ophthalmobracon	*kirkpatricki*
					Stenobracon	*deesae*
					Stenobracon	*nicevillei*
			Cardiochilinae		*Cardiochiles*	*hymeniae*
						nigricollis
					Toxoneuron	*nigriceps*
			Cheloninae		*Ascogaster*	*quadridentatus*
						reticulatus
					Chelonus	*annulipes*
						curvimaculata

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
					Chelonus	*heliopae*
						inanitus
						kellieae
						phthorimaeae
						texanus
					Phanerotoma	*bennetti*
						phyllotomae
						toreutae
			Doryctinae		*Dendrosoter*	*protuberans*
					Heterospilus	*coffeicola*
					Rhaconotus	*roslinensis*
					Spathius	*vulnificus*
			Euphorinae	Euphorini	*Aridelus*	*cameroni*
						rufus
					Microtonus	*hyperodae*
						sitonae
						stelleri
					Perilitus	*dubius*
				Meteorini	*Meteorus*	*campestris*
						pallipes
						ruficeps
						unicolor
			Macrocentrinae		*Macrocentrus*	*gifuensis*
						instabilis
						linearis
			Microgasterinae		*Apanteles*	*ater*
						bordagei
						dignus
						dilectus
						epinotaie
						etiellae
						forbesi

Division	Superfamily	Family	Subfamily	Tribe	Genus	Species
					Apanteles	*fumiferanae*
						maculitarsis
						murinanae
						obliquae
						solitarius
						subandinus
						syleptae
						targamae
						thompsoni
					Cotesia	*congregatus*
						flavipes
						marginiventris
						sesamiae
						xanthostigma
					Hypomicrogaster	*tiro*
					Microgaster	*tibialis*
					Microplitis	*croceipes*
						feltiae
						mediator
						plutellae
						rufiventris
						species
			Miracinae		*Mirax*	*minuta*
			Opiinae	Opiini	*Opius*	species
			Rogadinae		*Aleiodes*	*tristis*
					Chremylus	*elaphus*
					Pelecystoma	*harrisinae*
					Rogas	*nolophanae*
						species
						terminalis
						testaceus
		Ichneumonidae	Agriotypinae		*Agriotypus*	*armatus*

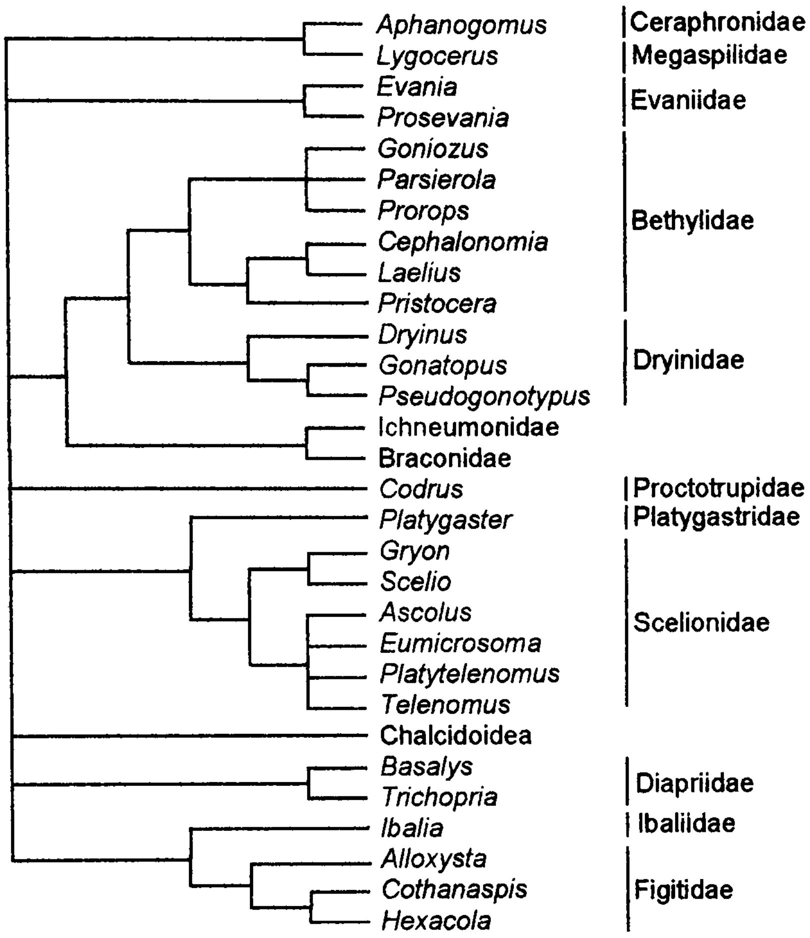
Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
			Banchinae	Banchini	*Banchus*	*flavescens*
				Glyptini	*Australoglypta*	*latrobei*
					Cephaloglypta	*murinanae*
					Glypta	*fumiferanae*
						haesitator
						fufiscutellaris
				Lissonotini	*Lissonota*	*complicator*
			Campopleginae		*Bathyplectes*	*anurus*
						stenostigma
						tristis
					Campoletis	*flavicincta*
					Campoplex	*haywardi*
						mutabilis
					Diadegma	*fenestrale*
						insulare
						mollipla
						rufipes
						semiclausen
						species
					Dolophron	*pedella*
					Hyposoter	*didymator*
						exiguae
						rivalis
					Lathrostizus	*euurae*
					Lemophagus	*curtus*
					Olesicampe	*benefactor*
						monticola
						ratzeburgi
					Sinophorus	*crassifemur*
					Tranosema	*rostrale*
			Cremastinae		*Eiphosoma*	*dentator*
					Pristomerus	species

Division	Superfamily	Family	Subfamily	Tribe	Genus	Species
					Temelucha	(*platensis* group)
			Cryptinae	Aptesini	*Pleolophus*	*basizonius*
						indistinctus
				Cryptini	*Agrothereutes*	*abbreviator*
						adustus
						extremalis
						tunetanus
					Gambroides	*javensis*
					Glabridorsum	*stokesii*
					Goryphus	*nursei*
					Itamoplex	*australis*
						inornatus
					Trathala	*flavoorbitalis*
				Hemitelini	*Aclastus*	*gracilis*
					Hemiteles	*ridibundus*
					Phygadeuon	*trichops*
					Sozites	*kerichoensis*
			Ctenopelmatinae	Mesoleiini	*Lamachus*	*eques*
				Perilissini	*Lophyroplectus*	*oblongopunctatus*
			Diplazontinae		*Diplazon*	*laetatorius*
					Syrphoctonus	*maculipennis*
			Ichneumoninae	Gyrodontini	*Afromelanichneumon*	*transvaalensis*
					Cratichneumon	*sublatus*
					Dentichasmias	*busseolae*
					Melanichneumon	*rubicundus*
					Pterocormus	*suspiciosus*
					Stenichneumon	*scutellator*
				Phaeogenini	*Centeterus*	*alternecoloratus*
					Phaeogenes	*maculicornis*
						nigridens
						semivulpinus
				Platylabini	*Peoecilostictus*	*cothurnatus*

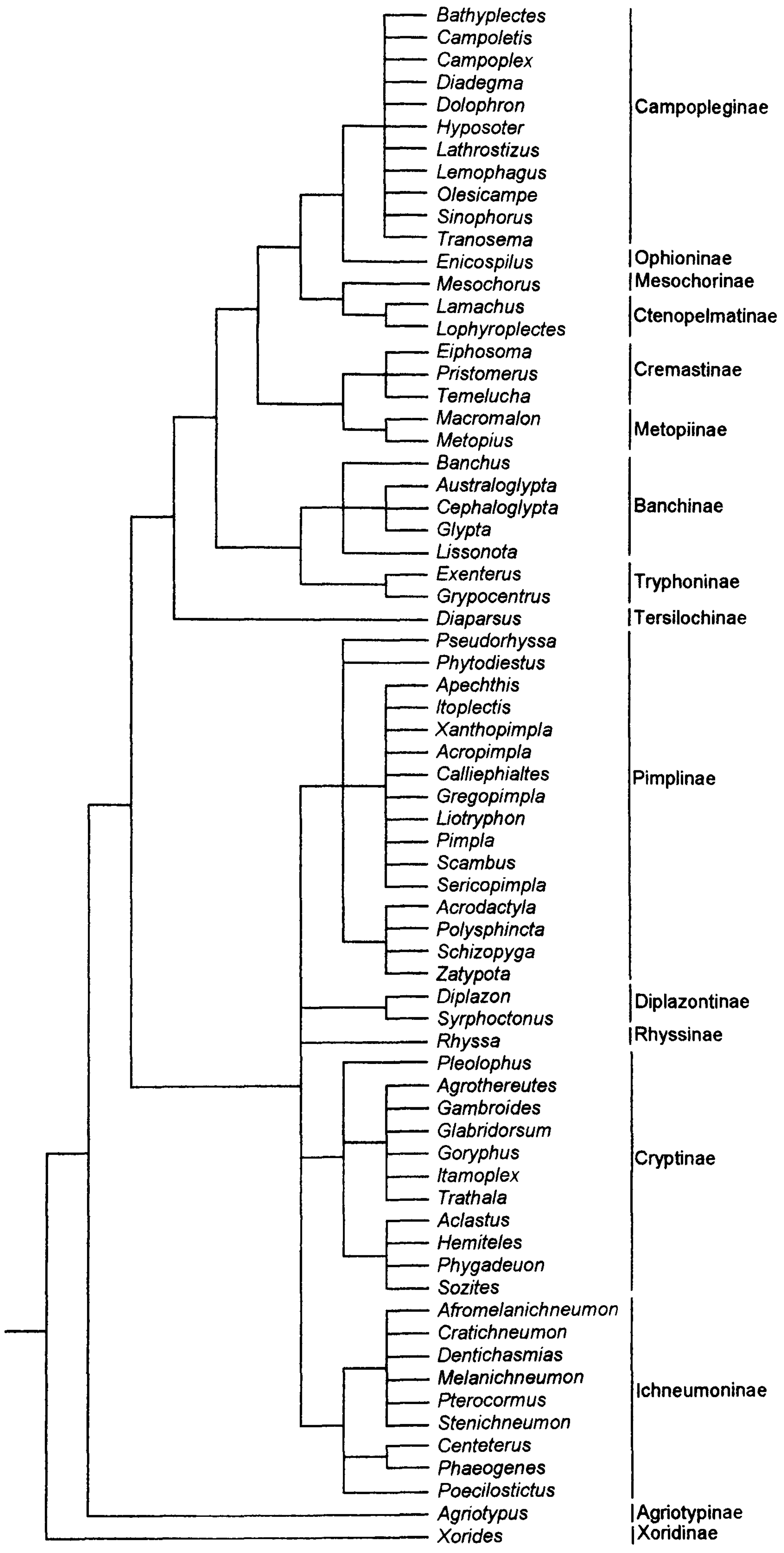
Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
			Mesochorinae		*Mesochorus*	*agilis*
						nigripes
			Metopiinae		*Macromalon*	*speices*
					Metopius	*discolor*
			Ophioninae		*Enicospilus*	species
			Pimplinae	Delomeristini	*Pseudorhyssa*	*maculicoxis*
				Phytodietini	*Phytodietus*	(*polysonias* group)
				Pimplini	*Acropimpla*	*pictipes*
					Apecthis	*quadridentata*
					Calliephialtes	*grapholithae*
					Gregopimpla	*inquisitor*
					Itoplectis	*cristatae*
						maculator
					Liotryphon	species
					Pimpla	*turionellae*
					Scambus	*brevicornis*
						foliae
					Sericopimpla	*sericata*
					Xanthopimpla	*citrina*
						stemmator
				Polysphinctini	*Acrodactyla*	*degener*
						quadrisculpta
					Polysphincta	*tuberosa*
					Schizopyga	*frigida*
					Zatypota	*albicoxa*
						bohemani
						percontatoria
			Rhyssinae	Rhyssini	*Rhyssa*	*persuasoria*
			Tersilochinae		*Diaparsus*	*carinifer*
			Tryphoninae	Exenterini	*Exenterus*	*abruptorius*
						adspersus
						amictorius

Division	**Superfamily**	**Family**	**Subfamily**	**Tribe**	**Genus**	**Species**
					Exenterus	*canadensis*
						tricolor
				Tryphonini	*Grypocentrus*	*albipes*
			Xoridinae		*Xorides*	*corcyrensis*
	Platygasteroidea	Platygasteridae	Platygasteriinae		*Platygaster*	*foersteri*
						oryzae
		Scelionidae			*Gryon*	*ajax*
						antestiae
						gnidus
					Scelio	*aegypticus*
					Scelio	*hieroglyphi*
						species
	Prototrupoidea	Diapriidae	Diapriinae		*Basalys*	*tritoma*
					Trichopria	*atrichomelinae*
						popei
		Proctotrupidae	Proctotrupinae		*Codrus*	*carolinensis*
			Telenominae		*Ascolus*	*seychellensis*
					Eumicrosoma	*beneficum*
					Platytelenomus	*busseolae*
					Telenomus	*alsophilae*
						calvus
						chloropus
						coelodasidis
						cosmopeplae
						costa-lima
						remus
						seychellensis
						ulyetti

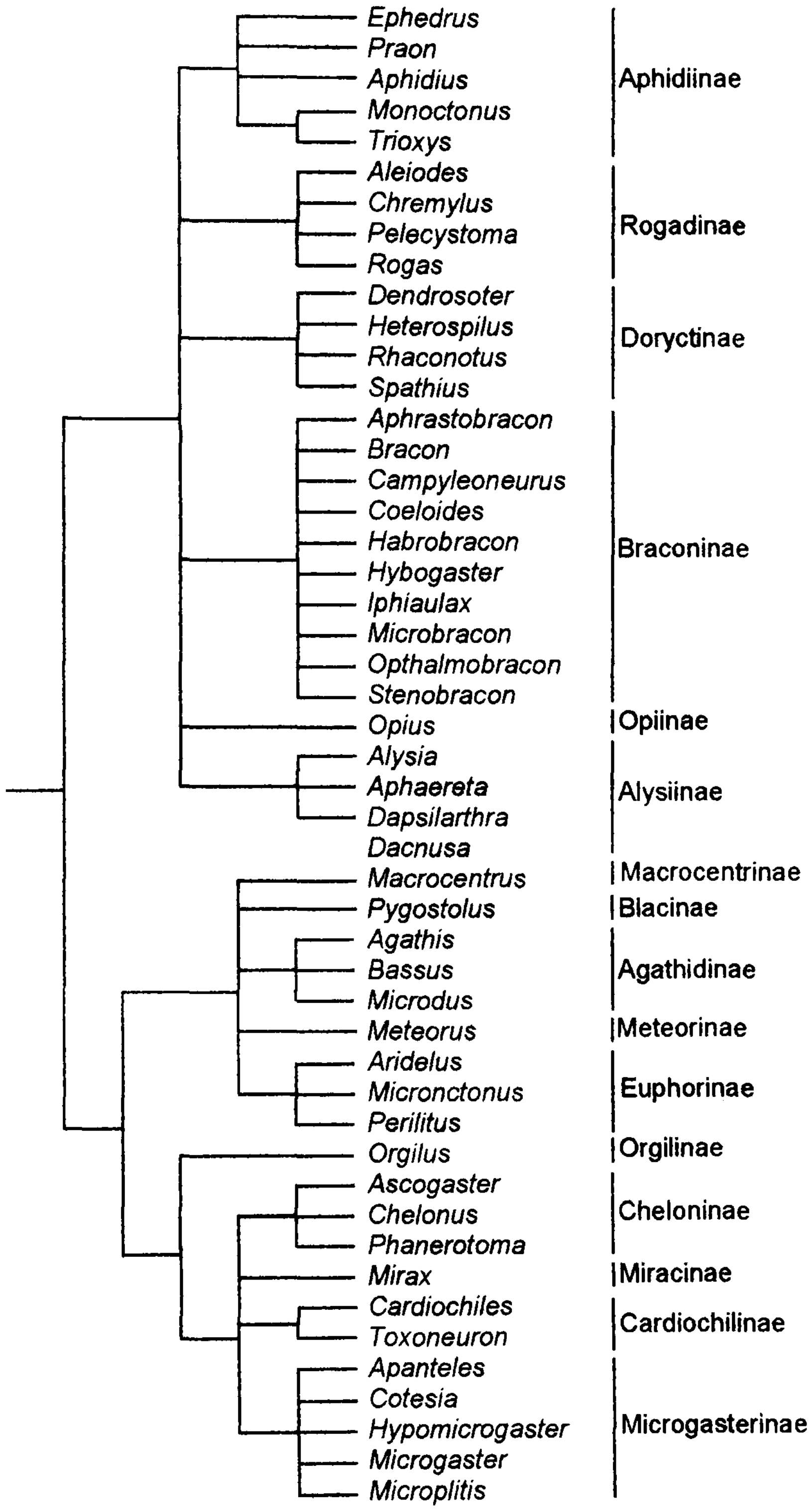
Appendix 3: Part 1. Conservative cladogram for the parasitic Hymenoptera (all polytomies are soft polytomies – individual species are placed within the relevant genus as soft polytomies).



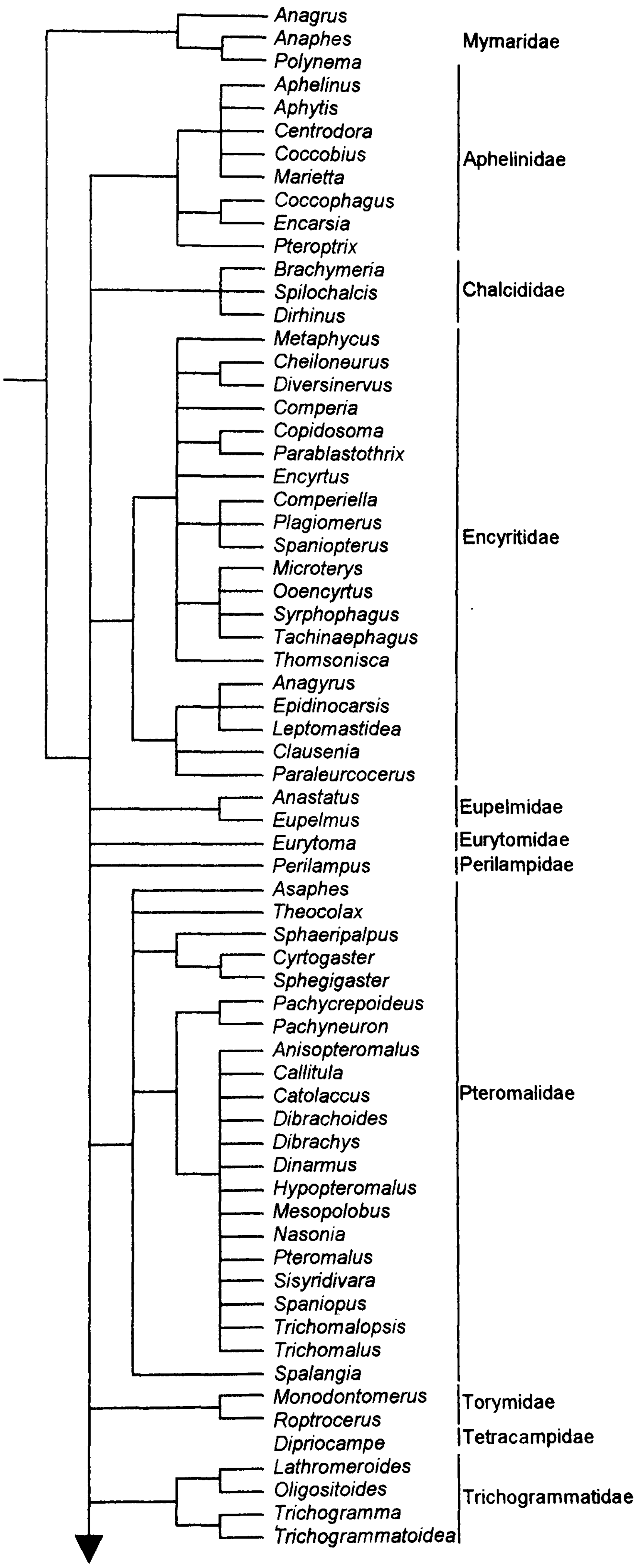
Appendix 3: Part 2. Ichneumonidae - conservative cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



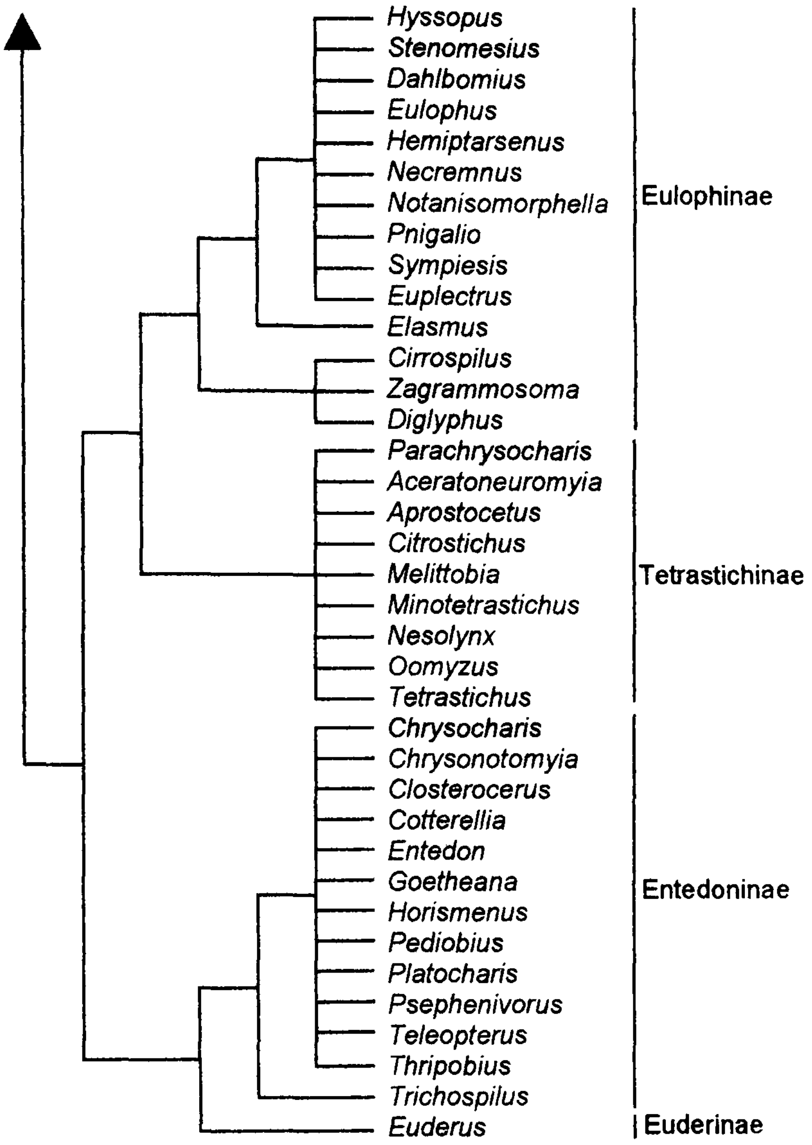
Appendix 3: Part 3. Braconidae - conservative cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



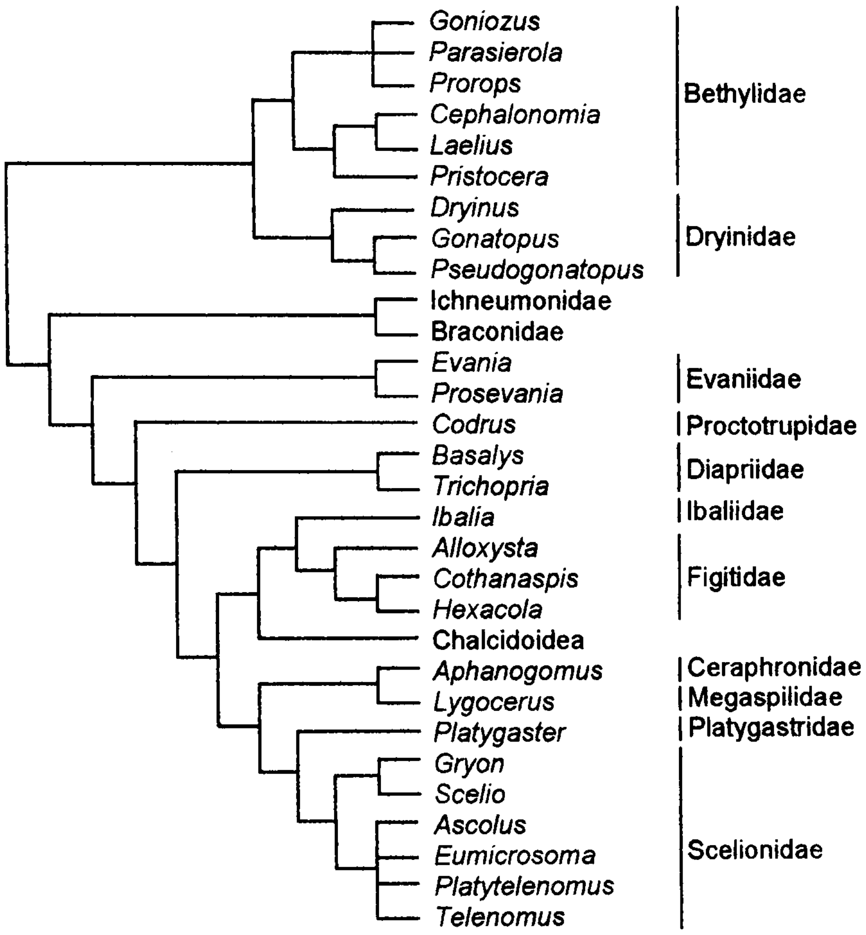
Appendix 3: Part 4a. Chalcidoidea - conservative cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



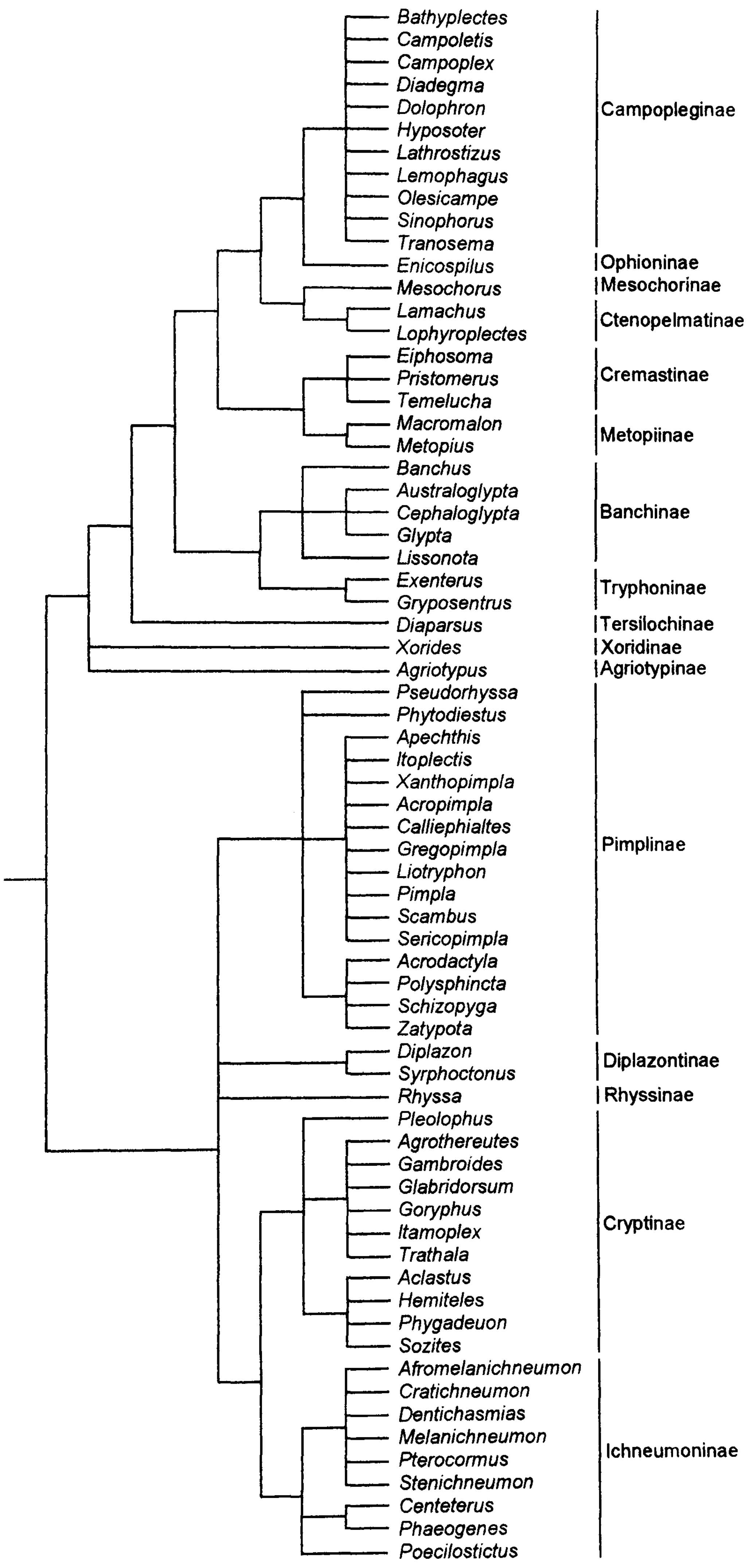
Appendix 3: Part 4b. Chalcidoidea - conservative cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



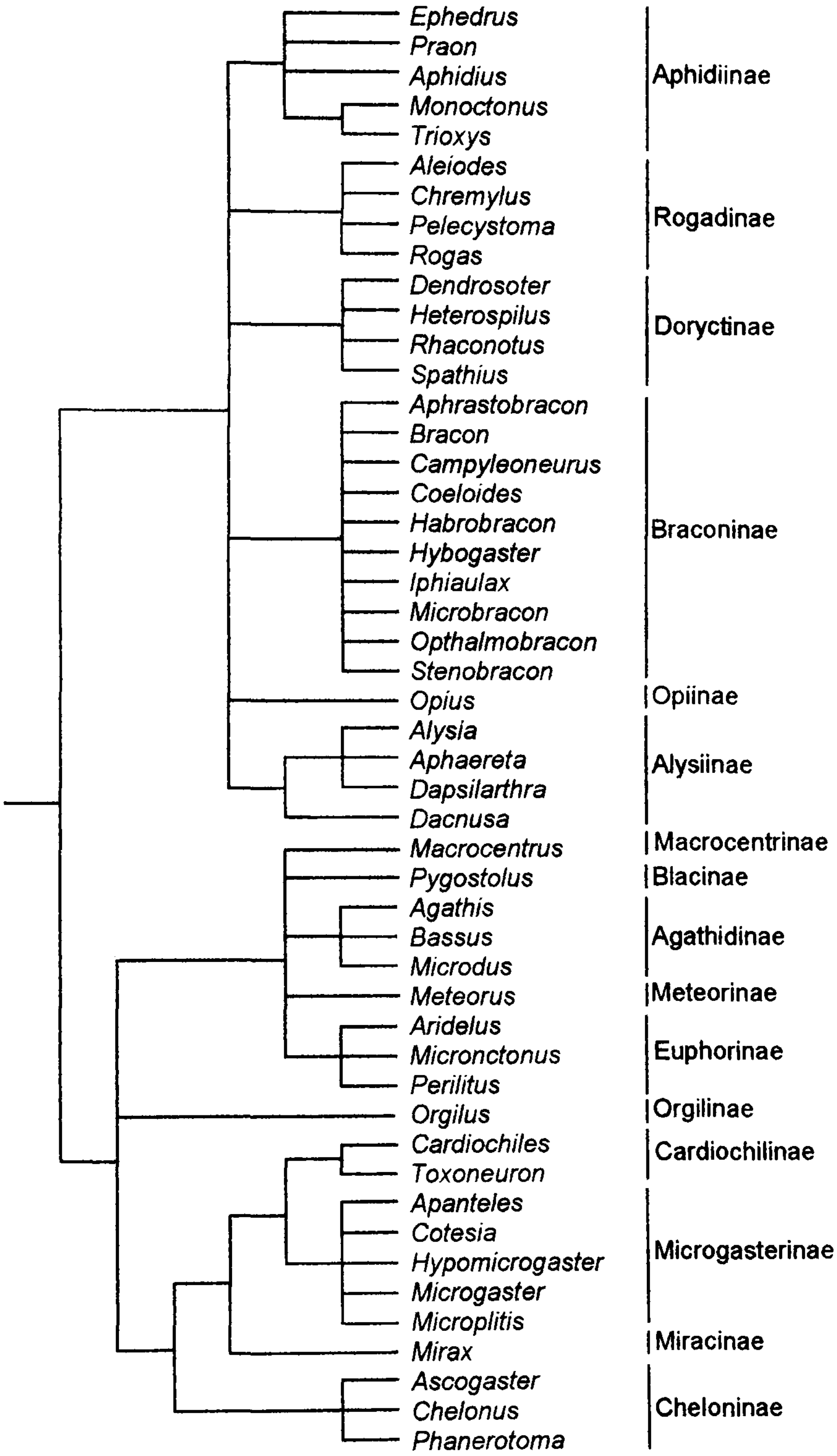
Appendix 4: Part 1. Highly resolved cladogram for the parasitic Hymenoptera (all polytomies are soft polytomies – individual species are placed within the relevant genus as soft polytomies).



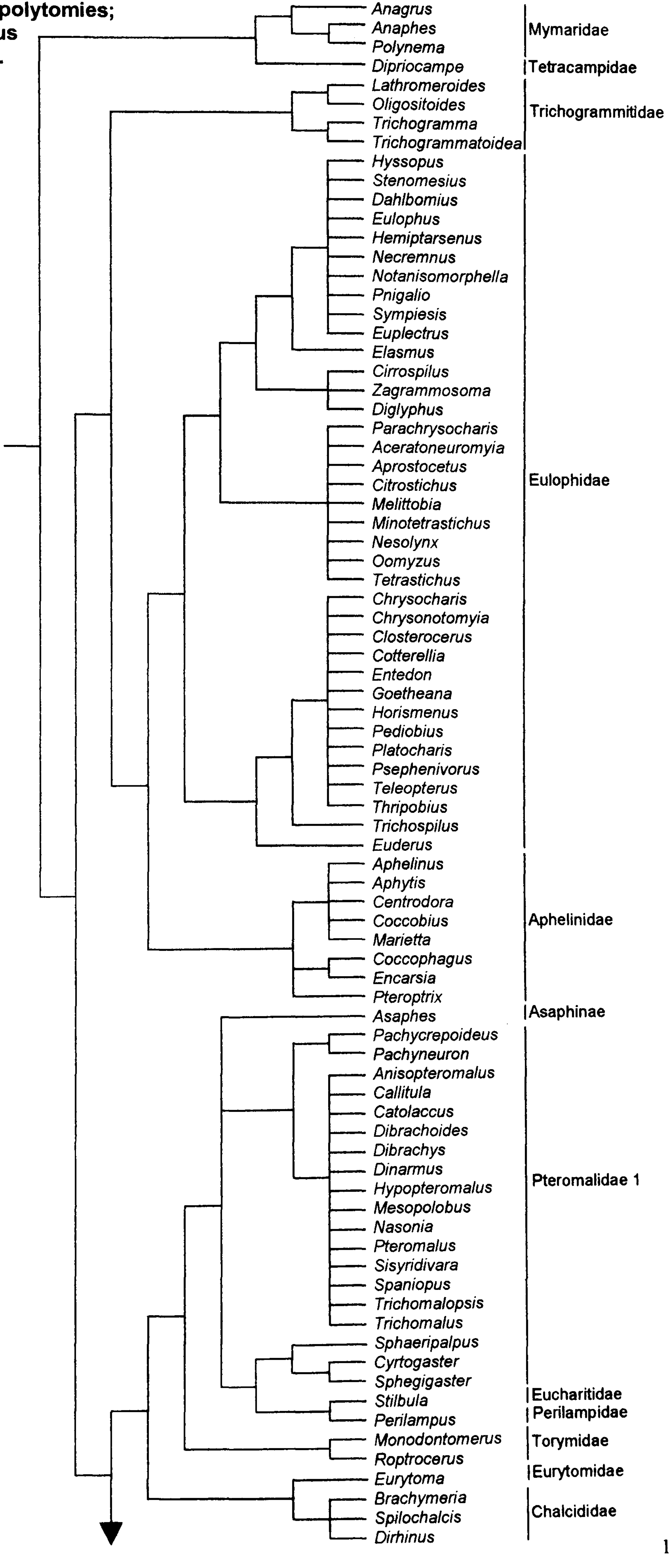
Appendix 4: Part 2. Ichneumonidae - highly resolved cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



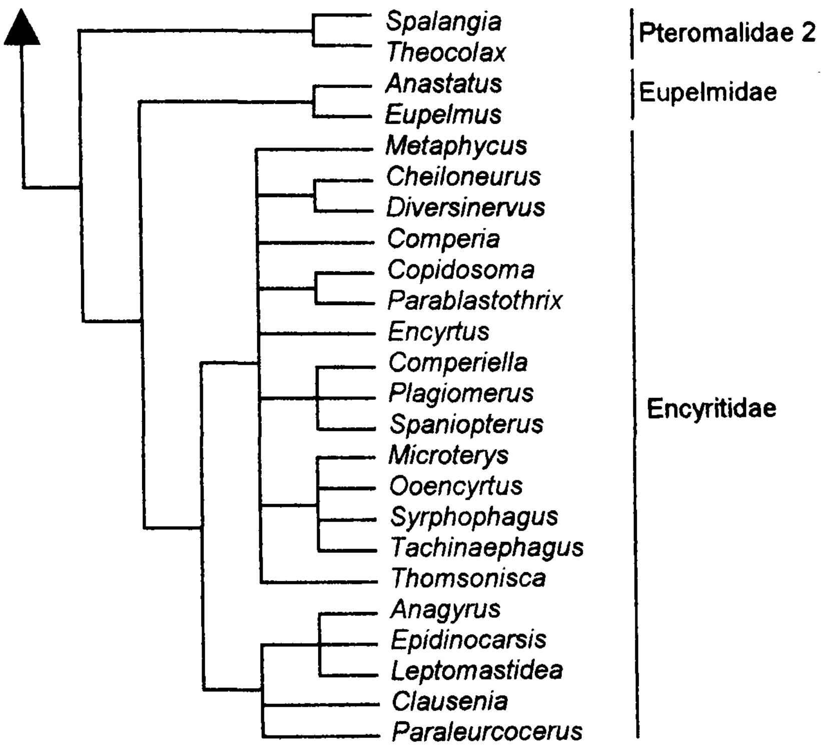
Appendix 4: Part 3. Braconidae - highly resolved cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



Appendix 4: Part 4a. Chalcidoidea - highly resolved cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



Appendix 4: Part 4b. Chalcidoidea - highly resolved cladogram for the parasitic Hymenoptera (soft polytomies; species within genus as soft polytomies).



Appendix 5: Ichneumonoidea (Hymenoptera) life history data set

Variables

1. Egg length (mm)
2. Egg width (mm)
3. Egg lifespan (days)
4. Parasitism – ectoparasitism (1); endoparasitism (2)
5. Development mode – idiobiosis (1); koinobiosis (2)
6. Larval development – solitary (1); gregarious (2)
7. Larval lifespan (days)
8. Feeding site – haemolymph (1); tissue (2)
9. Pupation site - inside host's body (1); under host's body (e.g. mummified aphid) (2); inside host's puparium but outside host's body (3); external to host's body and puparium (4)
10. Pupal lifespan (days)
11. Parasitoid adult length (mm)
12. Adult longevity (days)
13. Brood size
14. Fecundity
15. Parasitoid geographic range (square km)
16. Parasitoid distribution – temperate (1); tropical (2); temperate and tropical (3)
17. Maximum latitude of country where parasitoid is found
18. Minimum latitude of country where parasitoid is found
19. Host stage attacked – egg(1); nymph (2); larva (3); prepupa (4); pupa (5); adult (6); nymph / adult (7); prepupa / pupa (8); egg / larva / pupa (9); any host stage (10); larva / pupa (11); larva / prepupa (12); egg / larva (13); larva / pupa / adult (14); larva / prepupa / pupa (15)
20. Parasite window (days)
21. Host concealment – exposed (1); semi-concealed (2); concealed (3)
22. Host stage killed – larva (1); prepupa (2); pupa (3); adult (5); nymph / adult (6); larva / pupa (7); larva / prepupa (8); larva / prepupa / pupa (10)
23. Host adult body length (mm)
24. Host niche – external (1); leaf-miner (2); leaf-roller (3); web-spinner (4); casebearer (5); galler (6); borer (7); root feeder (8); predator (9); nest (10); in vegetation (11); pollen feeder (12); in stored grain (13); decaying plant material (14); frugivore (15); saprotroph (16)
25. Host geographic range (square km)
26. Host distribution – temperate (1); tropical (2); temperate and tropical (3)
27. Maximum latitude of country where host is found
28. Minimum latitude of country where host is found
29. Host range
30. Host order
31. Host species
32. The degree of study
33. List of countries where the parasitoid species has been recorded
34. List of countries where the host species has been recorded
35. References

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Family Braconidae																								
Subfamily Agathidinae																								
Tribe Agathidini																								
Agathis anglica											5				18535653	1	83n	35n			2		4.22	2
Agathis artemesiana											3.5	2.9			957999	1	69n	42n					3.4	
Agathis asteris											3.5				83858	1	49n	47n						
Agathis breviseta											3.5				22965320	1	83n	36n			2		3.1	5
Agathis calcarata				2	2	1					5.6		1		9629091	1	72n	25n	3		2		6.9	5
Agathis gibbosa	0.11	0.02	3.5	2	2	1	8.5			3	3.8	10.79	1	451	19599754.3	1	86n	25n	3		2		2.48	
Agathis laticincta				2	2	1				10	4.4		1		19599701	1	86n	25n	3		1			
Agathis unicolorata	0.1	0.02	5	2	2	1	10			3	4.7	17.08	1	470	2766889	3	22s	55s		3				
Baeognatha armeniaca											4				17938303	1	83n	36n					2.93	
Baeognatha nigra									4		3				17618958	1	83n	42n			2		3.06	5
Bassus arthurellus											4.4				9970610	1	86n	42n	3					
Cremnops desetor											8				24016790	3	83n	1n			3		6.78	15
Earinus elator						1					8				1204027	1	69n	46n			1			1
Earinus gloriatorius											5				19226522	1	83n	41n			2		7.02	2
Earinus limitaris				2	2						6.42				9970610	1	86n	42n	3		1		13.5	1
Earinus transversus											6.5				242910	1	58n	50n						
Earinus zeirapherae											4.25				19599701	1	86n	25n	3		3	1		7
Microdus dimidiator				2	2						5				1412870	1	55n	35n	3		3		4.08	7
Microdus pumilus	0.08	0.04	7	2	2	1				8	2	22	1	140	1185425	1	58n	43n	3		3		2.54	7
Microdus rufipes											5				1609033	1	58n	36n			3		6.78	15
Microdus tumidulus															1730277	1	58n	35n			2	3	4	2
Subfamily Alysiinae																								
Tribe Alysiini																								
Alysia manducator			2	2	2	1		2		12	6.25	3.5	1	549	25041731	3	58n	43s	3		3		12	16
Aphaereta apicalis											2				10946798	3	33n	34s			1			9
Aphaereta aotea						2					2.25				41528	1	36s	48s			3			16
Aphaereta colei				2	2	1							1		9629091	1	72n	25n				9		
Aphaereta genevensis				2	2	1					2.9	16.94	1		9629091	1	72n	25n	3		3		2.5	16
Aphaereta lonchaeae						1					2.5		1			1					3			16
Aphaereta minuta				2	2	2					1.78	9.53			173485	1	53n	35n	3		3	3	2	15
Aphaereta pallipes			4.29	2	2	2	6.5			5.71	2.13	4	11.2		9629091	1	72n	25n	3		3		2.5	16
Asobara rufescens				2	2										41528	1	53n	51n	3		3			14

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Asobara tabida				2	2	1			4		1.5		1		10659724	1	72n	25n	3		3	3	2.2	16
Chasmodon apterus											1.58				242910	1	58n	50n	11		3		2.5	7
Tribe Dacnusini																								
Dacnusa areolaris				2							1.36				269057	1	36s	48s			2		3	2
Dacnusa sibirica				2	2						1.5				242910	1	58n	50n	3		2		2	2
Subfamily Aphidiinae																								
Tribe Aphidiini																								
Aphidius ervi	0.05				2	1	7	2	1	6	1.5	5	1	101	39551770	3	86n	57s	7	4.5	1		2.6	1
Aphidius matricariae					1						1.95				16493439	1	72n	35s			1		1.5	1
Aphidius nigripes				2	2	1			1			15.34	1		9970610	1	86n	42n	7		1	5	3	1
Aphidius pisivorus				2		1			1		1.35		1			1			7		1		2.6	1
Aphidius rhopalosiphi			4	2	2	1	3	2	1	7	1.66	6.23	1		3457406	3	58n	57s	7		1		2.4	1
Aphidius smithi				2	2	1			1				1		4043889	3	34n	57s	7		1		2.6	1
Aphidius sonchi				2	2	1					2.09	9.92	1	215		1			7		1		1.9	1
Diaeretiella rapae				2	2	1		2	1	16	1.3	20	1	300	37484499	3	86n	35s	2		1	5	1.5	1
Dyscritulus planiceps						1					1.88								6		1			1
Lysiphlebus fabarum				2		1					1.08				357022	1	56n	46n			1		1.9	1
Lysiphlebus testaceipes				2					1		2				18077117	3	72n	57s			1		1.5	1
Monoctonus paulensis	0.14		3.17	2	2	1	5.33		1	6			1			1			7		1	5	2.6	1
Trioxys complanatus	0.07	0.03	2.19	2	2	1	4.73			3.04	1.3	28	1	180	18959391	3	72n	43s	7		1		1.5	1
Tribe Ephredrini																								
Ephedrus californicus				2	2	1		2	1	7.22		14		1200	9970610	1	86n	42n	7		1	5	2.6	1
Ephedrus plagiator				2	1	1				14.5	1.63		1	87	11752232	3	86n	57s	7		1		2.4	1
Tribe Praini																								
Praon exsoletum	0.07	0.02	2.88	2	2	1	3.88		1	4	1.7	47	1		20062721	3	72n	43s	6		1		1.5	1
Praon pequodorum				2	2	1			2		2				19599701	1	86n	25n			1		2.6	1
Praon volucre			4	2	2	1	18		2	8.5	2.07		1		21279330	3	86n	57s	6		1		2.6	1
Subfamily Blacinae																								
Tribe Blacini																								
Blacus exilis				2							1.86				17387678	3	83n	42n	3		3			7
Blacus koenigi											1.8				102173	1	47n	43n			3		3.25	7
Blacus nigricornis											1.82				41284	1	47n	46n	3		3			7

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Subfamily Braconinae																								
Tribe Braconini																								
Alienoclypeus insolitus											10.1				11587292	3	72n	15n			3		17	7
Bracon cajani	0.8	0.16	1.08	1	1		3.5				3.27	14				2			3	9				
Bracon cephi					1										9970610	1	86n	42n			3		7.8	7
Bracon gelechiae					2						3				9629091	1	72n	25n	3		2	3	3.6	3
Bracon lissogaster	0.74	0.11	2.75	1	1		7			8	3.5	19							3		3		7.8	7
Bracon kirkpatricki	0.81	0.16	0.83	1		2	3		3	3	2.6		6	132	17679551	3	72n	18s	3		3		4.98	7
Bracon mellitor	1.1	0.24	1	1		1	5.5			4.5	3.8	21.58	1	213	9629091	1	72n	25n	3	10.5	3	1	3.36	7
Bracon pineti				1	1		4				3.32				18949598	1	83n	42n	3		3			7
Bracon rhyacioniae				1												1			3		3			7
Bracon thurberiphagae	0.72	0.18	1.08	1	2	2	3.5		3	9.5		14	6.5		10614116	3	72n	23s	3	9	3		6.82	7
Habrobracon hebetor	0.5		2		1	2			2		3	40	10	614	9629091	1	72n	25n	3		3		5.16	13
Habrobracon lineatellae	0.54	0.18	1.1	1	1	2	2.46			5.46		72	7	854	9970610	1	86n	42n	3		3		4.14	7
Stenobracon deesae			1.1	1	1	1	5.4			16.79	11.87	29.5	1	58		2			3		3			
Tribe Coelidini																								
Coeloides pissodis											5				19599701	1	86n	25n			3		3	7
Coeloides scolyticida				1							4.38				102173	1	47n	43n			3			7
Subfamily Cardiochilinae																								
Schoenlandella diaphaniae															10768005	3	72n	4s			1		13.36	1
Toxoneuron nigriceps				2	2	1		2	4		7.15		1		21551731	3	86n	4s	3	14	1	10	14	1
Subfamily Charmontinae																								
Charmon extensor				2							4.18				93030	1	48n	45n	3		3			7
Charmon gracilis															9629091	1	72n	25n			2		9.22	4
Charmon rufipes				2											93030	1	48n	45n	3		3			7
Subfamily Cheloninae																								
Adelius subfasiatus						1							1		242910	1	58n	50n			2			2
Tribe Chelonini																								
Ascogaster quadridentata			2.5	2	2	1				7	4.42	24.5	1		9898148	1	72n	48s	1	7.5	3		6.78	15
Ascogaster reticulatus	0.21	0.06	1.5	2	2	1	14	2			4.17	12	1	170	337880	1	46n	24n	1	6		1	6.06	7
Chelonus asiaticus															1648000	1	40n	25n	3	30	2		6.52	4
Chelonus blackburni															9629091	1	72n	25n	1		3	1	4.98	7

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Chelonus curvimaculata	0.16	0.04	1.5	2	2	1	14.8			5.5	3.32	8.21	1	1237		1			3	8.67	1			
Chelonus heliopae	0.15	0.07	0.84	2	2	1	12.5			6	3.29	22	1	1300		2			1		1			
Chelonus inanitus				2	2	1				10.5	5.2		1			2			1		1			
Chelonus insularis				2	2	1							1		11587292	3	72n	15n	1		1	1	13.4	1
Chelonus curvimaculatus															8782874	3	16n	43s	1		3	1	4.98	7
Chelonus texanus				2	2	1				15	5		1			1			1		3		16.4	7
Tribe Phanerotomini																								
Phanerotoma flavistestacea				2	2	1													1		3	1	7.5	13
Subfamily Doryctinae																								
Tribe Doryctini																								
Dendrosoter protuberans	0.9		2	1	2	1	7.5			30.5	3		1	8	26939149	1	72n	25n	3		3		3.25	7
Doryctes mutillator				1											17074993	1	83n	42n	3		3			7
Doryctes undulatus				1											17074993	1	83n	42n	3		3			7
Tribe Hecabolini																								
Stenocorse bruchivora				1		1					4.5	100		67	9629091	1	72n	25n	11		3		6.5	7
Tribe Heterospilini																								
Heterospilus coffeicola	0.38	0.13	6	1	1	1	19				2.5		1			3			9	31.5	1		2	15
Heterospilus prosopidis				1		1		2				9	1	35	9629091	1	72n	25n	11	9	1		3	1
Tribe Spathiini																								
Spathius benefactor				1											19599701	1	86n	25n	3		3		3	7
Spathius brevicaudis				1		1					2.35				102173	1	47n	43n	3		3		3.25	7
Subfamily Euphorinae																								
Tribe Centistini																								
Pygostolus falcatus	0.31	0.08	5	2		1	11.5			7.5	3.59	11	1	46	9970610	1	86n	42n	6		3		50	8
Tribe Dinocampini																								
Dinocampus coccinellae				2	2	1			2		2.43				9872001	1	72n	25n	6		1	4	5.8	9
Tribe Euphorini																								
Microcotonus aethiopoides				2					3		4				51255542	3	86n	48s	6		3	4	4	11
Microcotonus caudatus				2	2	2			3				20.8		701292	1	70n	50n	6		1	4	15	1
Microcotomus colesi				2	2						3				9629091	1	72n	25n	3		1	4	5.25	1
Microcotonus hyperodae				2	2	1				15.58	2.1		1		12480752	3	5n	57s	10		3		3.5	7
Tribe Perilitini																								

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Meteorus arizonensis						1									9629091	1	72n	25n			1	1		1
Meteorus brevicauda															242910	1	58n	50n	3		3			7
Meteorus campestris			6	2	2					6		63		240	9629091	1	72n	25n	3		1	1	9.22	7
Meteorus leviventris				2		1									9629091	1	72n	25n	3		1		14.4	1
Meteorus trachynotus				2	2	1									19599701	1	86n	25n	3		2	3	3.6	3
Subfamily Exothecinae																								
Colastes braconius				1	1	1		2	3		1.13		1		242910	1	58n	50n	3	32	2		2.06	2
Exothecus braconius				1		1			3						242910	1	58n	50n	3		2		1.9	2
Phanomeris catenator				1	2				3		1.5				242910	1	58n	50n	3		2		2.73	2
Phanomeris dimidiata						1							1		242910	1	58n	50n			2		2.73	2
Phanomeris laevis				1	2				3		1.8				242910	1	58n	50n			2		3.15	2
Phanomeris phyllotomae	0.66	0.17	2	2			8		3		1.25	48			9629091	1	72n	25n	3	56	2		4.45	2
Subfamily Gnamptodontinae																								
Gnamptodon pumilio											0.8				313183	1	58n	50n					1.42	
Subfamily Helconinae																								
Tribe Brachistini																								
Eubazus semirugosius											5								1		3			7
Triaspis pallipes						1					1.75		1		242910	1	58n	50n					2.25	
Triaspis thoracicus											2.35				185180	1	37n	32n	3		3			7
Tribe Diospilini																								
Apsicolpus hudsoni						1		2	3		10.1				269057	1	36s	48s	3		3	1	20	7
Baeacis abietis				2							3.15				17074993	1	83n	42n	3		3			7
Diospilus capito											2.15				41284	1	47n	46n	3		1			12
Diospilus hiator															9970610	1	86n	42n	3		3		6.5	8
Subfamily Homolobinae																								
Homolobus truncator											4.8				9629091	1	72n	25n			1		13.2	1
Subfamily Hormiinae																								
Tribe Hormiini																								
Hormius moniliatus											1.2				115027	3	45n	15n			3		3.74	7
Hormius vulgaris															9629091	1	72n	25n			2			4
Subfamily Ichneutinae																								
Tribe Ichenutini																								

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Ichneutes levis				2	2						1.9								3		2	6		2
Ichneutes pikonematis															19599701	1	86n	25n			1			1
Subfamily Macrocentrinae																								
Macrocentrus ancylivorus											3.5				9629091	1	72n	25n	3	10.5	3		3.36	7
Macrocentrus cingulum				2	2	2						7		200	10392844	1	72n	25n	3		3		11.78	7
Macrocentrus iridescens									3		7				9970610	1	86n	42n	3		2		8.92	3
Macrocentrus nigridorsis				2		2			3						9970610	1	86n	42n	3		2	1	8.92	3
Subfamily Microgasterinae																								
Tribe Apantelini																								
Apanteles ater				2	2						2.25				11193373	1	86n	42n	3		2		8.92	3
Apanteles carpatus				2	2	1		2	4	6	2.5		1		36863600	3	86n	55s	3		3	1	6.8	18
Apanteles corvinus						1					2.4		1		18894137	1	83n	42n			2		1.88	2
Apanteles fumiferanae	0.29	0		2	2		20		4	10.5	3.5	26			19599701	1	86n	25n	3		3	1	8.38	7
Apanteles galleriae				2	2	1					2.7			239					3		2		13.26	10
Apanteles milleri											2.8				9629091	1	72n	25n						
Apanteles morrisi					2						2.8				9970610	1	86n	42n	3		3	1	8.38	7
Apanteles subandinus	0.32	0.07	0.92	2		1	9.5		4		3.86	17	1	345	10449189	3	11s	55s	3	5	3		3.64	7
Apanteles syleptae				2	2	1				5.5	3	11.21	1		923768	2	15n	5n	3	3	2		11.8	3
Dolichogenidea evonymellae				2		1			3		3.3	4			152522	1	53n	42n	3		3		12.9	7
Dolichogenidea absona				2							2.8				19599701	1	86n	25n	3		3	1	8.38	7
Pholetesor circumscriptus						1					2.2				23172817	3	83n	48s			2			2
Pseudapanteles dignus	0.35	0.06	1	2	2	1	7.5			9	2.23	10.21	1	182	11592420	3	72n	10n	3	8	2		2.5	2
Tribe Cotesiini																								
Cotesia congregata	0.14	0.04	2	2		2		2	3	4.5	2.47				28131757	1	86n	34s	3	8.3	1	1	28.2	1
Cotesia euphydryidis				2	2	2			2	7	2.2		28.1		9629091	1	72n	25n	3		2		17.5	4
Cotesia flavipes	0.14	0.04	3.5	2		2	11.5			8.5	1.72	3	42.6	262	25219206	3	46n	43s	3		3		10.08	7
Cotesia glomerata				2		2		1	2	8	3	14	60	1050	75332112	3	86n	48s	3		1	1	17.7	1
Cotesia jucunda											3				338145	1	70n	60n	3		1			1
Cotesia kariyai				2							1.2				337880	1	46n	24n	3		3		15.6	11
Cotesia kazak				2		1					3.5				9898148	1	72n	48s	3				13.8	
Cotesia marginiventris	0.88	0.17	1.13	2	2	1	4.75			4	3	5	1		11587292	3	72n	15n	3		1	1	13.2	1
Cotesia medicaginis				2	2	1					5		1								1		19.4	1

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Cotesia melanoscelus	0.31	0.06	5	2		1	11			7	2.67	24.5	1	1000	30997115	1	86n	21n	3		1		16.6	1
Cotesia melitaearum				2		2			2	15	4		7.03		581055	1	70n	50n	3		2	1	16.1	4
Cotesia ocneriae						2					2.2				2067296	1	53n	35n			1		17.2	1
Cotesia phobetri						2					1.8				9629091	1	72n	25n			1	1		1
Cotesia rubecula				2	2	1					3.1				36307527	3	86n	43s	3		1	1	17.7	1
Cotesia schizurae				2							1.8				19599701	1	86n	25n	3		1			1
Cotesia scitula						2			3		2.5		93		19599701	1	86n	25n	3	31.79	1		16	1
Cotesia vestalis				2		1			3				1		10502903	3	72n	1n	3		1	1	4.92	1
Cotesia yakutatensis						2					1.9				19599701	1	86n	25n	3		1		14.4	1
Glyptapanteles militaris				2		2					1.3				9629091	1	72n	25n	3		1		15.4	1
Glyptapanteles porthetriae											2.5				132892	1	59n	47n	3		1	1	17.2	1
Protapanteles immunis											3.5				338145	1	70n	60n	3		1			1
Tribe Microgastrini																								
Choeras tedellae				2	2	1					1.23		1			1			3		2			4
Choeras tiro				2						14	2.1				9970610	1	86n	42n	3	15.17				
Microgaster hospes				2	2	1									9629091	1	72n	25n	3		2	3	3.6	3
Microgaster tibialis	0.5	0.07	2.5	2		1	26.5				3.5		1	292		1			3					
Tribe Microplitini																								
Microplitis alaskensis				2		1									9629091	1	72n	25n	3		1		14.4	1
Microplitis croceipes	0.76	0.18	1.75	2	2	1		1	2	6	5.6	11.9	1	180	19599701	1	86n	25n	3	14	1		14	1
Microplitis demolitor				2	2	1		1	2	6	2.5		1		17311391	3	72n	43s	3		1		14	1
Microplitis mediator	0.35	0.08	1.54	2	2	1	11.3	2	3		2.86		1		31967267	1	86n	24n	3		1	1	14.2	1
Microplitis naenia						1					3.2				321776	1	58n	48n			1		13.2	1
Microplitis ocellatae						2			2		2.8				337880	1	46n	24n			1		28.8	1
Microplitis plutellae				2	2	1					1.5	20	1	232	9970610	1	86n	42n	3	20.5	2	1	4.92	2
Microplitis rufiventris	0.24	0.04	2	2	2	1	4.5			6.5	3.08		1		17074993	2	83n	42n	3		1	1	13.6	1
Microplitis tuberculifera						1					3.6				692874	1	69n	50n			1		14.2	1
Subfamily Microtypinae																								
Microtypus species															9629091	1	72n	25n			3		5.03	7
Microtypus wesmaelii															242910	1	58n	50n						
Subfamily Micracinae																								
Mirax minuta				2	2	1							1		9629091	1	72n	25n			2	3		2

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Mirax rufilabris						1					1.14		1		242910	1	58n	50n			1		1.32	1
Subfamily Opiinae																								
Biosteres arisanus				2							3				9629091	1	72n	25n	1		3		8	15
Biosteres melleus				2	2				4	30					9629091	1	72n	25n	3	14	3	3	3	15
Biosteres vandenboschii					2						3.46				9629091	1	72n	25n	3		3	3	8	15
Diachasmimorpha kraussi											3.1	27.6		111.7	17311391	3	72n	43s	3		3	3	8	15
Diachasmimorpha longicaudata				2							3.05				17626751	3	72n	26s	3		3	3	8.4	15
Diachasmimorpha tryoni															17311391	3	72n	43s	3	7	3	3	5	15
Doryctobracon areolatus					2						5				15653084	3	72n	55s	3		3	3	8.4	15
Doryctobracon crawfordi					2						4.8				2009301	3	33n	8n	3		3	3	9.1	15
Fopius arisanus				2	2	1			4				1		19599439	3	72n	43s	1		3	3	8	15
Opius canaliculatus				2	2	1									19599701	1	86n	25n	13	8	3	3	3	15
Opius dissitus				2	2	1															1		1.8	1
Opius lectus									4	30					9629091	1	72n	25n	3		3		3	15
Opius magnus				2	2	1									357022	1	58n	50n	3		3		3.5	15
Opius rhagoleticola					2	1					2.28				357022	1	58n	50n	3		3		3.5	15
Opius striatriventris				2	2				3						9629091	1	72n	25n	3		2		3	2
Psyttalia incisi				2	2						2.58				12916354	3	72n	8n	3		3	3	8	15
Utetes anastrephae					2										14354181	3	72n	55s	3		3	3	8.4	15
Subfamily Braconidae																								
Tribe Orgilini																								
Orgilus comptanae				2		1									9629091	1	72n	25n			2			2
Orgilus lepidus	0.27	0.06	1.5	2	2	1	8			9	4.5	17.58	1	791	7682300	3	11s	43s	3		3		3.64	7
Subfamily Pambolinae																								
Tribe Chremylini																								
Cedria paradoxa				1							0.7										1			
Subfamily Rhysipolinae																								
Rhysipolis decorator					1				3		3.1				242910	1	58n	50n	3		2	2	3.32	2
Rhysipolis hariolator					2						2.63				242910	1	58n	50n	3		2	3	2.56	2
Rhysipolis mediator				2	2				4		2.66				242910	1	58n	50n	3		2	2	2.3	2
Subfamily Rhyssalinae																								
Tribe Rhyssalini																								

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Oncophanes americanus				2	2	2			3						19599701	1	86n	25n	3		2	3	8.92	3
Oncophanes laevigatus				1	1	2			2				15		242910	1	58n	50n	3		2		7.04	3
Subfamily Rogadinae																								
Tribe Clinocentrini																								
Clinocentrus gracilpes				2	2				1		3.08				242910	1	58n	50n	3		2	3		4
Clinocentrus species																			3		2		6.02	4
Tribe Rogadini																								
Aleiodes circumscriptus											5				93030	1	48n	45n	3		3			7
Aleiodes gastritor	0.6	0.16										48			622339	1	70n	46n	3		1			1
Aleiodes nolophanae															9629091	1	72n	25n			1		11.2	1
Aleiodes praetor				2					1						242910	1	58n	50n	3					
Pelecystoma harrisinae	0.59	0.17	2	2			6			8	2	9.5		84		1			3		1			
Rogas malacosomatos				2	2	1			1		5				9970610	1	86n	42n	3		1	1		1
Rogas stigmator				2		2			1		2.9		29		19599701	1	86n	25n	3	30	1	1		1
Family Ichneumonidae																								
Subfamily Acaenitinae																								
Acaenitus dubiator				2	2						11.5				1022362	1	58n	36n	3		3		10	7
Phaenolobus terebrator											12				1022362	1	58n	36n			3		15	7
Subfamily Adelognathinae																								
Adelognathus species											3				9970610	1	86n	42n			1			1
Adelognathus brevicornis			0.25	1		2			3		3				242910	1	58n	50n			1			
Adelognathus granulatus			0.25	1		2			3		3				242910	1	58n	50n			1			
Adelognathus laevicollis			0.25	1		2			3		3				242910	1	58n	50n			1			
Adelognathus pusillus			0.25			2			2		3				242910	1	58n	50n			2			3
Subfamily Agriotypinae																								
Agriotypus armatus			7	1	1	1			4		6.76	9	1	51	2457171	1	69n	36n	11	30	2		8.5	5
Agriotypus changbaishanus				1	1						7.5				9572855	3	54n	18n	5		2			5
Agriotypus chaoi				1	1						6				329560	2	23n	9n			2			5
Agriotypus gracilis				1							6.5				337880	1	46n	24n	5		2		6.5	5
Agriotypus himalensis				1	1						9				3287263	3	34n	8n			2			5
Agriotypus jilinensis				1	1						7				9572855	3	54n	18n			2			5
Agriotypus kambaitensis				1	1						4.5				329847	2	7n	1n			2			5

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Agriotypus lui				1	1						7.8				9572855	3	54n	18n			2			5
Agriotypus maculiceps				1	1						6.5				9572855	3	54n	18n			2			5
Agriotypus masneri				1	1						7.2				329560	2	23n	9n			2			5
Agriotypus silvestris				1	1						6				337880	1	46n	24n			2			5
Agriotypus succinctus				1	1						6				9572855	3	54n	18n	5		2			5
Agriotypus tangi				1	1						4.5				9572855	3	54n	18n			2			5
Agriotypus townesi				1	1						5.2				32260	3	25n	22n			2			5
Agriotypus zhejiangensis				1	1						4.7				9572855	3	54n	18n			2			5
Agriotypus zhengi				1	1						7.2				9572855	3	54n	18n			2			5
Subfamily Anomaloninae																								
Tribe Gravenhorstiini																								
Agrypon flaveolatum									4		13.55				33723303.4	1	86n	42n	3		2			4
Parania prima											9.34				4227913	3	65n	35s			1		13.8	1
Subfamily Banchinae																								
Tribe Atrophini																								
Diradops bethunei					1						11				19599701	1	86n	25n			1			1
Lissonota dubia				2	2	1			4		5				43098	1	58n	55n	3		2	10	2.92	2
Tribe Banchini																								
Banchus flavescens	0.54	0.15	2	2		1	35		3		10.71		1		9970610	1	86n	42n	3		1	2		1
Tribe Glyptini																								
Glypta fumiferanae	0.43	0.18		2	2					9.5	8	20		103	21557902	3	86n	15n	3	37	3	1	8.02	7
Subfamily Campopleginae																								
Bathypectes group																								
Bathyplectes anurus	0.25	0.05	4	2	2	1	19.5	2	4		3.41		1	1200	19599701	1	86n	25n	3	43.5	1		5.25	7
Bathyplectes contracta				2		1					3.53		1		9629091	1	72n	25n	3		1		5.25	7
Bathyplectes curculionis	0.2	0.05		2		1			4	10	3.5	14	1	850	19599701	1	86n	25n	3		1		5.25	7
Bathyplectes stenostigma	0.25	0.05	4	2	2	1	10				4	13		1020							1			
Dusona group																								
Campoletis flavicincta	0.26	0.1	1.75	2	2	1	7.5			6.5	5.79	10	1		11587292	3	72n	15n	3	9.79	1		13.2	1
Campoletis grioti				2		1					6		1		9629091	1	72n	25n	3		1		13.2	1
Campoletis sonorensis				2	2	1		2	3	6	4.5		1		9629091	1	72n	25n			1	1	14	1
Campoplex cursitans				2		1					5		1		43098	1	58n	55n			2			9

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Campoplex frustranae				2		1			4		5		1		9629091	1	72n	25n			1	3	3.36	1
Campoplex punctulatus											6				242910	1	58n	50n	3		3		4.12	7
Diadegma chrysostictos	0.25	0.05	2.5	2	2	1	10.5				7.25	14	1		38682063	3	86n	21n			3		5.16	13
Diadegma insulare				2	1	1			4		6		1	516	22469952	3	86n	1n	3	20.5	1	2	4.92	1
Diadegma semiclausum			1.75	2	2		6.5			7.5	4.12	73		362	2477327	3	58n	11s	3		1		4.92	1
Dusona contumax	0.85	0.3		2	2		8				10	10.25			41284	1	47n	46n	3		1	2		1
Eriborus terebrans				2		1					8.5		1		9740085	1	72n	25n	3		3		12.9	8
Eriborus trochanteratus											7.5					3					3		6.84	13
Hyposoter didymator				2		1					6.49		1		10195201	1	72n	25n	3		1		14	1
Hyposoter exiguae			2	2	2	1	7.5	2		8.5	7.1	16.7	1		9629091	1	72n	25n	3		1		16.4	1
Hyposoter fugitivus				2	2	1					7		1								1		43	1
Hyposoter horticola				2		1			1	25	7.5	22	1		338145	1	70n	60n	3		2		16.1	4
Lathrostizus euurae	0.46	0.06		2	2					6	4.9				9629091	1	72n	25n	3	5.3	2			6
Phaedroctonus moderator				2	2						6.25				2314608	1	70n	36n	3		3	1		7
Phobocampe bicingulata											6				338145	1	70n	60n	3		1			1
Phobocampe lymantriae											5.5				132892	1	59n	47n	3		1			1
Phobocampe pallida				2	2	1			2		8		1		19599701	1	86n	25n	3		1	1		1
Tranosema pedella	0.31	0.09	21	2	2						3.66				9629091	1	72n	25n			2	6	4.45	2
Tranosema rostrale				2	1	1					6		1		9970610	1	86n	42n	3		3	1	8.38	7
Venturia canescens				2	2	1		2	4		7	36		2700	10589451	1	72n	25n	3		3		5.16	13
Gonotypus group																								
Gonotypus melanostoma				2		1					5		1		599932	1	58n	46n	3		3		2.5	7
Tribe Campoplegini																								
Sinophorus crassifemur						1				11	10.67	70	1		10327632	1	86n	42n	3		2		11.67	4
Sinophorus megalodontis	0.97	0.24		2		1			3				1		9970610	1	86n	42n	3		2		11.77	4
Sinophorus rhyacioniae															9629091	1	72n	25n	3		2	3		7
Subfamily Collyriinae																								
Collyria coxator				2							7.5				242910	1	58n	50n	1		3		7.03	7
Subfamily Cremastinae																								
Eiphosoma vitticolle				2		1	9				14.5		1		9629091	1	72n	25n	3		1		13.2	1
Pristomerus rufiabdominalis											7.5				110994	1	45n	42n	3		3		12.9	7
Pristomerus vulnerator						1					9	3.8			136707	1	45n	41n	3		3			7

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Trathala flavoorbitalis	0.51	0.17	3.5	2	2	1	15			7	7.8		1		9958938	3	72n	1n	3		3		6.38	7
Trathala species				2		1													3		3	1	7.5	13
Subfamily Cryptinae																								
Tribe Cryptini																								
Agrothereutina group																								
Agrothereutes lanceolatus				1	1	1					10	23.91	1		337880	1	46n	24n	15		2		13.26	10
Agrothereutes minousubae				1		1					10.25		1		337880	1	46n	24n	8		3			11
Agrothereutes abbreviatus	1.28	0.32	2	1			5	2	4	11	8								4		2		4.45	2
Agrothereutes tunetanus	1.25	0.25	1.54	2			7.29			8	9.5	42.5		38		1			5					
Gambrus ultimus				2		1			1		9.5		1		9629091	1	72n	25n	3		2	3	3.6	3
Hoplocryptus signatorius				1				2			7.22	40			242910	1	58n	50n	4		2		8	10
Gabuniina group																								
Xanthocryptus novozealandicus						1		2	3		12.5		1		269057	1	36s	48s	12		2	6	20	2
Mesostenina group																								
Mesostenus gracilis									4		9								5		3		5.58	13
Sphecophagina group																								
Sphecophaga vesparum				1							6.5	21			269057	1	36s	48s	5		2	3	11.03	10
Tribe Hemigasterini																								
Pleolophus larvicola	1.3	0.35	2.21	1	2	1	14.5			8	7.5	18	1		9970610	1	86n	42n	5		1			
Pleolophus indistinctus			3	1	2	1	2.1			11.79	5.75	28.71	1	54					3		1	3		1
Tribe Phygadeuontini																								
Acrolytina group																								
Sozites kerichoensis				2	2				2		3.26	5.2	1.6		592747	2	5n	6s	1	2	1			1
Endaseina group																								
Endasys subclavatus				1		1					7.25		1						4		3			
Gelina group																								
Gelis acarorum											4.59				338145	1	70n	60n			3		2.1	9
Gelis agilis											4.59	67			581055	1	70n	50n	3		3		2.1	9
Gelis tenellus				1							3.7				19599701	1	86n	25n	3		2			9
Matrina group																								
Mastrus ridibundus				1	1	2					7	40	4		9629091	1	72n	25n	3		3		6.78	15
Phygadeuontina group																								

Taxonomy	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Phygadeuon elegans				1	1	1					3.5		1						5		3		3.5	15
Phygadeuon exiguus				1	1	1					5		1						5		3		3.5	15
Phygadeuon wiesmanni				1	1	1					3.4		1		9970610	1	86n	42n	5	14	3		3	15
Subfamily Ctenopelmatinae																								
Tribe Ctenopelmatini																								
Homaspis interruptus				2		1					10		1		19599701	1	86n	25n	3		2		11.77	4
Tribe Mesoleini																								
Lamachus eques	0.7	0.15	15	2	2	1					9.52		1						3		1		7.2	1
Tribe Perilissini																								
Lathrolestes ensator			14	2	2	1	8		4		7.25	11	1	32	38332251	1	86n	25n	3	14	2		5.57	7
Lathrolestes luteolator			20	2	2	1	30		4		6.5		1		482164	1	56n	46n	3	35	1	3	7.2	1
Lathrolestes nigricollis				2							4.2				2666390	1	86n	25n	3		2		2.17	2
Lophyroplectus oblongopunctatus	0.54	0.13	20	2	2	1	30				10.57	9.5	1	194	10213520	1	86n	25n	3		1		7.2	1
Subfamily Diplazontinae																								
Diplazon laetatorius			3.5	2	2	1	22.5			11	5.94	37			242910	1	58n	50n	3					
Diplazon pectoratorius				2							7.2				242910	1	58n	50n	13		1		13	1
Diplazon tetragonus											5.5				242910	1	58n	50n	3		1		13	1
Diplazon tibiatorius				2							7.43				242910	1	58n	50n	13					
Enizemum ornatum				1							7.35				9970610	1	86n	42n	3		1		13	1
Syrphophilus trinctorius				2		1					5.58		1		242910	1	58n	50n	13		1		13	1
Subfamily Eucerotinae																								
Euceros albitarsus											10				242910	1	58n	50n			2			9
Euceros frigidus				1	2						7.6			1000					3					
Subfamily Ichneumoninae																								
Tribe Alomyini																								
Diadromus pulchellus			1.5	2	1	1					6				543965	1	52n	43n	11		2			2
Dirophanes hariolus				2							7.25				9629091	1	72n	25n	5		3	3	8.38	7
Dirophanes maculicornis					1						8.03				21557902	3	86n	15n	5		3	3	8.38	7
Tycherus nigridens	1	0.29	2	2	1	1	7.5			4.4	8	43	1						5		3			
Tycherus osculator						1					6.31	390	1		10514575	1	86n	42n	8		3	3	6.16	11
Tribe Ichneumonini																								
Cratichneumon sublatus					1						11.55				19599701	1	86n	25n	5	0.5	1	3		1

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Ichneumon caloscelis					1						11.5								5		1			
Ichneumon gracilicornis						1					13	72	1		338145	1	70n	60n	5	18	3		16.1	11
Tribe Mesoleiini																								
Mesoleius species									4						19599701	1	86n	25n			1			1
Olesicampe melanogaster			2	2	2	1				19	7	19	1	350	9970610	1	86n	42n	3		1		7.7	1
Olesicampe geniculata				2	2	1			4		7	25	1	323	10054468	1	86n	42n	3		1	10	36.37	1
Olesicampe macellator				2	2						8				357022	1	56n	46n	3		1	6	8.87	1
Olesicampe monticola				2	2	1					8.16	19	1		912617	1	58n	46n	3		2	2	9.27	4
Subfamily Labeninae																								
Tribe Groteini																								
Grotea angunia				1							15.5								3		2			2
Subfamily Mesochorinae																								
Mesochorus agilis	0.12	0.3	3	2	2	1	18.4			10	1.5	31.4	1		9629091	1	72n	25n	3		2		3.28	9
Stictopisthus laticeps											3.66				242910	1	58n	50n			2			2
Subfamily Metopiinae																								
Exochus nigripalpis tectulum											6.5								3		3	3	8.38	7
Triclistus crassus									4		5.95				9970610	1	86n	42n					10	
Triclistus emarginalus											3				9970610	1	86n	42n			2			2
Triclistus podagricus											4.5								3		3			7
Triclistus species															9970610	1	86n	42n			3			7
Triclistus xylostellae											5.7				9970610	1	86n	42n			1		4.92	1
Subfamily Neorhacodinae																								
Neorhacodes enslini				2							2.4				586952	1	70n	35n	3		2			10
Subfamily Ophioninae																								
Ophion flavidus						2					17.5				9629091	1	72n	25n	3		1		13.2	1
Ophion parvulus				2	2				2		10.5				242910	1	58n	50n				1		
Subfamily Orthopelmatinae																								
Orthopelma mediator											4.2				449964	1	69n	55n			2		2.1	6
Orthopelma species				2											9970610	1	86n	42n			2		2.1	6
Subfamily Pimplinae																								
Lytarmes maculipennis											18.25				329847	2	7n	1n	3		3			7
Tribe Delomeristini																								

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Perithous divinator	2.2	0.3		1		1		2			8.75	20	1		19599701	1	86n	25n	4		1		7	1
Tribe Ephialtini																								
Acrodactyla degener				1						15	3.94				242910	1	58n	50n			1		3	1
Apechthis ontario						1					9.5		1		19599701	1	86n	25n	5		3	3	8.38	7
Calliephialtes notanda									3		9.5				9970610	1	86n	42n	3		2		6.9	6
Exeristes comstockii				2							9.5				9629091	1	72n	25n	3		3		8.38	7
Exeristes roborator				1							15								3		2		13.26	10
Liotryphon strobilellae				1	1						8.3				19139458	1	83n	42n	3		3			7
Polysphincta tuberosa				1						13	6.08				242910	1	58n	50n	2		1		6	1
Scambus foliae	1.4	0.2	2	1			5		3		7.75			167	9629091	1	72n	25n			2		4.45	2
Scambus atrocoxalis				1							5.25					1			3		3			2
Scambus brevicornis	1.4	0.3	1.5	1	1	1	6.83			6.5	6.73	42	1		10663484	1	86n	42n	3		3		2.5	7
Scambus canadensis											3.93				9629091	1	72n	25n	3		3			7
Scambus capitator				2											1336551	1	69n	36n	3		2			2
Scambus hispae						2					7.5				9629091	1	72n	25n	5		1		5.94	1
Sericopimpla sericata	2	0.3	3.75	1	1	1	21			10	12	140	1	30					3					
Schiizopyga frigida				1	1					14.71	7.46				242910	1	58n	50n	7		1		7	1
Zatypota albicoxa				1	2					20	5				242910	1	58n	50n			1			1
Zatypota bohemani				1						17.67	4.12				242910	1	58n	50n	2		1		2.25	1
Zatypota percontatoria				1	1					12.33	4.71				242910	1	58n	50n	7		1		2.25	1
Tribe Pimplini																								
Itoplectis conquisitor				2	1	1					10								11	22	2		4.76	3
Itoplectis maculator					2					20	8.01				93030	1	48n	45n	11	8	3	3		7
Itoplectis naranyae				2		1					9.9	45	1			3			5		2		13.26	10
Itoplectis quadricingulata						1					11		1		19599701	1	86n	25n	5		1			1
Pimpla turionellae			3	2	1	1	8			19	8.81	42.93		329					5		2		13.26	10
Theronia atalantae						1					10.5		1		9761983	1	72n	25n			2		11.16	5
Subfamily Poemiinae																								
Pseudorhyssa sternata			2	1		2	12.5	2	3		20.84	28	3						3		3		28.15	7
Subfamily Rhyssinae																								
Megarhyssa atrata				1		1			3		40		1		19599701	1	86n	25n	3			3	40	
Rhyssa persuasoria			2	1	1	1					28.15		1		7754112	3	52n	43s	3		3		21.53	15

Taxonomy	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Subfamily Stilbopinae																								
Stilbops limneriaeformis				2	2						5				1867642	1	70n	42n	1		3	1	4.42	7
Stilbops ruficornis											7.25				242910	1	58n	50n	1		3			7
Stilbops vetulus											5.65				242910	1	58n	50n					4.22	
Subfamily Tryphoninae																								
Tribe Exenterini																								
Exenterus abruptorius	0.35	0.28	1.1	1	2	1	31.5		4		9.25								3		1		7.2	1
Tribe Oedemopsini																								
Oedemopsis scabricula				1		1					6.75		1		242910	1	58n	50n	3		2			3
Tribe Phytodietini																								
Netelia vinulae				1		2					17				242910	1	58n	50n	3		1			1
Phytodietus fumiferanae				2	2						7.5				21557902	3	86n	15n	3		3	3	8.38	7
Tribe Tryphonini																								
Grypocentrus albipes	0.31	0.15	4.5				13.5			15	3.1	15.6		96	20306390	1	86n	25n	3		2		2.17	2
Grypocentrus apicalis				1	2						4								3		2			2
Subfamily Xoridinae																								
Xorides brachylabris				1							11.5										3			7
Xorides corcyrensis			4	1		1	11			33.5	16.5		1			1			14					

Taxonomy	**25**	**26**	**27**	**28**	**29**		**30**	**31**	**32**
Family Braconidae									
Subfamily Agathidinae									
Tribe Agathidini									
Agathis anglica	905702	1	58n	35n	9	Lepidoptera	Epinotia mercuriana		2
Agathis artemesiana	858099	1	69n	42n	2	Lepidoptera	Coleophora granulatella		2
Agathis asteris	83858	1	49n	47n	2	Lepidoptera	Coleophora halophilella		2
Agathis breviseta	83858	1	49n	47n	15	Lepidoptera	Coleophora albitarsella		2
Agathis calcarata					12	Lepidoptera	Acrobasis caryivorella		3
Agathis gibbosa					10	Lepidoptera	Mompha stellella		4
Agathis laticincta					7	Lepidoptera	Coleophora fletcherella		3
Agathis unicolorata									3
Baeognatha armeniaca					3	Lepidoptera	Anarsia eleagnella		1
Baeognatha nigra	17932141	1	83n	42n	2	Lepidoptera	Coleophora flavipennella		2
Bassus arthurellus	9970610	1	86n	42n	2	Lepidoptera	Cocchylis arthuri		5
Cremnops desetor	9629091	1	72n	25n	7	Lepidoptera	Cydia pomonella		2
Earinus elator	587346	1	58n	36n	3	Lepidoptera	Agrochola circellaris		1
Earinus gloriatorius	9659619	1	72n	25n	7	Lepidoptera	Agonopterix ciliella		2
Earinus limitaris	9970610	1	86n	42n	1	Lepidoptera	Momima hibisci		4
Earinus transversus	242910	1	58n	50n	3		Polycommata species		2
Earinus zeirapherae	9970610	1	86n	42n	6	Lepidoptera	Zeiraphera canadensis		10
Microdus dimidiator		1			2	Lepidoptera	Spilonota ocellana		1
Microdus pumilus	20210629	1	86n	24n	1	Lepidoptera	Coleophora laricella		3
Microdus rufipes					6	Lepidoptera	Cydia pomonella		1
Microdus tumidulus	1730277	1	58n	35n	1	Lepidoptera	Dichrorampha acuminatana		1
Subfamily Alysiinae									
Tribe Alysiini									
Alysia manducator					8	Diptera	Calliphora vicina		6
Aphaereta apicalis									3
Aphaereta aotea	7951357	3	11s	48s	1	Diptera	Musca vestusissima		1
Aphaereta colei	9872001	1	72n	25n	1	Diptera	Aulacigaster leucopeza		7
Aphaereta genevensis	9629091	1	72n	25n	2	Diptera	Drosophila virilis		15
Aphaereta lonchaeae		1			1	Diptera	Lonchaea polita		2
Aphaereta minuta	131957	1	43n	35n	5	Diptera	Drosophila hydei		30
Aphaereta pallipes	9629091	1	72n	25n	10	Diptera	Drosophila virilis		13

Taxonomy	25	26	27	28	29	30	31	32
Asobara rufescens	41528	1	53n	51n	2	Diptera	Scaptomyza pallida	9
Asobara tabida	12596038	1	86n	35n	18	Diptera	Drosophila subobscura	98
Chasmodon apterus	242910	1	58n	50n	3	Diptera	Oscinella frit	18
Tribe Dacnusini								
Dacnusa areolaris	269057	1	36s	48s	4	Diptera	Chromatomyia syngenesiae	3
Dacnusa sibirica	242910	1	58n	50n	3	Diptera	Liriomyza bryoniae	19
Subfamily Aphidiinae								
Tribe Aphidiini								
Aphidius ervi	21169632	3	86n	57s	23	Hemiptera	Acyrthosiphon pisum	161
Aphidius matricariae	28422250	3	86n	15n	3	Hemiptera	Diuraphis noxia	8
Aphidius nigripes	9970610	1	86n	42n	1	Hemiptera	Macrosiphum euphorbiae	12
Aphidius pisivorus		1			2	Hemiptera	Acyrthosiphon pisum	14
Aphidius rhopalosiphi	1586599	3	58n	57s	9	Hemiptera	Sitobion avenae	30
Aphidius smithi	4043889		34n	57s	3	Hemiptera	Acyrthosiphon pisum	18
Aphidius sonchi					1	Hemiptera	Hyperomyzus lactucae	3
Diaeretiella rapae	11035308	1	72n	35s	30	Hemiptera	Diuraphis noxia	73
Dyscritulus planiceps					1	Hemiptera	Drepanosiphum species	15
Lysiphlebus fabarum	357022	1	56n	46n	7	Hemiptera	Aphis fabae fabae	2
Lysiphlebus testaceipes	9629091	1	72n	25n	30	Hemiptera	Schizaphis graminum	32
Monoctonus paulensis	19599701	1	86n	25n	4	Hemiptera	Acyrthosiphon pisum	16
Trioxys complanatus	17311391	3	72n	43s	2	Hemiptera	Theirioaphis trifolii	26
Tribe Ephredrini								
Ephedrus californicus	9970610	1	86n	42n	6	Hemiptera	Acyrthosiphon pisum	54
Ephedrus plagiator					9	Hemiptera	Sitobion avenae	13
Tribe Praini								
Praon exsoletum	9629091	1	72n	25n	2	Hemiptera	Theirioaphis maculata	6
Praon pequodorum	19599701	1	86n	25n	8	Hemiptera	Acyrthosiphon pisum	15
Praon volucre	19599701	1	86n	25n	26	Hemiptera	Acyrthosiphon pisum	8
Subfamily Blacinae								
Tribe Blacini								
Blacus exilis	17387678	1	83n	42n	1	Lepidoptera	Cydia strobilella	2
Blacus koenigi	195203	1	48n	43n	1	Coleoptera	Scolytus intricatus	1

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Blacus nigricornis	41284	1	47n	46n	1	Coleoptera	Meligethes species		1
Subfamily Braconinae									
Tribe Braconini									
Alienoclypeus insolitus	35149170	3	72n	43s	1	Coleoptera	Scyphophorus acupunctatus		1
Bracon cajani									2
Bracon cephi	9970610	1	86n	42n	1	Hymenoptera	Cephus cinctus		4
Bracon gelechiae	9629091	1	72n	25n	2	Lepidoptera	Ancylis comptana		2
Bracon lissogaster	9970610	1	86n	42n	2	Hymenoptera	Cephus cinctus		6
Bracon kirkpatricki	22291975	3	72n	43s	15	Lepidoptera	Pectinophora gossypiella		11
Bracon mellitor	9629091	1	72n	25n	2	Lepidoptera	Rhyacionia frustrana		4
Bracon pineti	18949598	1	83n	42n	5	Lepidoptera	Cydia strobilella		12
Bracon rhyacioniae	678279	1	52n	43n	1	Lepidoptera	Cydia strobilella		1
Bracon thurberiphagae	10608988	3	72n	28s	5	Lepidoptera	Ancylostomia stercorea		4
Habrobracon hebetor	9629091	1	72n	25n	7	Lepidoptera	Plodia interpunctella		61
Habrobracon lineatellae	17652910	1	86n	43s	1	Lepidoptera	Anarsia lineatella		3
Stenobracon deesae									2
Tribe Coelidini									
Coeloides pissodis	19599701	1	86n	25n	3	Coleoptera	Dendroctonus frontalis		2
Coeloides scolyticida	102173	1	47n	43n		Coleoptera			7
Subfamily Cardiochilinae									
Schoenlandella diaphaniae	9629091	1	72n	25n	2	Lepidoptera	Diaphania hyalinata		2
Toxoneuron nigriceps	19599701	1	86n	25n	13	Lepidoptera	Heliothis virescens		12
Subfamily Charmontinae									
Charmon extensor	678279	1	52n	43n	1	Lepidoptera	Cydia strobilella		1
Charmon gracilis	9629091	1	72n	25n	2	Lepidoptera	Choristoneura occidentalis		1
Charmon rufipes	17753272	1	83n	42n	1	Lepidoptera	Cydia strobilella		1
Subfamily Cheloninae									
Adelius subfasiatus	242910	1	58n	50n		Lepidoptera			1
Tribe Chelonini									
Ascogaster quadridentata	9629091	1	72n	25n	2	Lepidoptera	Cydia pomonella		11
Ascogaster reticulatus	611318	1	58n	24n	8	Lepidoptera	Adoxophyes orana		12
Chelonus asiaticus	1648000	1	40n	25n	1	Lepidoptera	Oxypteron wertheimsteini		6

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Chelonus blackburni	22291975	3	72n	43s	1	Lepidoptera	Pectinophora gossypiella		14
Chelonus curvimaculata									2
Chelonus heliopae									3
Chelonus inanitus									2
Chelonus insularis	9629091	1	72n	25n	6	Lepidoptera	Spodoptera praefica		17
Chelonus curvimaculatus	22291975	3	72n	43s	2	Lepidoptera	Pectinophora gossypiella		5
Chelonus texanus					2	Lepidoptera	Helicoverpa zea		3
Tribe Phanerotomini									
Phanerotoma flavistestacea	7682300	3	11s	43s	1	Lepidoptera	Anagasta kuehniella		1
Subfamily Doryctinae									
Tribe Doryctini									
Dendrosoter protuberans	751139	1	59n	43n	2	Coleoptera	Scolytus intricatus		23
Doryctes mutillator	17753272	1	83n	42n	1	Lepidoptera	Cydia strobilella		1
Doryctes undulatus	17753272	1	83n	42n	1	Lepidoptera	Cydia strobilella		1
Tribe Hecabolini									
Stenocorse bruchivora	11587292	3	72n	15n	1	Coleoptera	Zabrotes subfasciatus		11
Tribe Heterospilini									
Heterospilus coffeicola		3			1	Coleoptera	Hypothenemushampei		3
Heterospilus prosopidis	9629091	1	72n	25n	5	Coleoptera	Callosobruchus chinensis		58
Tribe Spathiini									
Spathius benefactor	19599701	1	86n	25n	3	Coleoptera	Scolytus multistriatus		7
Spathius brevicaudis	751139	1	59n	43n	2	Coleoptera	Scolytus intricatus		2
Subfamily Euphorinae									
Tribe Centistini									
Pygostolus falcatus	19599701	1	86n	25n	1	Coleoptera	Sitona hispidula		3
Tribe Dinocampini									
Dinocampus coccinellae	9872001	1	72n	25n	5	Coleoptera	Coccinella septempunctata		8
Tribe Euphorini									
Microcotonus aethiopoides	7951357	3	11s	43s	7	Coleoptera	Sitona discoideus		85
Microcotonus caudatus	17726056	1	83n	24n	1	Coleoptera	Harpalus rufipes		5
Microcotomus colesi	9629091	1	72n	25n	1	Coleoptera	Hypera postica		1
Microcotonus hyperodae	8194267	3	58n	43s	2	Coleoptera	Listronotus bonariensis		22

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Tribe Perilitini									
Meteorus arizonensis	9629091	1	72n	25n	1	Lepidoptera	Grammia geneura		1
Meteorus brevicauda	242910	1	58n	50n	1	Coleoptera	Zeugophora subspinosa		1
Meteorus campestris	9629091	1	72n	25n	2	Lepidoptera	Choristoneura occidentalis		4
Meteorus leviventris	9629091	1	72n	25n	1	Lepidoptera	Autographa californica		1
Meteorus trachynotus	9629091	1	72n	25n	5	Lepidoptera	Ancylis comptana		22
Subfamily Exothecinae									
Colastes braconius	83858	1	49n	47n	13	Lepidoptera	Cameraria ohridella		2
Exothecus braconius	242910	1	58n	50n	1	Lepidoptera	Phyllonorycter querifoliella		1
Phanomeris catenator	242910	1	58n	50n	9	Hymenoptera	Fenusa ulmi		2
Phanomeris dimidiata	242910	1	58n	50n	1	Hymenoptera	Fenusa ulmi		1
Phanomeris laevis	242910	1	58n	50n	5	Hymenoptera	Heterarthrus aceris		2
Phanomeris phyllotomae	11104364	1	86n	25n	1	Hymenoptera	Phyllotoma nemoratus		2
Subfamily Gnamptodontinae									
Gnamptodon pumilio	313183	1	58n	50n	4	Lepidoptera	Nepticula lapponica		1
Subfamily Helconinae									
Tribe Brachistini									
Eubazus semirugosius						Coleoptera			1
Triaspis pallipes	242910	1	58n	50n	2	Coleoptera	Orchestes fagi		1
Triaspis thoracicus	17912263	1	83n	30n	1	Coleoptera	Bruchus dentipes		9
Tribe Diospilini									
Apsicolpus hudsoni	269057	1	36s	48s	1	Coleoptera	Oemona hirta		4
Baeacis abietis	17753272	1	83n	42n	1	Lepidoptera	Cydia strobilella		1
Diospilus capito	41284	1	47n	46n	1	Coleoptera	Meligethes species		1
Diospilus hiator	9629091	1	72n	25n	2	Coleoptera	Polydrusus impressifrons		1
Subfamily Homolobinae									
Homolobus truncator	12395980	1	72n	55s	1	Lepidoptera	Spodoptera frugiperda		2
Subfamily Hormiinae									
Tribe Hormiini									
Hormius moniliatus	110994	1	45n	42n	1	Lepidoptera	Gelechia senticetella		2
Hormius vulgaris	9629091	1	72n	25n	1	Lepidoptera	Tetralopha robustella		2
Subfamily Ichneutinae									

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Tribe Ichenutini								
Ichneutes levis					1	Hymenoptera	Scolioneura betulae	1
Ichneutes pikonematis	19599701	1	86n	25n	1	Hymenoptera	Pikonema alaskensis	2
Subfamily Macrocentrinae								
Macrocentrus ancylivorus	9629091	1	72n	25n	1	Lepidoptera	Rhyacionia frustrana	3
Macrocentrus cingulum	9629091	1	72n	25n	2	Lepidoptera	Ostrinia nubialis	5
Macrocentrus iridescens	9970610	1	86n	42n	3	Lepidoptera	Choristoneura rosaceana	4
Macrocentrus nigridorsis	9970610	1	86n	42n	2	Lepidoptera	Choristoneura rosaceana	2
Subfamily Microgasterinae								
Tribe Apantelini								
Apanteles ater					16	Lepidoptera	Choristoneura rosaceana	5
Apanteles carpatus	7682300	3	11s	43s	18	Lepidoptera	Tineola bisselliella	10
Apanteles corvinus	242910	1	58n	50n	9	Lepidoptera	Phyllonorycter oxyacanthae	3
Apanteles fumiferanae	19599701	1	86n	25n	9	Lepidoptera	Choristoneura fumiferana	29
Apanteles galleriae	337880	1	46n	24n	2	Lepidoptera	Galleria mellonella	5
Apanteles milleri	9629091	1	72n	25n	1	Lepidoptera	Dioryctria reniculelloides	2
Apanteles morrisi	19599701	1	86n	25n	2	Lepidoptera	Choristoneura fumiferana	3
Apanteles subandinus	7682300	3	11s	43s	3	Lepidoptera	Phthorimaea operculella	7
Apanteles syleptae	923768	2	15n	5n	1	Lepidoptera	Sylepta derogata	4
Dolichogenidea evonymellae	152522	1	53n	42n	4	Lepidoptera	Paranthrene tabaniformis	4
Dolichogenidea absona	19599701	1	86n	25n	1	Lepidoptera	Choristoneura fumiferana	5
Pholetesor circumscriptus	242910	1	58n	50n	14	Lepidoptera	Phyllonorycter pomonella	3
Pseudapanteles dignus	11739842	3	72n	15n	3	Lepidoptera	Keiferia lycopersciella	3
Tribe Cotesiini								
Cotesia congregata	9629091	1	72n	25n	2	Lepidoptera	Ceratomia catalpae	19
Cotesia euphydryidis	9629091	1	72n	25n	2	Lepidoptera	Euphydryas phaeton	3
Cotesia flavipes	1388842	3	37n	6s	3	Lepidoptera	Chilo partellus	11
Cotesia glomerata	20560164	1	86n	24n	8	Lepidoptera	Pieris rapae	99
Cotesia jucunda	622339	1	70n	46n	1	Lepidoptera	Epirrita autumnata	8
Cotesia kariyai	17165400	3	70n	48s	1	Lepidoptera	Pseudaletia seperata	6
Cotesia kazak	9948918	3	49n	43s	3	Lepidoptera	Helicoverpa armigera	3
Cotesia marginiventris	9629091	1	72n	25n	13	Lepidoptera	Spodoptera frugiperda	26

Taxonomy	25	26	27	28	29	30		31	32
Cotesia medicaginis	11587292	3	72n	15n	1	Lepidoptera	Colias eurytheme		1
Cotesia melanoscelus	10213520	1	86n	42n	1	Lepidoptera	Leucoma salicis		4
Cotesia melitaearum	581055	1	70n	50n	4	Lepidoptera	Melitaea cinxia		14
Cotesia ocneriae	20070473	1	86n	24n	1	Lepidoptera	Lymantria dispar		1
Cotesia phobetri	9629091	1	72n	25n	1	Lepidoptera	Grammia geneura		2
Cotesia rubecula	67241	1	53n	41n	2	Lepidoptera	Pieris rapae		27
Cotesia schizurae	19599701	1	86n	25n	4	Lepidoptera	Heterocampa guttivitta		2
Cotesia scitula	19599701	1	86n	25n	1	Lepidoptera	Simyra henrici		2
Cotesia vestalis	31382286	3	86n	48s	1	Lepidoptera	Plutella xylostella		22
Cotesia yakutatensis	19599701	1	86n	25n	2	Lepidoptera	Autographa californica		2
Glyptapanteles militaris	9629091	1	72n	25n	1	Lepidoptera	Pseudaletia unipuncta		5
Glyptapanteles porthetriae	20070473	1	86n	24n	1	Lepidoptera	Lymantria dispar		16
Protapanteles immunis	581055	1	70n	50n	1	Lepidoptera	Epirrita autumnata		1
Tribe Microgastrini									
Choeras tedellae		1			1	Lepidoptera	Tetralopha robustella		3
Choeras tiro	9970610	1	86n	42n	1	Lepidoptera	Cnesphasia virguareana		3
Microgaster hospes	9629091	1	72n	25n	1	Lepidoptera	Ancylis comptana		1
Microgaster tibialis									3
Tribe Microplitini									
Microplitis alaskensis	19599701	1	86n	25n	1	Lepidoptera	Autographa californica		1
Microplitis croceipes	19599701	1	86n	25n	4	Lepidoptera	Heliothis virescens		12
Microplitis demolitor	9629091	1	72n	25n	5	Lepidoptera	Pseudoplusia includens		15
Microplitis mediator	9970610	1	86n	42n	9	Lepidoptera	Mamestra configurata		15
Microplitis naenia	321776	1	58n	48n	2	Lepidoptera	Orthosia cruda		1
Microplitis ocellatae	288052776	3	83n	18n	4	Lepidoptera	Smerinthus planus		1
Microplitis plutellae	9970610	1	86n	42n	2	Lepidoptera	Plutella xylostella		13
Microplitis rufiventris					4	Lepidoptera	Spodoptera littoralis		12
Microplitis tuberculifera		1			3	Lepidoptera	Diachrysia chrysitis		1
Subfamily Microtypinae									
Microtypus species	9629091	1	72n	25n	1	Lepidoptera	Acrobasis vacinii		2
Microtypus wesmaelii	242910	1	58n	50n	1	Lepidoptera	Acrobasis species		2
Subfamily Micracinae									

Taxonomy	25	26	27	28	29	30	31	32
Mirax minuta	9629091	1	72n	25n	3	Lepidoptera	Stigmella juglandifoliella	3
Mirax rufilabris	313183	1	58n	50n	5	Lepidoptera	Nepticula plagicolella	1
Subfamily Opiinae								
Biosteres arisanus	9629091	1	72n	25n	2	Diptera	Dacus dorsalis	7
Biosteres melleus	19599701	1	86n	25n	1	Diptera	Rhagoletis pomonella	12
Biosteres vandenboschii	9629091	1	72n	25n	1	Diptera	Dacus dorsalis	10
Diachasmimorpha kraussi	9629091	1	72n	25n	9	Diptera	Dacus dorsalis	10
Diachasmimorpha longicaudata	11760684	3	72n	23s	12	Diptera	Anastrepha suspensa	53
Diachasmimorpha tryoni	9629091	1	72n	25n	4	Diptera	Ceratitus capitata	22
Doryctobracon areolatus	9629091	1	72n	25n	7	Diptera	Anastrepha suspensa	31
Doryctobracon crawfordi	1958201	3	33n	15n	4	Diptera	Anastrepha ludens	22
Fopius arisanus	9629091	1	72n	25n	18	Diptera	Dacus dorsalis	28
Opius canaliculatus	19599701	1	86n	25n	1	Diptera	Rhagoletis pomonella	2
Opius dissitus	9629091	1	72n	25n	1	Diptera	Liriomyza sativae	1
Opius lectus	19599701	1	86n	25n	1	Diptera	Rhagoletis pomonella	12
Opius magnus	357022	1	58n	50n	5	Diptera	Rhagoletis cerasi	2
Opius rhagoleticola	357022	1	58n	50n	5	Diptera	Rhagoletis cerasi	2
Opius striatriventris	9629091	1	72n	25n	1	Diptera	Phytomyza ilicicola	6
Psyttalia incisi	9629091	1	72n	25n	2	Diptera	Dacus dorsalis	2
Utetes anastrephae	1958201	3	33n	15n	4	Diptera	Anastrepha obliqua	31
Subfamily Braconidae								
Tribe Orgilini								
Orgilus comptanae	9629091	1	72n	25n	1	Lepidoptera	Ancylis comptana	1
Orgilus lepidus	7682300	3	11s	43s	1	Lepidoptera	Phthorimaea operculella	6
Subfamily Pambolinae								
Tribe Chremylini								
Cedria paradoxa								1
Subfamily Rhysipolinae								
Rhysipolis decorator	242910	1	58n	50n	5	Lepidoptera	Caloptula alchimiella	1
Rhysipolis hariolator	242910	1	58n	50n	2	Lepidoptera	Parornix betulae	1
Rhysipolis mediator	242910	1	58n	50n	1	Lepidoptera	Mompha raschkiella	1
Subfamily Rhyssalinae								

Taxonomy	25	26	27	28	29		30	31	32
Tribe Rhyssalini									
Oncophanes americanus					3	Lepidoptera	Choristoneura rosaceana		13
Oncophanes laevigatus	242910	1	58n	50n	5	Lepidoptera	Agonopterix nervosa		1
Subfamily Rogadinae									
Tribe Clinocentrini									
Clinocentrus gracilpes	242910	1	58n	50n	1	Lepidoptera	Anthophila fabriciana		1
Clinocentrus species	19599701	1	86n	25n	1	Lepidoptera	Zeiraphera improbana		1
Tribe Rogadini									
Aleiodes circumscriptus	678279	1	52n	43n	4	Lepidoptera	Cydia strobiella		2
Aleiodes gastritor	622339	1	70n	46n	3	Lepidoptera	Epirrita autumnata		19
Aleiodes nolophanae	9629091	1	72n	25n	1	Lepidoptera	Plathypena scabra		2
Aleiodes praetor	242910	1	58n	50n		Lepidoptera			2
Pelecystoma harrisinae					1	Lepidoptera			3
Rogas malacosomatos	19599701	1	86n	25n	4	Lepidoptera	Malacosoma americanum		3
Rogas stigmator	19599701	1	86n	25n	4	Lepidoptera	Simyra henrici		5
Family Ichneumonidae									
Subfamily Acaenitinae									
Acaenitus dubiator	242910	1	58n	50n	1	Coleoptera	Cleonis piger		11
Phaenolobus terebrator	242910	1	58n	50n	3	Coleoptera	Oberea linearis		2
Subfamily Adelognathinae									
Adelognathus species	19599701	1	86n	25n	1	Hymenoptera	Pikonema alaskensis		2
Adelognathus brevicornis						Hymenoptera			1
Adelognathus granulatus	242910	1	58n	50n		Hymenoptera			1
Adelognathus laevicollis	242910	1	58n	50n		Hymenoptera			1
Adelognathus pusillus	242910	1	58n	50n	2	Hymenoptera	Phyllocolpa species		1
Subfamily Agriotypinae									
Agriotypus armatus	692874	1	69n	50n	8	Trichoptera	Silo pallipes		37
Agriotypus changbaishanus	9572855	3	54n	18n		Trichoptera			1
Agriotypus chaoi	329560	2	23n	9n	1	Trichoptera	Psilotreta species		1
Agriotypus gracilis	337880	1	46n	24n	2	Trichoptera	Goera japonica		2
Agriotypus himalensis	3287263	3	34n	8n	2	Trichoptera	Neophylax n.sp. albimaculatus		2
Agriotypus jilinensis	9572855	3	54n	18n		Trichoptera			1

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Agriotypus kambaitensis	329847	2	7n	1n		Trichoptera		1
Agriotypus lui	9572855	3	54n	18n		Trichoptera		1
Agriotypus maculiceps	9572855	3	54n	18n		Trichoptera		1
Agriotypus masneri	329560	2	23n	9n		Trichoptera		1
Agriotypus silvestris	337880	1	46n	24n	2	Trichoptera	Neophylax japonicus	1
Agriotypus succinctus	9572855	3	54n	18n		Trichoptera		1
Agriotypus tangi	9572855	3	54n	18n		Trichoptera		1
Agriotypus townesi	32260	3	25n	22n		Trichoptera		1
Agriotypus zhejiangensis	9572855	3	54n	18n		Trichoptera		1
Agriotypus zhengi	9572855	3	54n	18n		Trichoptera		1
Subfamily Anomaloninae								
Tribe Gravenhorstiini								
Agrypon flaveolatum	10551400	1	86n	24n	1	Lepidoptera	Operophtera brumata	54
Parania prima	4501351	3	65n	35s	2	Lepidoptera	Helicoverpa armigera	1
Subfamily Banchinae								
Tribe Atrophini								
Diradops bethunei	9629091	1	72n	25n	2	Lepidoptera	Heterocampa amneo	4
Lissonota dubia	43098	1	58n	55n	1	Lepidoptera	Epinotia tedellus	12
Tribe Banchini								
Banchus flavescens	19599701	1	86n	25n	5	Lepidoptera	Mamestra configurata	49
Tribe Glyptini								
Glypta fumiferanae	19599701	1	86n	25n	5	Lepidoptera	Choristoneura pinus pinus	45
Subfamily Campopleginae								
Bathypectes group								
Bathyplectes anurus	19599701	1	86n	25n	1	Coleoptera	Hypera postica	31
Bathyplectes contracta	9629091	1	72n	25n	1	Coleoptera	Hypera postica	1
Bathyplectes curculionis	19599701	1	86n	25n	2	Coleoptera	Hypera postica	25
Bathyplectes stenostigma								1
Dusona group								
Campoletis flavicincta	9629091	1	72n	25n	4	Lepidoptera	Spodoptera frugiperda	5
Campoletis grioti	9629091	1	72n	25n	1	Lepidoptera	Spodoptera frugiperda	7
Campoletis sonorensis	9629091	1	72n	25n	31	Lepidoptera	Pseudoplusia includens	1

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Campoplex cursitans	43098	1	58n	55n	1	Hymenoptera	Apanteles tedellae		12
Campoplex frustranae	9629091	1	72n	25n	1	Lepidoptera	Rhyacionia frustrana		5
Campoplex punctulatus	242910	1	58n	50n	2	Lepidoptera	Cydia dorsana		5
Diadegma chrysostictos	9629091	1	72n	25n	35	Lepidoptera	Plodia interpunctella		18
Diadegma insulare	24035229	3	86n	11s	5	Lepidoptera	Plutella xylostella		117
Diadegma semiclausum	24035229	3	86n	11s	1	Lepidoptera	Plutella xylostella		18
Dusona contumax	327292	1	58n	46n	3	Lepidoptera	Agriopis aurantiaria		10
Eriborus terebrans	9842258	1	72n	25n	2	Lepidoptera	Paranthrene tabaniformis		3
Eriborus trochanteratus	7682300	3	11s	43s	1	Lepidoptera	Corcyra cephalonica		1
Hyposoter didymator					2	Lepidoptera	Heliothis virescens		3
Hyposoter exiguae	9629091	1	72n	25n	7	Lepidoptera	Helicoverpa zea		37
Hyposoter fugitivus					1	Lepidoptera	Manduca sexta		1
Hyposoter horticola	338145	1	70n	60n	2	Lepidoptera	Melitaea cinixa		1
Lathrostizus euurae	9629091	1	72n	25n	2	Hymenoptera	Euura lasiolepis		11
Phaedroctonus moderator	19139458	1	83n	42n	2	Lepidoptera	Cydia strobilella		1
Phobocampe bicingulata	338145	1	70n	60n	1	Lepidoptera	Epirrita autumnata		1
Phobocampe lymantriae	20070473	1	86n	24n	1	Lepidoptera	Lymantria dispar		2
Phobocampe pallida	19599701	1	86n	25n	1	Lepidoptera	Heterocampa guttivitta		1
Tranosema pedella	20733455	1	86n	25n	1	Hymenoptera	Phyllotoma nemorata		1
Tranosema rostrale	19599701	1	86n	25n	1	Lepidoptera	Choristoneura fumiferana		4
Venturia canescens	9629091	1	72n	25n	11	Lepidoptera	Plodia interpunctella		84
Gonotypus group									
Gonotypus melanostoma	242910	1	58n	50n	1	Lepidoptera	Coleophora alticolella		8
Tribe Campoplegini									
Sinophorus crassifemur					3	Hymenoptera	Acantholyda posticalis		4
Sinophorus megalodontis		1			1	Hymenoptera	Acantholyda erythrocephala		4
Sinophorus rhyacioniae	9629091	1	72n	25n	1	Lepidoptera	Rhyacionia zozana		2
Subfamily Collyriinae									
Collyria coxator	9872001	1	72n	25n	2	Hymenoptera	Cephus pygmaeus		3
Subfamily Cremastinae									
Eiphosoma vitticolle	12395980	1	72n	55s	1	Lepidoptera	Spodoptera frugiperda		6
Pristomerus rufiabdominalis	110994	1	45n	42n	1	Lepidoptera	Paranthrene tabaniformis		1

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Pristomerus vulnerator	136707	1	45n	41n	7	Lepidoptera Gypsonoma aceriana		12
Trathala flavoorbitalis	2572297	3	46n	11s	4	Lepidoptera Hellula undalis		9
Trathala species	7682300	3	11s	43s	2	Lepidoptera Anagasta kuehniella		1
Subfamily Cryptinae								
Tribe Cryptini								
Agrothereutina group								
Agrothereutes lanceolatus	337880	1	46n	24n	4	Lepidoptera Galleria mellonella		11
Agrothereutes minousubae	337880	1	46n	24n	1	Lepidoptera Pryeria sinica		14
Agrothereutes abbreviatus	11104364	1	86n	42n	6	Hymenoptera Phyllotoma nemorata		1
Agrothereutes tunetanus								2
Gambrus ultimus	9629091	1	72n	25n	3	Lepidoptera Ancylis comptana		4
Hoplocryptus signatorius	242910	1	58n	50n	4	Hymenoptera Prosopis brevicornis		1
Gabuniina group								
Xanthocryptus novozealandicus	269057	1	36s	48s	1	Coleoptera Oemona hirta		4
Mesostenina group								
Mesostenus gracilis	17311391	3	72n	43s	1	Lepidoptera Cadra figulilella		10
Sphecophagina group								
Sphecophaga vesparum	511967	1	58n	48s	2	Hymenoptera Vespula vulgaris		19
Tribe Hemigasterini								
Pleolophus larvicola								2
Pleolophus indistinctus	19599701	1	86n	25n	1	Hymenoptera Pikonema alaskensis		3
Tribe Phygadeuontini								
Acrolytina group								
Sozites kerichoensis	592747	2	5n	6s	2	Coleoptera Entypotrachelus meyeri		7
Endaseina group								
Endasys subclavatus								1
Gelina group								
Gelis acarorum	581055	1	70n	50n	3	Hymenoptera Cotesia melitaearum		13
Gelis agilis	581055	1	70n	50n	3	Hymenoptera Cotesia melitaearum		20
Gelis tenellus	65301	1	56n	54n	9	Hymenoptera Apanteles melanoscelus		6
Matrina group								
Mastrus ridibundus	9629091	1	72n	25n	1	Lepidoptera Cydia pomonella		15

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Phygadeuontina group									
Phygadeuon elegans	357022	1	56n	46n	1	Diptera	Rhagoletis cerasi		2
Phygadeuon exiguus	28260892	3	83n	18n	2	Diptera	Rhagoletis alternata		2
Phygadeuon wiesmanni	19599701	1	86n	25n	6	Diptera	Rhagoletis pomonella		5
Subfamily Ctenopelmatinae									
Tribe Ctenopelmatini									
Homaspis interruptus					3	Hymenoptera	Acantholyda erythrocephala		2
Tribe Mesoleini									
Lamachus eques	21288815	1	86n	24n	1	Hymenoptera	Neodiprion sertifer		2
Tribe Perilissini									
Lathrolestes ensator	38332251	1	86n	25n	1	Hymenoptera	Hoplocampa testudinae		22
Lathrolestes luteolator	21288815	1	86n	24n	1	Hymenoptera	Neodiprion sertifer		1
Lathrolestes nigricollis	2666390	1	86n	25n	1	Hymenoptera	Fenusa pusilla		16
Lophyroplectus oblongopunctatus	21288815	1	86n	24n	1	Hymenoptera	Neodiprion sertifer		2
Subfamily Diplazontinae									
Diplazon laetatorius						Diptera			12
Diplazon pectoratorius	313183	1	58n	50n	4	Diptera	Syrphus ribesii		1
Diplazon tetragonus	313183	1	58n	50n	6	Diptera	Syrphus ribesii		1
Diplazon tibiatorius	242910	1	58n	50n		Diptera			2
Enizemum ornatum	313183	1	58n	50n	8	Diptera	Syrphus ribesii		13
Syrphophilus trinctorius	313183	1	58n	50n	2	Diptera	Syrphus ribesii		3
Subfamily Eucerotinae									
Euceros albitarsus	242910	1	58n	50n	1	Hymenoptera	Ophion species		1
Euceros frigidus						Hymenoptera			2
Subfamily Ichneumoninae									
Tribe Alomyini									
Diadromus pulchellus	10213520	1	86n	42n	2	Lepidoptera	Acrolepiopsis assectella		76
Dirophanes hariolus	19599701	1	86n	25n	1	Lepidoptera	Choristoneura fumiferana		1
Dirophanes maculicornis	19599701	1	86n	25n	1	Lepidoptera	Choristoneura fumiferana		10
Tycherus nigridens									1
Tycherus osculator	543965	1	52n	43n	3	Lepidoptera	Zeiraphera diniana		9
Tribe Ichneumonini									

Taxonomy	25	26	27	28	29	30		31	32
Cratichneumon sublatus	19599701	1	86n	25n	1	Lepidoptera	Heterocampa guttivitta		13
Ichneumon caloscelis									1
Ichneumon gracilicornis	338145	1	70n	60n	1	Lepidoptera	Melitaea cinixa		13
Tribe Mesoleiini									
Mesoleius species	19599701	1	86n	25n	1	Hymenoptera	Pikonema alaskensis		1
Olesicampe melanogaster	19937581	1	86n	24n	1	Hymenoptera	Pristiphora erichsonii		2
Olesicampe geniculata	19599701	1	86n	25n	1	Hymenoptera	Pristiphora geniculata		12
Olesicampe macellator	357022	1	56n	46n	1	Hymenoptera	Diprion pini		8
Olesicampe monticola	242910	1	58n	50n	2	Hymenoptera	Cephalcia lariciphila		14
Subfamily Labeninae									
Tribe Groteini									
Grotea angunia						Hymenoptera			1
Subfamily Mesochorinae									
Mesochorus agilis	9629091	1	72n	25n	1	Hymenoptera	Bathyplectes curculionis		3
Stictopisthus laticeps	242910	1	58n	50n	1	Hymenoptera	Apanteles nanus		1
Subfamily Metopiinae									
Exochus nigripalpis tectulum	19599701	1	86n	25n	2	Lepidoptera	Choristoneura fumiferana		8
Triclistus crassus	9970610	1	86n	42n	2	Lepidoptera	Operophtera brumata		1
Triclistus emarginalus	9970610	1	86n	42n	1	Lepidoptera	Phyllonorycter elmaella		1
Triclistus podagricus	19599701	1	86n	25n	1	Lepidoptera	Zeiraphera canadensis		12
Triclistus species	19599701	1	86n	25n	1	Lepidoptera	Zeiraphera canadensis		12
Triclistus xylostellae	24035229	3	86n	11s	1	Lepidoptera	Plutella xylostella		1
Subfamily Neorhacodinae									
Neorhacodes enslini	242910	1	58n	50n	3	Hymenoptera	Spilomena enslini		2
Subfamily Ophioninae									
Ophion flavidus	12395980	1	72n	55s	2				21
Ophion parvulus	242910	1	58n	50n					1
Subfamily Orthopelmatinae									
Orthopelma mediator	449964	1	69n	55n	1	Hymenoptera	Diplolepis rosae		2
Orthopelma species	9970610	1	86n	42n	1	Hymenoptera	Diplolepis triforma		13
Subfamily Pimplinae									
Lytarmes maculipennis	329847	2	7n	1n	1	Coleoptera			3

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Tribe Delomeristini								
Perithous divinator	242910	1	58n	50n	6	Hymenoptera	Pemphredon lethifer	2
Tribe Ephialtini								
Acrodactyla degener	18145853	1	83n	42n	7	Araneae	Theridion varians	1
Apechthis ontario	19599701	1	86n	25n	5	Lepidoptera	Choristoneura fumiferana	6
Calliephialtes notanda	9970610	1	86n	42n	1	Lepidoptera	Gnorimoschema gallaeosolidaginis	1
Exeristes comstockii	9629091	1	72n	25n	7	Lepidoptera	Choristoneura fumiferana	3
Exeristes roborator	337880	1	46n	24n	6	Lepidoptera	Galleria mellonella	22
Liotryphon strobilellae	19139458	1	83n	42n	2	Lepidoptera	Cydia strobiella	3
Polysphincta tuberosa	242910	1	58n	50n	9	Araneae	Gibbaranea gibbosa	2
Scambus foliae	9629091	1	72n	25n	1	Hymenoptera	Phyllotoma nemerata	1
Scambus atrocoxalis	1336551	1	52n	36n	1	Lepidoptera	Cydia strobiella	1
Scambus brevicornis	242910	1	58n	50n	4	Lepidoptera	Coleophora alticolella	14
Scambus canadensis	9629091	1	72n	25n	2	Lepidoptera	Endothenis daeckeana	1
Scambus capitator	1336551	1	69n	36n	1	Lepidoptera	Cydia strobiella	2
Scambus hispae	9629091	1	72n	25n	3	Lepidoptera	Lymnaecia phragmitella	8
Sericopimpla sericata								2
Schiizopyga frigida	242910	1	58n	50n	1	Araneae	Clubiona species	2
Zatypota albicoxa	242910	1	58n	50n	1	Araneae	Tegenaria species	2
Zatypota bohemani	353904	1	58n	42n	1	Araneae	Theridion mystaceum	2
Zatypota percontatoria	353904	1	58n	42n	1	Araneae	Theridion mystaceum	2
Tribe Pimplini								
Itoplectis conquisitor		1			80	Lepidoptera	Plutella porrectella	73
Itoplectis maculator	93030	1	48n	45n	1	Lepidoptera	Cydia strobiella	2
Itoplectis naranyae	337880	1	46n	24n	1	Lepidoptera	Galleria mellonella	6
Itoplectis quadricingulata	9629091	1	72n	25n	4	Lepidoptera	Rhyacionia zozana	7
Pimpla turionellae	337880	1	46n	24n	91	Lepidoptera	Galleria mellonella	40
Theronia atalantae	9629091	1	72n	25n	2	Lepidoptera	Thyridopteryx ephemeraeformis	2
Subfamily Poemiinae								
Pseudorhyssa sternata	7754112	3	52n	43s	1	Hymenoptera	Rhyssa persuasoria	3
Subfamily Rhyssinae								
Megarhyssa atrata	9970610	1	86n	42n	1	Hymenoptera	Tremex columba	23

Taxonomy	**25**	**26**	**27**	**28**	**29**	**30**		**31**	**32**
Rhyssa persuasoria	7754112	3	52n	43s	8	Hymenoptera	Sirex noctilo		22
Subfamily Stilbopinae									
Stilbops limneriaeformis	70273	1	55n	52n	1	Lepidoptera	Nematopogon schwarziellus		2
Stilbops ruficornis	242910	1	58n	50n	1	Lepidoptera	Nematopogon metallica		2
Stilbops vetulus	242910	1	58n	50n	1	Lepidoptera	Adela reaumurella		1
Subfamily Tryphoninae									
Tribe Exenterini									
Exenterus abruptorius	21288815	1	86n	24n	1	Hymenoptera	Neodiprion sertifer		5
Tribe Oedemopsini									
Oedemopsis scabricula	242910	1	58n	50n		Lepidoptera			1
Tribe Phytodietini									
Netelia vinulae	242910	1	58n	50n	1	Lepidoptera	Cerura vinula		1
Phytodietus fumiferanae	19599701	1	86n	25n	3	Lepidoptera	Choristoneura fumiferana		6
Tribe Tryphonini									
Grypocentrus albipes	20306390	1	86n	25n	1	Hymenoptera	Fenusa pusilla		6
Grypocentrus apicalis					1	Hymenoptera	Profenusa pygmaea		1
Subfamily Xoridinae									
Xorides brachylabris									1
Xorides corcyrensis									2

Taxonomy	**33**
Family Braconidae	
Subfamily Agathidinae	
Tribe Agathidini	
Agathis anglica	Albania,Austria,Bulgaria,Cyprus,Greece,UK,Italy,Finland,Netherlands, Croatia,Macedonia,Hungary,Russia
Agathis artemesiana	Austria,Bulgaria,UK,Ireland,Sweden
Agathis asteris	Austria
Agathis breviseta	Belgium,Bulgaria,Ireland,Turkey,Switzerland,Macedonia,Germany,Russia, Hungary,Poland,Netherlands,Finland,UK,Sweden,Spain,Latvia,Mongolia, Czechoslovakia,Romania,France
Agathis calcarata	USA
Agathis gibbosa	USA,Canada,Bermuda
Agathis laticincta	USA,Canada
Agathis unicolorata	Argentina
Baeognatha armeniaca	Austria,Turkey,Russia
Baeognatha nigra	Russia,France
Bassus arthurellus	Canada
Cremnops desetor	Hungary,Finland,Switzerland,France,Austria,Belgium,Germany,India, Italy,Russia,Sweden,Poland,Ukraine,Latvia,Malaysia,Czechoslovakia, Macedonia
Earinus elator	Austria,Germany,UK,Ireland,Sweden
Earinus gloriatorius	Belgium,Germany,UK,Netherlands,Hungary,Ireland,Sweden,Russia, Macedonia,Austria,Latvia,Poland,Switzerland,Finland
Earinus limitaris	Canada
Earinus transversus	UK
Earinus zeirapherae	Canada,USA
Microdus dimidiator	France,Germany,Greece,Netherlands,Poland,Macedonia
Microdus pumilus	UK,France,Germany,Netherlands
Microdus rufipes	Bulgaria,UK,Sweden,Turkey,Macedonia
Microdus tumidulus	France,Germany,UK,Greece,Ireland,Italy,Netherlands,Switzerland
Subfamily Alysiinae	
Tribe Alysiini	
Alysia manducator	Russia,Netherlands,Australia,UK
Aphaereta apicalis	Mexico,Ecuador,Brazil,Panama,Cuba,WestIndies
Aphaereta aotea	NewZealand
Aphaereta colei	USA
Aphaereta genevensis	USA
Aphaereta lonchaeae	
Aphaereta minuta	Netherlands,Greece
Aphaereta pallipes	USA
Asobara rufescens	Netherlands
Asobara tabida	Greece,France,USA,UK,Ireland,Netherlands
Chasmodon apterus	UK
Tribe Dacnusini	
Dacnusa areolaris	NewZealand
Dacnusa sibirica	UK
Subfamily Aphidiinae	
Tribe Aphidiini	
Aphidius ervi	Lebanon,Australia,Denmark,Ireland,Serbia,Germany,China,Canada,USA, NewZealand,France,Italy,Chile,UK
Aphidius matricariae	Czechoslovakia,Pakistan,Greece,Turkey,Macedonia,USA,SouthAfrica, France,India
Aphidius nigripes	Canada
Aphidius pisivorus	
Aphidius rhopalosiphi	UK,France,Chile,Denmark,Ireland,Pakistan,Turkey,Greece,Hungary
Aphidius smithi	Chile,India
Aphidius sonchi	

Taxonomy	**33**
Diaeretiella rapae	Canada,Mexico,Panama,Germany,UK,Netherlands,France,India,Syria, India,USA,SouthAfrica
Dyscritulus planiceps	
Lysiphlebus fabarum	Germany
Lysiphlebus testaceipes	PuertoRico,Australia,USA,Chile
Monoctonus paulensis	
Trioxys complanatus	Australia,USA,Iran
Tribe Ephredrini	
Ephedrus californicus	Canada
Ephedrus plagiator	Chile,Denmark,France,Turkey,USA
Tribe Praini	
Praon exsoletum	Italy,USA,Cyprus,Iran,Pakistan,Australia
Praon pequodorum	USA,Canada
Praon volucre	UK,Chile,Denmark,France,Hungary,USA,Canada
Subfamily Blacinae	
Tribe Blacini	
Blacus exilis	Russia,Poland
Blacus koenigi	Serbia
Blacus nigricornis	Switzerland
Subfamily Braconinae	
Tribe Braconini	
Alienoclypeus insolitus	USA,Mexico
Bracon cajani	
Bracon cephi	Canada
Bracon gelechiae	USA
Bracon lissogaster	
Bracon kirkpatricki	Kenya,USA,Egypt,Barbados,Mexico,Sudan,Uganda,Angola,Senegal, IvoryCoast
Bracon mellitor	USA
Bracon pineti	Sweden,Germany,Finland,Norway,Russia,Poland,Hungary
Bracon rhyacioniae	
Bracon thurberiphagae	Trinidad,Guyana,Grenada,Dominica,Montserrat,Antigua,USA
Habrobracon hebetor	USA
Habrobracon lineatellae	Canada
Stenobracon deesae	
Tribe Coelidini	
Coeloides pissodis	USA,Canada
Coeloides scolyticida	Serbia
Subfamily Cardiochilinae	
Schoenlandella diaphaniae	Colombia,USA
Toxoneuron nigriceps	USA,Canada,Colombia,Philippines,Thailand
Subfamily Charmontinae	
Charmon extensor	Hungary
Charmon gracilis	USA
Charmon rufipes	Hungary
Subfamily Cheloninae	
Adelius subfasiatus	UK
Tribe Chelonini	
Ascogaster quadridentata	NewZealand,USA
Ascogaster reticulatus	Japan
Chelonus asiaticus	Iran
Chelonus blackburni	USA
Chelonus curvimaculata	
Chelonus heliopae	
Chelonus inanitus	
Chelonus insularis	USA,Mexico
Chelonus curvimaculatus	Australia,Ethiopia

Taxonomy	**33**
Chelonus texanus	
Tribe Phanerotomini	
Phanerotoma flavistestacea	
Subfamily Doryctinae	
Tribe Doryctini	
Dendrosoter protuberans	Austria,Slovakia,USA,Serbia,Russia
Doryctes mutillator	Russia
Doryctes undulatus	Russia
Tribe Hecabolini	
Stenocorse bruchivora	USA
Tribe Heterospilini	
Heterospilus coffeicola	
Heterospilus prosopidis	USA
Tribe Spathiini	
Spathius benefactor	USA,Canada
Spathius brevicaudis	Serbia
Subfamily Euphorinae	
Tribe Centistini	
Pygostolus falcatus	Canada
Tribe Dinocampini	
Dinocampus coccinellae	UK,USA
Tribe Euphorini	
Microcotonus aethiopoides	Canada,USA,France,Sweden,Croatia,Romania,Russia,Italy,Algeria,Spain, Portugal,NewZealand,Australia,Morocco,Greece,Uzbekistan,Ukraine, Tunisia
Microcotonus caudatus	UK,Sweden,Finland,Ireland
Microcotomus colesi	USA
Microcotonus hyperodae	NewZealand,Argentina,Brazil,Chile,Urgaguay
Tribe Perilitini	
Meteorus arizonensis	USA
Meteorus brevicauda	UK
Meteorus campestris	USA
Meteorus leviventris	USA
Meteorus trachynotus	USA,Canada
Subfamily Exothecinae	
Colastes braconius	UK
Exothecus braconius	UK
Phanomeris catenator	UK
Phanomeris dimidiata	UK
Phanomeris laevis	UK
Phanomeris phyllotomae	USA
Subfamily Gnamptodontinae	
Gnamptodon pumilio	UK,Ireland
Subfamily Helconinae	
Tribe Brachistini	
Eubazus semirugosius	
Triaspis pallipes	UK
Triaspis thoracicus	Syria
Tribe Diospilini	
Apsicolpus hudsoni	NewZealand
Baeacis abietis	Russia
Diospilus capito	Switzerland
Diospilus hiator	Canada
Subfamily Homolobinae	
Homolobus truncator	USA
Subfamily Hormiinae	
Tribe Hormiini	

Taxonomy	**33**
Hormius moniliatus	Bulgaria,CapeVerde
Hormius vulgaris	USA
Subfamily Ichneutinae	
Tribe Ichenutini	
Ichneutes levis	
Ichneutes pikonematis	USA,Canada
Subfamily Macrocentrinae	
Macrocentrus ancylivorus	USA
Macrocentrus cingulum	USA,France,Korea
Macrocentrus iridescens	Canada
Macrocentrus nigridorsis	Canada
Subfamily Microgasterinae	
Tribe Apantelini	
Apanteles ater	Canada,Germany,UK,France,Czechoslovakia
Apanteles carpatus	USA,Canada,Finland,Japan,Switzerland,Sweden,Germany,PuertoRico, SouthAfrica,Singapore,Australia,NewZealand,Tanzania,UK,Grenada, DemRepCongo,Ghana,Fiji,Argentina
Apanteles corvinus	UK,Germany,Hungary,Poland,Sweden,Russia,Romania,Switzerland, Austria
Apanteles fumiferanae	USA,Canada
Apanteles galleriae	
Apanteles milleri	USA
Apanteles morrisi	Canada
Apanteles subandinus	Argentina,Australia
Apanteles syleptae	Nigeria
Dolichogenidea evonymellae	Bulgaria,Netherlands
Dolichogenidea absona	Canada,USA
Pholetesor circumscriptus	UK,Germany,Sweden,Ireland,Italy,Austria,Denmark,Finland,NewZealand, Belgium,Hungary,Morocco,Mongolia,Russia,Netherlands,Spain,Poland, Japan,Romania,Czechoslovakia,Macedonia
Pseudapanteles dignus	USA,Mexico,Trinidad&Tobago
Tribe Cotesiini	
Cotesia congregata	USA,Canada,PortoRico,Jamaica,Brazil
Cotesia euphydryidis	USA
Cotesia flavipes	Australia,Barbados,Malaysia,China,India,Indonesia,Japan,Mauritius, Pakistan,SriLanka,Singapore,Taiwan,Kenya,Madagascar
Cotesia glomerata	Algeria,Australia,Austria,Barbados,Belgium,Brazil,Bulgaria,Netherlands, Denmark,Fiji,Finland,USA,France,Germany,India,Ireland,UK,Switzerland, Japan,Latvia,Malta,Spain,Italy,Uraguay,Morocco,Norway,NewZealand, Lebanon,Poland,Romania,Russia,Serbia,Sweden,Ukraine,Turkey,China, Canada,Cyprus,Czechoslovakia,Macedonia
Cotesia jucunda	Finland
Cotesia kariyai	Japan
Cotesia kazak	NewZealand,USA
Cotesia marginiventris	USA,Mexico
Cotesia medicaginis	
Cotesia melanoscelus	Canada,Finland,Germany,Italy,Sweden,UK,Poland,Russia,Belgium, Austria,Macedonia,Netherlands,Romania,Switzerland,Czechoslovakia, Ukraine,Hungary,Morocco
Cotesia melitaearum	UK,Finland
Cotesia ocneriae	Austria,Albania,Bosnia,Bulgaria,Croatia,Hungary,Greece,Turkey,Serbia, Ukraine,Macedonia
Cotesia phobetri	USA
Cotesia rubecula	UK,France,Switzerland,Russia,Austria,Netherlands,NewZealand, Australia,Germany,Canada
Cotesia schizurae	USA,Canada
Cotesia scitula	USA,Canada

Taxonomy	**33**
Cotesia vestalis	France,Malaysia,USA
Cotesia yakutatensis	USA,Canada
Glyptapanteles militaris	USA
Glyptapanteles porthetriae	Austria,Slovakia
Protapanteles immunis	Finland
Tribe Microgastrini	
Choeras tedellae	
Choeras tiro	Canada
Microgaster hospes	USA
Microgaster tibialis	
Tribe Microplitini	
Microplitis alaskensis	USA
Microplitis croceipes	USA,Canada
Microplitis demolitor	USA,Australia
Microplitis mediator	Canada,Finland,Greenland,Japan,Latvia,Mongolia,Russia,Sweden
Microplitis naenia	UK,Czechoslovakia
Microplitis ocellatae	Japan
Microplitis plutellae	Canada
Microplitis rufiventris	Russia
Microplitis tuberculifera	Sweden,UK
Subfamily Microtypinae	
Microtypus species	USA
Microtypus wesmaelii	UK
Subfamily Micracinae	
Mirax minuta	USA
Mirax rufilabris	UK
Subfamily Opiinae	
Biosteres arisanus	USA
Biosteres melleus	USA
Biosteres vandenboschii	USA
Diachasmimorpha kraussi	Australia,USA
Diachasmimorpha longicaudata	USA,Mexico,Guatemala,Malaysia,Indonesia,Philippines,India
Diachasmimorpha tryoni	USA,Australia
Doryctobracon areolatus	USA,Argentina,Guatemala,CostaRica,Colombia,Mexico
Doryctobracon crawfordi	Mexico,CostaRica
Fopius arisanus	Mexico,USA,Malaysia,Australia
Opius canaliculatus	Canada,USA
Opius dissitus	
Opius lectus	USA
Opius magnus	Germany
Opius rhagoleticola	Germany
Opius striatriventris	USA
Psyttalia incisi	USA,India
Utetes anastrephae	Mexico,USA,Argentina
Subfamily Braconidae	
Tribe Orgilini	
Orgilus comptanae	USA
Orgilus lepidus	Australia
Subfamily Pambolinae	
Tribe Chremylini	
Cedria paradoxa	
Subfamily Rhysipolinae	
Rhysipolis decorator	UK
Rhysipolis hariolator	UK
Rhysipolis mediator	UK
Subfamily Rhyssalinae	
Tribe Rhyssalini	

Taxonomy	**33**
Oncophanes americanus	Canada,USA
Oncophanes laevigatus	UK
Subfamily Rogadinae	
Tribe Clinocentrini	
Clinocentrus gracilpes	UK
Clinocentrus species	
Tribe Rogadini	
Aleiodes circumscriptus	Hungary
Aleiodes gastritor	UK,Finland,Switzerland
Aleiodes nolophanae	USA
Aleiodes praetor	UK
Pelecystoma harrisinae	
Rogas malacosomatos	Canada
Rogas stigmator	Canada,USA
Family Ichneumonidae	
Subfamily Acaenitinae	
Acaenitus dubiator	Turkey,UK
Phaenolobus terebrator	Turkey,UK
Subfamily Adelognathinae	
Adelognathus species	Canada
Adelognathus brevicornis	UK
Adelognathus granulatus	UK
Adelognathus laevicollis	UK
Adelognathus pusillus	UK
Subfamily Agriotypinae	
Agriotypus armatus	UK,Austria,France,Germany,Sweden,Turkey
Agriotypus changbaishanus	China
Agriotypus chaoi	Vietnam
Agriotypus gracilis	Japan
Agriotypus himalensis	India
Agriotypus jilinensis	China
Agriotypus kambaitensis	Malaysia
Agriotypus lui	China
Agriotypus maculiceps	China
Agriotypus masneri	Vietnam
Agriotypus silvestris	Japan
Agriotypus succinctus	China
Agriotypus tangi	China
Agriotypus townesi	Taiwan
Agriotypus zhejiangensis	China
Agriotypus zhengi	China
Subfamily Anomaloninae	
Tribe Gravenhorstiini	
Agrypon flaveolatum	Canada
Parania prima	SouthAfrica,Nigeria,Uganda,Angola,Botswana
Subfamily Banchinae	
Tribe Atrophini	
Diradops bethunei	USA,Canada
Lissonota dubia	Denmark
Tribe Banchini	
Banchus flavescens	Canada
Tribe Glyptini	
Glypta fumiferanae	USA, Mexico,Canada
Subfamily Campopleginae	
Bathypectes group	
Bathyplectes anurus	USA, Canada
Bathyplectes contracta	USA

Taxonomy	**33**
Bathyplectes curculionis	USA,Canada
Bathyplectes stenostigma	
Dusona group	
Campoletis flavicincta	USA,Mexico
Campoletis grioti	USA
Campoletis sonorensis	USA
Campoplex cursitans	Denmark
Campoplex frustranae	USA
Campoplex punctulatus	UK
Diadegma chrysostictos	UK,Netherlands,Germany,Russia,Morocco,Belgium,France,Canada,USA, Czechoslovakia
Diadegma insulare	Canada, USA, Venezuala, Mexico
Diadegma semiclausum	UK,Malaysia,Indonesia
Dusona contumax	Switzerland
Eriborus terebrans	Bulgaria,USA
Eriborus trochanteratus	
Hyposoter didymator	France,USA,Israel
Hyposoter exiguae	USA
Hyposoter fugitivus	
Hyposoter horticola	Finland
Lathrostizus euurae	USA
Phaedroctonus moderator	Switzerland,Sweden,Germany,Finland,Hungary,Italy,France,Bulgaria, Czechoslovakia
Phobocampe bicingulata	Finland
Phobocampe lymantriae	Austria,Slovakia
Phobocampe pallida	USA,Canada
Tranosema pedella	USA
Tranosema rostrale	Canada
Venturia canescens	Netherlands,France,UK,USA,Greece
Gonotypus group	
Gonotypus melanostoma	UK,Germany
Tribe Campoplegini	
Sinophorus crassifemur	Germany,Canada
Sinophorus megalodontis	Canada
Sinophorus rhyacioniae	USA
Subfamily Collyriinae	
Collyria coxator	UK
Subfamily Cremastinae	
Eiphosoma vitticolle	USA
Pristomerus rufiabdominalis	Bulgaria
Pristomerus vulnerator	Bulgaria,Macedonia
Trathala flavoorbitalis	USA, Malaysia
Trathala species	
Subfamily Cryptinae	
Tribe Cryptini	
Agrothereutina group	
Agrothereutes lanceolatus	Japan
Agrothereutes minousubae	Japan
Agrothereutes abbreviatus	
Agrothereutes tunetanus	
Gambrus ultimus	USA
Hoplocryptus signatorius	UK
Gabuniina group	
Xanthocryptus novozealandicus	NewZealand
Mesostenina group	
Mesostenus gracilis	
Sphecophagina group	

Taxonomy	33
Sphecophaga vesparum	NewZealand
Tribe Hemigasterini	
Pleolophus larvicola	Canada
Pleolophus indistinctus	
Tribe Phygadeuontini	
Acrolytina group	
Sozites kerichoensis	Kenya
Endaseina group	
Endasys subclavatus	
Gelina group	
Gelis acarorum	Finland
Gelis agilis	Finland,UK
Gelis tenellus	Canada, USA
Matrina group	
Mastrus ridibundus	USA
Phygadeuontina group	
Phygadeuon elegans	
Phygadeuon exiguus	
Phygadeuon wiesmanni	Canada
Subfamily Ctenopelmatinae	
Tribe Ctenopelmatini	
Homaspis interruptus	USA,Canada
Tribe Mesoleini	
Lamachus eques	
Tribe Perilissini	
Lathrolestes ensator	Netherlands,Ukraine,Russia,Switzerland,Poland,Italy,USA,Canada, Germany
Lathrolestes luteolator	Austria,Germany,Switzerland
Lathrolestes nigricollis	USA,Canada,France,Austria,Czechoslovakia
Lophyroplectus oblongopunctatus	UK,Canada
Subfamily Diplazontinae	
Diplazon laetatorius	UK
Diplazon pectoratorius	UK
Diplazon tetragonus	UK
Diplazon tibiatorius	UK
Enizemum ornatum	Canada
Syrphophilus trinctorius	UK
Subfamily Eucerotinae	
Euceros albitarsus	UK
Euceros frigidus	
Subfamily Ichneumoninae	
Tribe Alomyini	
Diadromus pulchellus	France
Dirophanes hariolus	USA
Dirophanes maculicornis	Canada,USA,Mexico
Tycherus nigridens	
Tycherus osculator	France,Canada
Tribe Ichneumonini	
Cratichneumon sublatus	USA,Canada
Ichneumon caloscelis	
Ichneumon gracilicornis	Finland
Tribe Mesoleiini	
Mesoleius species	USA,Canada
Olesicampe melanogaster	Canada
Olesicampe geniculata	Canada, Austria
Olesicampe macellator	Germany
Olesicampe monticola	Poland,UK,Germany

Taxonomy	**33**
Subfamily Labeninae	
Tribe Groteini	
Grotea angunia	
Subfamily Mesochorinae	
Mesochorus agilis	USA
Stictopisthus laticeps	UK
Subfamily Metopiinae	
Exochus nigripalpis tectulum	
Triclistus crassus	Canada
Triclistus emarginalus	Canada
Triclistus podagricus	
Triclistus species	Canada
Triclistus xylostellae	Canada
Subfamily Neorhacodinae	
Neorhacodes enslini	UK,Finland,Cyprus
Subfamily Ophioninae	
Ophion flavidus	USA
Ophion parvulus	UK
Subfamily Orthopelmatinae	
Orthopelma mediator	Sweden
Orthopelma species	Canada
Subfamily Pimplinae	
Lytarmes maculipennis	Malaysia
Tribe Delomeristini	
Perithous divinator	UK,Canada
Tribe Ephialtini	
Acrodactyla degener	UK
Apechthis ontario	Canada,USA
Calliephialtes notanda	Canada
Exeristes comstockii	USA
Exeristes roborator	
Liotryphon strobilellae	Sweden,Finland,Germany,Norway,Hungary,Bulgaria,Russia,Poland, Czechoslovakia
Polysphincta tuberosa	UK
Scambus foliae	USA
Scambus atrocoxalis	
Scambus brevicornis	Canada,Sweden,UK
Scambus canadensis	USA
Scambus capitator	Switzerland,France,Italy,Sweden
Scambus hispae	USA
Sericopimpla sericata	
Schiizopyga frigida	UK
Zatypota albicoxa	UK
Zatypota bohemani	UK
Zatypota percontatoria	UK
Tribe Pimplini	
Itoplectis conquisitor	
Itoplectis maculator	Hungary
Itoplectis naranyae	
Itoplectis quadricingulata	USA,Canada
Pimpla turionellae	
Theronia atalantae	USA,Austria,Slovakia
Subfamily Poemiinae	
Pseudorhyssa sternata	
Subfamily Rhyssinae	
Megarhyssa atrata	USA,Canada
Rhyssa persuasoria	Australia,Switzerland,Belgium

Taxonomy	**33**
Subfamily Stilbopinae	
Stilbops limneriaeformis	Ireland,France,Netherlands,Germany,Hungary,Poland,Finland,Bulgaria
Stilbops ruficornis	UK
Stilbops vetulus	UK
Subfamily Tryphoninae	
Tribe Exenterini	
Exenterus abruptorius	
Tribe Oedemopsini	
Oedemopsis scabricula	UK
Tribe Phytodietini	
Netelia vinulae	UK
Phytodietus fumiferanae	Canada,USA,Mexico
Tribe Tryphonini	
Grypocentrus albipes	Austria,Czechoslovakia,France,USA,Canada
Grypocentrus apicalis	
Subfamily Xoridinae	
Xorides brachylabris	
Xorides corcyrensis	

Taxonomy	**34**
Family Braconidae	
Subfamily Agathidinae	
Tribe Agathidini	
Agathis anglica	Albania,Austria,Bulgaria,Cyprus,UK.Greece,Italy
Agathis artemesiana	Austria,Bulgaria,UK,Ireland,Sweden
Agathis asteris	Austria
Agathis breviseta	Austria
Agathis calcarata	
Agathis gibbosa	
Agathis laticincta	
Agathis unicolorata	
Baeognatha armeniaca	
Baeognatha nigra	Russia,France,UK,Ireland
Bassus arthurellus	Canada
Cremnops desetor	USA
Earinus elator	Denmark,Italy,UK
Earinus gloriatorius	Belgium, USA
Earinus limitaris	Canada
Earinus transversus	UK
Earinus zeirapherae	Canada
Microdus dimidiator	
Microdus pumilus	USA,UK,Canada,Japan,Italy
Microdus rufipes	
Microdus tumidulus	France,Germany,UK,Greece,Ireland,Italy,Netherlands,Switzerland
Subfamily Alysiinae	
Tribe Alysiini	
Alysia manducator	
Aphaereta apicalis	
Aphaereta aotea	NewZealand,Australia
Aphaereta colei	USA,UK
Aphaereta genevensis	USA
Aphaereta lonchaeae	
Aphaereta minuta	Greece
Aphaereta pallipes	USA
Asobara rufescens	Netherlands
Asobara tabida	Canada,Sweden,UK,France,Greece,Italy,Switzerland,Hungary,Turkey, Netherlands
Chasmodon apterus	UK
Tribe Dacnusini	
Dacnusa areolaris	NewZealand
Dacnusa sibirica	UK
Subfamily Aphidiinae	
Tribe Aphidiini	
Aphidius ervi	UK,Italy,Chile,USA,NewZealand,Canada
Aphidius matricariae	Czechoslovakia,Pakistan,Greece,Turkey,Macedonia,France,Mexico, SouthAfrica
Aphidius nigripes	Canada
Aphidius pisivorus	
Aphidius rhopalosiphi	UK,France,Chile,Denmark
Aphidius smithi	Chile,India
Aphidius sonchi	
Diaeretiella rapae	SouthAfrica,Syria,USA
Dyscritulus planiceps	
Lysiphlebus fabarum	Germany
Lysiphlebus testaceipes	USA
Monoctonus paulensis	USA,Canada

Taxonomy	**34**
Trioxys complanatus	Australia,USA
Tribe Ephredrini	
Ephedrus californicus	Canada
Ephedrus plagiator	
Tribe Praini	
Praon exsoletum	USA
Praon pequodorum	USA,Canada
Praon volucre	USA,Canada
Subfamily Blacinae	
Tribe Blacini	
Blacus exilis	Russia,Poland
Blacus koenigi	Hungary,Serbia
Blacus nigricornis	Switzerland
Subfamily Braconinae	
Tribe Braconini	
Alienoclypeus insolitus	USA,Mexico,Italy,Netherlands,Indonesia,Kenya,Cuba,SouthAfrica, Tanzania,CostaRico,
Bracon cajani	
Bracon cephi	Canada
Bracon gelechiae	USA
Bracon lissogaster	Canada
Bracon kirkpatricki	Kenya,USA,Australia,Ethiopia,India
Bracon mellitor	USA
Bracon pineti	Sweden,Germany,Finland,Norway,Hungary,Russia,Poland
Bracon rhyacioniae	Hungary,Switzerland,France
Bracon thurberiphagae	Guyana,Grenada,Dominica,Montserrat,Antigua,USA
Habrobracon hebetor	USA
Habrobracon lineatellae	Canada,Australia
Stenobracon deesae	
Tribe Coelidini	
Coeloides pissodis	USA,Canada
Coeloides scolyticida	Serbia
Subfamily Cardiochilinae	
Schoenlandella diaphaniae	USA
Toxoneuron nigriceps	Canada,USA
Subfamily Charmontinae	
Charmon extensor	Hungary,Switzerland,France
Charmon gracilis	USA
Charmon rufipes	Russia,Hungary,Switzerland,France
Subfamily Cheloninae	
Adelius subfasiatus	UK
Tribe Chelonini	
Ascogaster quadridentata	USA
Ascogaster reticulatus	Japan,UK,Belgium
Chelonus asiaticus	Iran
Chelonus blackburni	Kenya,USA,Australia,Ethiopia,India
Chelonus curvimaculata	
Chelonus heliopae	
Chelonus inanitus	
Chelonus insularis	USA
Chelonus curvimaculatus	Kenya,USA,Australia,Ethiopia,India
Chelonus texanus	
Tribe Phanerotomini	
Phanerotoma flavistestacea	Australia
Subfamily Doryctinae	
Tribe Doryctini	
Dendrosoter protuberans	UK,Germany,Slovakia,Serbia

Taxonomy	**34**
Doryctes mutillator	Russia,Hungary,Switzerland,France
Doryctes undulatus	Russia,Hungary,Switzerland,France
Tribe Hecabolini	
Stenocorse bruchivora	USA,Mexico
Tribe Heterospilini	
Heterospilus coffeicola	
Heterospilus prosopidis	USA
Tribe Spathiini	
Spathius benefactor	USA,Canada
Spathius brevicaudis	UK,Germany,Slovakia,Serbia
Subfamily Euphorinae	
Tribe Centistini	
Pygostolus falcatus	USA,Canada
Tribe Dinocampini	
Dinocampus coccinellae	UK,USA
Tribe Euphorini	
Microcotonus aethiopoides	NewZealand,Australia
Microcotonus caudatus	UK,Ireland,Japan,Russia
Microcotomus colesi	USA
Microcotonus hyperodae	NewZealand,UK,Australia
Tribe Perilitini	
Meteorus arizonensis	USA
Meteorus brevicauda	UK
Meteorus campestris	USA
Meteorus leviventris	USA
Meteorus trachynotus	USA
Subfamily Exothecinae	
Colastes braconius	Austria
Exothecus braconius	UK
Phanomeris catenator	UK
Phanomeris dimidiata	UK
Phanomeris laevis	UK
Phanomeris phyllotomae	Canada,UK,Sweden,Germany,Austria
Subfamily Gnamptodontinae	
Gnamptodon pumilio	UK,Ireland
Subfamily Helconinae	
Tribe Brachistini	
Eubazus semirugosius	
Triaspis pallipes	UK
Triaspis thoracicus	Russia,Syria,Afghanistan
Tribe Diospilini	
Apsicolpus hudsoni	NewZealand
Baeacis abietis	Russia,Hungary,Switzerland,France
Diospilus capito	Switzerland
Diospilus hiator	USA
Subfamily Homolobinae	
Homolobus truncator	USA,Argentina
Subfamily Hormiinae	
Tribe Hormiini	
Hormius moniliatus	Bulgaria
Hormius vulgaris	USA
Subfamily Ichneutinae	
Tribe Ichenutini	
Ichneutes levis	
Ichneutes pikonematis	USA,Canada
Subfamily Macrocentrinae	
Macrocentrus ancylivorus	USA

Taxonomy	**34**
Macrocentrus cingulum	USA
Macrocentrus iridescens	Canada
Macrocentrus nigridorsis	Canada
Subfamily Microgasterinae	
Tribe Apantelini	
Apanteles ater	
Apanteles carpatus	Australia
Apanteles corvinus	UK
Apanteles fumiferanae	USA,Canada
Apanteles galleriae	Japan
Apanteles milleri	USA
Apanteles morrisi	USA,Canada
Apanteles subandinus	Australia
Apanteles syleptae	Nigeria
Dolichogenidea evonymellae	Bulgaria,Netherlands
Dolichogenidea absona	USA,Canada
Pholetesor circumscriptus	UK
Pseudapanteles dignus	Bahamas,Cuba,Haiti,Mexico,USA
Tribe Cotesiini	
Cotesia congregata	USA
Cotesia euphydryidis	USA
Cotesia flavipes	Kenya,Pakistan
Cotesia glomerata	Canda,Finland,Japan,Netherlands,USA,UK
Cotesia jucunda	Finland,Switzerland,UK
Cotesia kariyai	China,Finland,France,Germany,India,Indonesia,Japan,NewZealand Netherlands
Cotesia kazak	Austria,Australia,IvoryCoast,Italy,Kenya,Tanzania
Cotesia marginiventris	USA
Cotesia medicaginis	USA,Mexico
Cotesia melanoscelus	Canada,UK
Cotesia melitaearum	UK,Finland
Cotesia ocneriae	Austria,Slovakia,USA,Canada,Japan
Cotesia phobetri	USA
Cotesia rubecula	Macedonia,Netherlands
Cotesia schizurae	Canada,USA
Cotesia scitula	USA,Canada
Cotesia vestalis	India,NewZealand,Australia,Canada,France,USA
Cotesia yakutatensis	USA,Canada
Glyptapanteles militaris	USA
Glyptapanteles porthetriae	Austria,Slovakia,USA,Canada,Japan
Protapanteles immunis	Finland,UK
Tribe Microgastrini	
Choeras tedellae	
Choeras tiro	Canada
Microgaster hospes	USA
Microgaster tibialis	
Tribe Microplitini	
Microplitis alaskensis	USA,Canada
Microplitis croceipes	USA,Canada
Microplitis demolitor	USA
Microplitis mediator	Canada
Microplitis naenia	UK,Czechoslovakia
Microplitis ocellatae	China,Korea,Mongolia,Russia,Taiwan,Japan
Microplitis plutellae	Canada
Microplitis rufiventris	
Microplitis tuberculifera	
Subfamily Microtypinae	

Taxonomy	**34**
Microtypus species	USA
Microtypus wesmaelii	UK
Subfamily Micracinae	
Mirax minuta	USA
Mirax rufilabris	UK,Ireland
Subfamily Opiinae	
Biosteres arisanus	USA
Biosteres melleus	USA,Canada
Biosteres vandenboschii	USA
Diachasmimorpha kraussi	USA
Diachasmimorpha longicaudata	USA,Mexico,Bahamas,Cuba,Dominica,Haiti,Jamica,PuertoRico
Diachasmimorpha tryoni	USA
Doryctobracon areolatus	USA
Doryctobracon crawfordi	Mexico
Fopius arisanus	USA
Opius canaliculatus	USA,Canada
Opius dissitus	USA
Opius lectus	USA,Canada
Opius magnus	Germany
Opius rhagoleticola	Germany
Opius striatriventris	USA
Psyttalia incisi	USA
Utetes anastrephae	Mexico
Subfamily Braconidae	
Tribe Orgilini	
Orgilus comptanae	USA
Orgilus lepidus	Australia
Subfamily Pambolinae	
Tribe Chremylini	
Cedria paradoxa	
Subfamily Rhysipolinae	
Rhysipolis decorator	UK
Rhysipolis hariolator	UK
Rhysipolis mediator	UK
Subfamily Rhyssalinae	
Tribe Rhyssalini	
Oncophanes americanus	
Oncophanes laevigatus	UK
Subfamily Rogadinae	
Tribe Clinocentrini	
Clinocentrus gracilpes	UK
Clinocentrus species	USA,Canada
Tribe Rogadini	
Aleiodes circumscriptus	Hungary,Switzerland,France
Aleiodes gastritor	Finland,Switzerland,UK
Aleiodes nolophanae	USA
Aleiodes praetor	UK
Pelecystoma harrisinae	
Rogas malacosomatos	USA,Canada
Rogas stigmator	USA,Canada
Family Ichneumonidae	
Subfamily Acaenitinae	
Acaenitus dubiator	UK
Phaenolobus terebrator	UK
Subfamily Adelognathinae	
Adelognathus species	Canada, USA
Adelognathus brevicornis	

Taxonomy	**34**
Adelognathus granulatus	UK
Adelognathus laevicollis	UK
Adelognathus pusillus	UK
Subfamily Agriotypinae	
Agriotypus armatus	UK,Sweden
Agriotypus changbaishanus	China
Agriotypus chaoi	Vietnam
Agriotypus gracilis	Japan
Agriotypus himalensis	India
Agriotypus jilinensis	China
Agriotypus kambaitensis	Malaysia
Agriotypus lui	China
Agriotypus maculiceps	China
Agriotypus masneri	Vietnam
Agriotypus silvestris	Japan
Agriotypus succinctus	China
Agriotypus tangi	China
Agriotypus townesi	Taiwan
Agriotypus zhejiangensis	China
Agriotypus zhengi	China
Subfamily Anomaloninae	
Tribe Gravenhorstiini	
Agrypon flaveolatum	Canada,UK,Japan
Parania prima	UK,Belgium,SouthAfrica,Nigeria,Uganda,Angola,Botswana
Subfamily Banchinae	
Tribe Atrophini	
Diradops bethunei	USA
Lissonota dubia	Denmark
Tribe Banchini	
Banchus flavescens	Canada,America
Tribe Glyptini	
Glypta fumiferanae	USA,Canada
Subfamily Campopleginae	
Bathypectes group	
Bathyplectes anurus	USA,Canada
Bathyplectes contracta	USA
Bathyplectes curculionis	USA,Canada
Bathyplectes stenostigma	
Dusona group	
Campoletis flavicincta	USA
Campoletis grioti	USA
Campoletis sonorensis	USA
Campoplex cursitans	Denmark
Campoplex frustranae	USA
Campoplex punctulatus	UK
Diadegma chrysostictos	USA
Diadegma insulare	USA, Canada, Mexico,Malaysia,Indonesia,UK
Diadegma semiclausum	USA, Canada, Mexico,Malaysia,Indonesia,UK
Dusona contumax	Denmark,UK,Switzerland
Eriborus terebrans	Bulgaria,USA,Serbia
Eriborus trochanteratus	Australia
Hyposoter didymator	
Hyposoter exiguae	USA
Hyposoter fugitivus	
Hyposoter horticola	Finland
Lathrostizus euurae	USA
Phaedroctonus moderator	Sweden,Finland,Germany,Norway,Hungary,Bulgaria,Poland,Russia,

Taxonomy	**34**
	Czechoslovakia
Phobocampe bicingulata	Finland
Phobocampe lymantriae	Austria,Slovakia,USA,Canada,Japan
Phobocampe pallida	USA,Canada
Tranosema pedella	USA,Canada,UK,Sweden,Germany,Austria
Tranosema rostrale	USA,Canada
Venturia canescens	USA
Gonotypus group	
Gonotypus melanostoma	UK
Tribe Campoplegini	
Sinophorus crassifemur	
Sinophorus megalodontis	
Sinophorus rhyacioniae	USA
Subfamily Collyriinae	
Collyria coxator	USA,UK
Subfamily Cremastinae	
Eiphosoma vitticolle	USA,Argentina
Pristomerus rufiabdominalis	Bulgaria
Pristomerus vulnerator	Bulgaria,Macedonia
Trathala flavoorbitalis	Malaysia,Japan,Indonesia
Trathala species	Australia
Subfamily Cryptinae	
Tribe Cryptini	
Agrothereutina group	
Agrothereutes lanceolatus	Japan
Agrothereutes minousubae	Japan
Agrothereutes abbreviatus	Canada,UK,Sweden,Germany,Austria
Agrothereutes tunetanus	
Gambrus ultimus	USA
Hoplocryptus signatorius	UK
Gabuniina group	
Xanthocryptus novozealandicus	NewZealand
Mesostenina group	
Mesostenus gracilis	USA,Australia
Sphecophagina group	
Sphecophaga vesparum	NewZealand, UK
Tribe Hemigasterini	
Pleolophus larvicola	
Pleolophus indistinctus	USA,Canada
Tribe Phygadeuontini	
Acrolytina group	
Sozites kerichoensis	Kenya
Endaseina group	
Endasys subclavatus	
Gelina group	
Gelis acarorum	Finland,UK
Gelis agilis	Finland,UK
Gelis tenellus	Lithunia
Matrina group	
Mastrus ridibundus	USA
Phygadeuontina group	
Phygadeuon elegans	Germany
Phygadeuon exiguus	UK,France,Russia,China,Japan,Slovenia,Bulgaria,Germany
Phygadeuon wiesmanni	USA,Canada
Subfamily Ctenopelmatinae	
Tribe Ctenopelmatini	
Homaspis interruptus	

Taxonomy	**34**
Tribe Mesoleini	
Lamachus eques	Canada,Germany,Italy,Sweden,USA,UK,Japan
Tribe Perilissini	
Lathrolestes ensator	Netherlands,Ukraine,Russia,Switzerland,Poland,Italy,Germany,Canada, USA
Lathrolestes luteolator	Canada,Germany,Italy,Sweden,USA,UK,Japan
Lathrolestes nigricollis	Canada,France,Austria,Czechoslovakia,USA
Lophyroplectus oblongopunctatus	Canada,Germany,Italy,Sweden,USA,UK,Japan
Subfamily Diplazontinae	
Diplazon laetatorius	
Diplazon pectoratorius	UK,Ireland
Diplazon tetragonus	UK,Ireland
Diplazon tibiatorius	UK
Enizemum ornatum	UK,Ireland
Syrphophilus trinctorius	UK,Ireland
Subfamily Eucerotinae	
Euceros albitarsus	UK
Euceros frigidus	
Subfamily Ichneumoninae	
Tribe Alomyini	
Diadromus pulchellus	UK,Canada
Dirophanes hariolus	Canada,USA
Dirophanes maculicornis	Canada,USA
Tycherus nigridens	
Tycherus osculator	France
Tribe Ichneumonini	
Cratichneumon sublatus	USA,Canada
Ichneumon caloscelis	
Ichneumon gracilicornis	Finland
Tribe Mesoleiini	
Mesoleius species	USA,Canada
Olesicampe melanogaster	Canada,USA,Japan
Olesicampe geniculata	Canada, USA
Olesicampe macellator	Germany
Olesicampe monticola	UK
Subfamily Labeninae	
Tribe Groteini	
Grotea angunia	
Subfamily Mesochorinae	
Mesochorus agilis	USA
Stictopisthus laticeps	UK
Subfamily Metopiinae	
Exochus nigripalpis tectulum	Canada,USA
Triclistus crassus	Canada
Triclistus emarginalus	Canada
Triclistus podagricus	Canada,USA
Triclistus species	Canada,USA
Triclistus xylostellae	USA, Canada, Mexico,Malaysia,Indonesia,UK
Subfamily Neorhacodinae	
Neorhacodes enslini	UK
Subfamily Ophioninae	
Ophion flavidus	USA,Argentina
Ophion parvulus	UK
Subfamily Orthopelmatinae	
Orthopelma mediator	Sweden
Orthopelma species	Canada
Subfamily Pimplinae	

Taxonomy	34
Lytarmes maculipennis	Malaysia
Tribe Delomeristini	
Perithous divinator	UK
Tribe Ephialtini	
Acrodactyla degener	Sweden,Russia,Lithunia,Poland,UK
Apechthis ontario	Canada,USA
Calliephialtes notanda	Canada
Exeristes comstockii	USA
Exeristes roborator	Japan
Liotryphon strobilellae	Sweden,Finland,Germany,Norway,Hungary,Bulgaria,Czechoslovakia, Poland,Russia
Polysphincta tuberosa	UK
Scambus foliae	USA
Scambus atrocoxalis	Switzerland,France,Italy,Sweden
Scambus brevicornis	UK
Scambus canadensis	USA
Scambus capitator	Switzerland,France,Italy,Sweden
Scambus hispae	USA
Sericopimpla sericata	
Schiizopyga frigida	UK
Zatypota albicoxa	UK
Zatypota bohemani	Bulgaria,UK
Zatypota percontatoria	Bulgaria,UK
Tribe Pimplini	
Itoplectis conquisitor	
Itoplectis maculator	Hungary
Itoplectis naranyae	Japan
Itoplectis quadricingulata	USA
Pimpla turionellae	Japan
Theronia atalantae	USA
Subfamily Poemiinae	
Pseudorhyssa sternata	Australia,Switzerland,Belgium
Subfamily Rhyssinae	
Megarhyssa atrata	Canada
Rhyssa persuasoria	Australia,Switzerland,Belgium
Subfamily Stilbopinae	
Stilbops limneriaeformis	Ireland
Stilbops ruficornis	UK
Stilbops vetulus	UK
Subfamily Tryphoninae	
Tribe Exenterini	
Exenterus abruptorius	Canada,Germany,Italy,Sweden,USA,UK,Japan
Tribe Oedemopsini	
Oedemopsis scabricula	UK
Tribe Phytodietini	
Netelia vinulae	UK
Phytodietus fumiferanae	Canada,USA
Tribe Tryphonini	
Grypocentrus albipes	Austria,Czechoslovakia,France,Canada,USA
Grypocentrus apicalis	
Subfamily Xoridinae	
Xorides brachylabris	
Xorides corcyrensis	

Taxonomy	**35**
Family Braconidae	
Subfamily Agathidinae	
Tribe Agathidini	
Agathis anglica	280,347
Agathis artemesiana	280,347
Agathis asteris	280,347
Agathis breviseta	280,347
Agathis calcarata	47,347
Agathis gibbosa	47,192,347
Agathis laticincta	47,347
Agathis unicolorata	47,347
Baeognatha armeniaca	280
Baeognatha nigra	280,347
Bassus arthurellus	339
Cremnops desetor	280,347
Earinus elator	280
Earinus gloriatorius	280,347
Earinus limitaris	71
Earinus transversus	280,347
Earinus zeirapherae	347,418
Microdus dimidiator	280
Microdus pumilus	47,280
Microdus rufipes	280
Microdus tumidulus	280
Subfamily Alysiinae	
Tribe Alysiini	
Alysia manducator	5,47,248,323,41
Aphaereta apicalis	419,420
Aphaereta aotea	419
Aphaereta colei	67,419,420
Aphaereta genevensis	248,303
Aphaereta lonchaeae	419
Aphaereta minuta	400,401,406,407,420
Aphaereta pallipes	47,248,421
Asobara rufescens	402
Asobara tabida	4,32,79,96,97,103,139,171,201,215,216,401
Chasmodon apterus	260,261,420
Tribe Dacnusini	
Dacnusa areolaris	70
Dacnusa sibirica	69,373
Subfamily Aphidiinae	
Tribe Aphidiini	
Aphidius ervi	64,138,142,159,165,188,197,198,263,292,336,367,377
Aphidius matricariae	1,47,106,176,189,254,263,333,353,368
Aphidius nigripes	63,65
Aphidius pisivorus	62,63
Aphidius rhopalosiphi	115,116,264,297,352,367,368
Aphidius smithi	18,60,62,235,313,367
Aphidius sonchi	47,154
Diaeretiella rapae	1,100,160,176,234,304,321,338,353,368,399
Dyscritulus planiceps	408
Lysiphlebus fabarum	169,368
Lysiphlebus testaceipes	68,134,169,217,235,368,426
Monoctonus paulensis	47,64,169,233
Trioxys complanatus	47,190,249,254
Tribe Ephredrini	

Taxonomy	**35**
Ephedrus californicus	61,63,64,66,154,213,233,337,362
Ephedrus plagiator	32,47,66,116,352,367,368
Tribe Praini	
Praon exsoletum	47,190,204
Praon pequodorum	62,63,169
Praon volucre	47,204,264,333,367
Subfamily Blacinae	
Tribe Blacini	
Blacus exilis	49,214
Blacus koenigi	242
Blacus nigricornis	52
Subfamily Braconinae	
Tribe Braconini	
Alienoclypeus insolitus	245
Bracon cajani	47
Bracon cephi	262
Bracon gelechiae	114,282
Bracon lissogaster	47,262
Bracon kirkpatricki	51,74
Bracon mellitor	47,114,404
Bracon pineti	49
Bracon rhyacioniae	49
Bracon thurberiphagae	37,47
Habrobracon hebetor	8,9,47,138,150,182,203,286,287,374
Habrobracon lineatellae	39,47
Stenobracon deesae	47
Tribe Coelidini	
Coeloides pissodis	219,246
Coeloides scolyticida	32,240
Subfamily Cardiochilinae	
Schoenlandella diaphaniae	154,186
Toxoneuron nigriceps	47,82,186,405
Subfamily Charmontinae	
Charmon extensor	49
Charmon gracilis	332
Charmon rufipes	49
Subfamily Cheloninae	
Adelius subfasiatus	346
Tribe Chelonini	
Ascogaster quadridentata	47,159,428
Ascogaster reticulatus	47,175,267
Chelonus asiaticus	156
Chelonus blackburni	59
Chelonus curvimaculata	47,59,169
Chelonus heliopae	47,48
Chelonus inanitus	47
Chelonus insularis	7,179,224,252,256,283
Chelonus curvimaculatus	59
Chelonus texanus	47,372
Tribe Phanerotomini	
Phanerotoma flavistestacea	75
Subfamily Doryctinae	
Tribe Doryctini	
Dendrosoter protuberans	47,144,242,425
Doryctes mutillator	49
Doryctes undulatus	49
Tribe Hecabolini	

Taxonomy	**35**
Stenocorse bruchivora	38,192
Tribe Heterospilini	
Heterospilus coffeicola	47,274
Heterospilus prosopidis	30,32,210,218,274,390,391
Tribe Spathiini	
Spathius benefactor	148
Spathius brevicaudis	236,242
Subfamily Euphorinae	
Tribe Centistini	
Pygostolus falcatus	47,245
Tribe Dinocampini	
Dinocampus coccinellae	23,81,221
Tribe Euphorini	
Microcotonus aethiopoides	21,23,132,133,183,205,206,209,220
Microcotonus caudatus	230
Microcotomus colesi	209
Microcotonus hyperodae	20,47,132,250
Tribe Perilitini	
Meteorus arizonensis	371
Meteorus brevicauda	341
Meteorus campestris	47,146
Meteorus leviventris	253
Meteorus trachynotus	239,269,285,334
Subfamily Exothecinae	
Colastes braconius	137,340
Exothecus braconius	346
Phanomeris catenator	312,340
Phanomeris dimidiata	346
Phanomeris laevis	312,340
Phanomeris phyllotomae	84,312
Subfamily Gnamptodontinae	
Gnamptodon pumilio	346
Subfamily Helconinae	
Tribe Brachistini	
Eubazus semirugosius	32
Triaspis pallipes	346
Triaspis thoracicus	378
Tribe Diospilini	
Apsicolpus hudsoni	411
Baeacis abietis	49
Diospilus capito	52
Diospilus hiator	245
Subfamily Homolobinae	
Homolobus truncator	324
Subfamily Hormiinae	
Tribe Hormiini	
Hormius moniliatus	299
Hormius vulgaris	166
Subfamily Ichneutinae	
Tribe Ichenutini	
Ichneutes levis	311
Ichneutes pikonematis	382
Subfamily Macrocentrinae	
Macrocentrus ancylivorus	114
Macrocentrus cingulum	92
Macrocentrus iridescens	25,239,398
Macrocentrus nigridorsis	225,398

Taxonomy	**35**
Subfamily Microgasterinae	
Tribe Apantelini	
Apanteles ater	47,246,348,399
Apanteles carpatus	153,154,348
Apanteles corvinus	348
Apanteles fumiferanae	47,145,270,271,272,332,348
Apanteles galleriae	154,160,394
Apanteles milleri	145,192
Apanteles morrisi	56,192,269
Apanteles subandinus	47,178,348
Apanteles syleptae	47,288
Dolichogenidea evonymellae	122
Dolichogenidea absona	56,192,332,348
Pholetesor circumscriptus	159,346,348
Pseudapanteles dignus	47,348
Tribe Cotesiini	
Cotesia congregata	28,47,153,328,348,369
Cotesia euphydryidis	348,366
Cotesia flavipes	21,47,159,276,348
Cotesia glomerata	119,121,141,152,199,223,245,281,282,289,290,329,348,409
Cotesia jucunda	380
Cotesia kariyai	379
Cotesia kazak	386
Cotesia marginiventris	15,47,177,200,252,387
Cotesia medicaginis	154
Cotesia melanoscelus	47,159,348
Cotesia melitaearum	222,263
Cotesia ocneriae	172
Cotesia phobetri	371
Cotesia rubecula	50,87,119,129,154,245,348,409
Cotesia schizurae	3,348
Cotesia scitula	57
Cotesia vestalis	118,136,154,184
Cotesia yakutatensis	253,348
Glyptapanteles militaris	179
Glyptapanteles porthetriae	172,284
Protapanteles immunis	380
Tribe Microgastrini	
Choeras tedellae	47,166
Choeras tiro	47,245
Microgaster hospes	285
Microgaster tibialis	32,47
Tribe Microplitini	
Microplitis alaskensis	253
Microplitis croceipes	47,82,154,385
Microplitis demolitor	153,163,244,306
Microplitis mediator	13,47,151,154,279,305,379
Microplitis naenia	279
Microplitis ocellatae	279
Microplitis plutellae	47,315,425
Microplitis rufiventris	47,154,162,208,374
Microplitis tuberculifera	154
Subfamily Microtypinae	
Microtypus species	166
Microtypus wesmaelii	344
Subfamily Micracinae	
Mirax minuta	47,168

Taxonomy	**35**
Mirax rufilabris	346
Subfamily Opiinae	
Biosteres arisanus	364
Biosteres melleus	105
Biosteres vandenboschii	313,365
Diachasmimorpha kraussi	330
Diachasmimorpha longicaudata	90,91,229,251,314,356,357,358
Diachasmimorpha tryoni	90,314,358
Doryctobracon areolatus	6,229,356
Doryctobracon crawfordi	6,229
Fopius arisanus	19,27,229,319
Opius canaliculatus	2,310
Opius dissitus	154
Opius lectus	105
Opius magnus	173
Opius rhagoleticola	173
Opius striatriventris	241
Psyttalia incisi	314,330
Utetes anastrephae	6,229,356
Subfamily Braconidae	
Tribe Orgilini	
Orgilus comptanae	285
Orgilus lepidus	32,47,178
Subfamily Pambolinae	
Tribe Chremylini	
Cedria paradoxa	32
Subfamily Rhysipolinae	
Rhysipolis decorator	340
Rhysipolis hariolator	340
Rhysipolis mediator	340
Subfamily Rhyssalinae	
Tribe Rhyssalini	
Oncophanes americanus	25,226,285
Oncophanes laevigatus	340
Subfamily Rogadinae	
Tribe Clinocentrini	
Clinocentrus gracilpes	339
Clinocentrus species	227
Tribe Rogadini	
Aleiodes circumscriptus	49,340
Aleiodes gastritor	159,345,380,416
Aleiodes nolophanae	300
Aleiodes praetor	186,340
Pelecystoma harrisinae	47,340
Rogas malacosomatos	247
Rogas stigmator	57,247
Family Ichneumonidae	
Subfamily Acaenitinae	
Acaenitus dubiator	32,108,147,211,342
Phaenolobus terebrator	109,211
Subfamily Adelognathinae	110,381
Adelognathus species	110
Adelognathus brevicornis	110
Adelognathus granulatus	110
Adelognathus laevicollis	110
Adelognathus pusillus	110
Subfamily Agriotypinae	

Taxonomy	**35**
Agriotypus armatus	36,47,98,99,295
Agriotypus changbaishanus	36
Agriotypus chaoi	36
Agriotypus gracilis	36,98
Agriotypus himalensis	36,98
Agriotypus jilinensis	36
Agriotypus kambaitensis	36
Agriotypus lui	36
Agriotypus maculiceps	36
Agriotypus masneri	36
Agriotypus silvestris	36
Agriotypus succinctus	36
Agriotypus tangi	36
Agriotypus townesi	36
Agriotypus zhejiangensis	36
Agriotypus zhengi	36
Subfamily Anomaloninae	
Tribe Gravenhorstiini	
Agrypon flaveolatum	24,94,102,126,156,191,237,238
Parania prima	120
Subfamily Banchinae	
Tribe Atrophini	
Diradops bethunei	3,375
Lissonota dubia	265
Tribe Banchini	
Banchus flavescens	12,13,47,244,391,392,420,421,422
Tribe Glyptini	
Glypta fumiferanae	47,146,232,239,268,269,272,278,306,331,333,362
Subfamily Campopleginae	
Bathypectes group	
Bathyplectes anurus	26,85,149,209,299
Bathyplectes contracta	80
Bathyplectes curculionis	85,101,130,149,159,209
Bathyplectes stenostigma	85
Dusona group	
Campoletis flavicincta	7,154,174,371
Campoletis grioti	15,16
Campoletis sonorensis	154
Campoplex cursitans	265
Campoplex frustranae	114
Campoplex punctulatus	212
Diadegma chrysostictos	107,154
Diadegma insulare	47,112,113,119,184,193,194,195,196,243,257,258,290,314,328,350, 358,423
Diadegma semiclausum	47,113,118,195,410
Dusona contumax	415
Eriborus terebrans	123
Eriborus trochanteratus	155
Hyposoter didymator	385
Hyposoter exiguae	55,104,151,152,154,192,252,380,383
Hyposoter fugitivus	154
Hyposoter horticola	222
Lathrostizus euurae	72
Phaedroctonus moderator	49
Phobocampe bicingulata	379
Phobocampe lymantriae	172
Phobocampe pallida	3

Taxonomy	**35**
Tranosema pedella	84
Tranosema rostrale	47,56,154
Venturia canescens	29,111,135,151,154,155,158,164,203,312,317,353
Gonotypus group	
Gonotypus melanostoma	319
Tribe Campoplegini	
Sinophorus crassifemur	14,47,231
Sinophorus megalodontis	14,231
Sinophorus rhyacioniae	2,77
Subfamily Collyriinae	
Collyria coxator	32,109,308
Subfamily Cremastinae	
Eiphosoma vitticolle	15
Pristomerus rufiabdominalis	123
Pristomerus vulnerator	32,122,123,124
Trathala flavoorbitalis	47,154,354
Trathala species	75
Subfamily Cryptinae	
Tribe Cryptini	
Agrothereutina group	
Agrothereutes lanceolatus	395,396
Agrothereutes minousubae	348
Agrothereutes abbreviatus	84
Agrothereutes tunetanus	47,308
Gambrus ultimus	57,73,284
Hoplocryptus signatorius	76
Gabuniina group	
Xanthocryptus novozealandicus	410
Mesostenina group	
Mesostenus gracilis	203
Sphecophagina group	
Sphecophaga vesparum	10,22,388
Tribe Hemigasterini	
Pleolophus larvicola	47,307
Pleolophus indistinctus	47,307,381
Tribe Phygadeuontini	
Acrolytina group	
Sozites kerichoensis	35,47,207
Endaseina group	
Endasys subclavatus	307
Gelina group	
Gelis acarorum	222
Gelis agilis	222,263,281
Gelis tenellus	126,127,145,365,429
Matrina group	
Mastrus ridibundus	40,41
Phygadeuontina group	
Phygadeuon elegans	173
Phygadeuon exiguus	173
Phygadeuon wiesmanni	143,173
Subfamily Ctenopelmatinae	
Tribe Ctenopelmatini	
Homaspis interruptus	14,231
Tribe Mesoleini	
Lamachus eques	310
Tribe Perilissini	
Lathrolestes ensator	403,427,428

Taxonomy	**35**
Lathrolestes luteolator	310
Lathrolestes nigricollis	87,117,311
Lophyroplectus oblongopunctatus	185,231
Subfamily Diplazontinae	
Diplazon laetatorius	47,81,308,324,325
Diplazon pectoratorius	325
Diplazon tetragonus	77,325
Diplazon tibiatorius	77,325
Enizemum ornatum	77,81,245,324,325
Syrphophilus trinctorius	77,324,325
Subfamily Eucerotinae	
Euceros albitarsus	109
Euceros frigidus	307,308
Subfamily Ichneumoninae	
Tribe Alomyini	
Diadromus pulchellus	17,33,34,42,43,44,301,317,321,327
Dirophanes hariolus	145
Dirophanes maculicornis	47,56,239,333
Tycherus nigridens	47
Tycherus osculator	417
Tribe Ichneumonini	
Cratichneumon sublatus	3
Ichneumon caloscelis	32
Ichneumon gracilicornis	222
Tribe Mesoleiini	
Mesoleius species	381
Olesicampe melanogaster	315,382
Olesicampe geniculata	159,315,316,416
Olesicampe macellator	167
Olesicampe monticola	14,45,47,228
Subfamily Labeninae	
Tribe Groteini	
Grotea angunia	32
Subfamily Mesochorinae	
Mesochorus agilis	101
Stictopisthus laticeps	345
Subfamily Metopiinae	
Exochus nigripalpis tectulum	56,95,146
Triclistus crassus	126
Triclistus emarginalus	83
Triclistus podagricus	292,417
Triclistus species	292,417
Triclistus xylostellae	25
Subfamily Neorhacodinae	
Neorhacodes enslini	76,109
Subfamily Ophioninae	
Ophion flavidus	16,140,147,174,323
Ophion parvulus	185
Subfamily Orthopelmatinae	
Orthopelma mediator	32,369
Orthopelma species	349
Subfamily Pimplinae	
Lytarmes maculipennis	93
Tribe Delomeristini	
Perithous divinator	76,245
Tribe Ephialtini	
Acrodactyla degener	344

Taxonomy	**35**
Apechthis ontario	56,145,239,268
Calliephialtes notanda	326
Exeristes comstockii	31,49,114
Exeristes roborator	219,411,412
Liotryphon strobilellae	49
Polysphincta tuberosa	47,344
Scambus foliae	84
Scambus atrocoxalis	49
Scambus brevicornis	47,226,259,319
Scambus canadensis	170
Scambus capitator	49
Scambus hispae	73,95,114
Sericopimpla sericata	47,349
Schiizopyga frigida	47,344
Zatypota albicoxa	47,344
Zatypota bohemani	47,344
Zatypota percontatoria	47,344
Tribe Pimplini	
Itoplectis conquisitor	11,57,73,95,180,181,202,219,239,269,284,317,325,358,387,412,413
Itoplectis maculator	49,409
Itoplectis naranyae	394
Itoplectis quadricingulata	146,226,277,331
Pimpla turionellae	46,47,53,54,128,202,293,294,317,330,374,409,414
Theronia atalantae	73,172
Subfamily Poemiinae	
Pseudorhyssa sternata	360
Subfamily Rhyssinae	
Megarhyssa atrata	161,275
Rhyssa persuasoria	32,47,78,359,360
Subfamily Stilbopinae	
Stilbops limneriaeformis	109,341
Stilbops ruficornis	32,109
Stilbops vetulus	109
Subfamily Tryphoninae	
Tribe Exenterini	
Exenterus abruptorius	47,310
Tribe Oedemopsini	
Oedemopsis scabricula	185
Tribe Phytodietini	
Netelia vinulae	185
Phytodietus fumiferanae	56,146,331,333
Tribe Tryphonini	
Grypocentrus albipes	86,117
Grypocentrus apicalis	311
Subfamily Xoridinae	
Xorides brachylabris	32
Xorides corcyrensis	47

Appendix 6: Taxonomy for the Ichneumonoidea

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
Braconidae	Agathidinae	Agathidini		*Agathis*	*anglica*
					artemesiana
					asteris
					breviseta
					calcarata
					gibbosa
					laticincta
					unicolorata
				Baeognatha	*armeniaca*
					nigra
				Bassus	*arthurellus*
				Cremnops	*desetor*
				Earinus	*elator*
					gloriatorius
					limitaris
					transversus
					zeirapherae
				Microdus	*dimidiator*
					pumilus
					rufipes
					tumidulus
	Alysiinae	Alysiini		*Alysia*	*manducator*
				Aphaereta	*apicalis*
					aotea
					colei
					genevensis
					lonchaeae
					minuta
					pallipes
				Asobara	*rufescens*

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Asobara	*tabida*
				Chasmodon	*apterus*
		Dacnusini		*Dacnusa*	*areolaris*
					sibirica
	Aphidiinae	Aphidiini		*Aphidius*	*ervi*
					matricariae
					nigripes
					pisivorus
					rhopalosiphi
					smithi
					sonchi
				Diaeretiella	*rapae*
				Dyscritulus	*planiceps*
				Lysiphlebus	*fabarum*
					testaceipes
				Monoctonus	*paulensis*
				Trioxys	*complanatus*
		Ephredrini		*Ephedrus*	*californicus*
					plagiator
		Praini		*Praon*	*exsoletum*
					pequodorum
					volucre
	Blacinae	Blacini		*Blacus*	*exilis*
					koenigi
					nigricornis
	Braconinae	Braconini		*Alienoclypeus*	*insolitus*
				Bracon	*cajani*
					cephi
					gelechiae
					lissogaster
					kirkpatricki
					mellitor

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Bracon	*pineti*
					rhyacioniae
					thurberiphagae
				Habrobracon	*hebetor*
					lineatellae
				Stenobracon	*deesae*
		Coelidini		*Coeloides*	*pissodis*
					scolyticida
	Cardiochilinae			*Schoenlandella*	*diaphaniae*
				Toxoneuron	*nigriceps*
	Charmontinae			*Charmon*	*extensor*
					gracilis
					rufipes
	Cheloninae			*Adelius*	*subfasiatus*
		Chelonini		*Ascogaster*	*quadridentata*
					reticulatus
				Chelonus	*asiaticus*
					blackburni
					curvimaculata
					heliopae
					inanitus
					insularis
					curvimaculatus
					texanus
		Phanerotomini		*Phanerotoma*	*flavistestacea*
	Doryctinae	Doryctini		*Dendrosoter*	*protuberans*
				Doryctes	*mutillator*
					undulatus
		Hecabolini		*Stenocorse*	*bruchivora*
		Heterospilini		*Heterospilus*	*coffeicola*
					prosopidis
		Spathiini		*Spathius*	*benefactor*

Family	Subfamily	Tribe	Group	Genus	Species
				Spathius	*brevicaudis*
	Euphorinae	Centistini		*Pygostolus*	*falcatus*
		Dinocampini		*Dinocampus*	*coccinellae*
		Euphorini		*Microcotonus*	*aethiopoides*
					caudatus
					colesi
					hyperodae
		Perilitini		*Meteorus*	*arizonensis*
					brevicauda
					campestris
					leviventris
					trachynotus
	Exothecinae			*Colastes*	*braconius*
				Exothecus	*braconius*
				Phanomeris	*catenator*
					dimidiata
					laevis
					phyllotomae
	Gnamptodontinae			*Gnamptodon*	*pumilio*
	Helconinae	Brachistini		*Eubazus*	*semirugosius*
				Triaspis	*pallipes*
					thoracicus
		Diospilini		*Apsicolpus*	*hudsoni*
				Baeacis	*abietis*
				Diospilus	*capito*
					hiator
	Homolobinae			*Homolobus*	*truncator*
	Hormiinae	Hormiini		*Hormius*	*moniliatus*
					vulgaris
	Ichneutinae	Ichenutini		*Ichneutes*	*levis*
					pikonematis
	Macrocentrinae			*Macrocentrus*	*ancylivorus*

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Macrocentrus	*cingulum*
					iridescens
					nigridorsis
	Microgasterinae	Apantelini		*Apanteles*	*ater*
					carpatus
					corvinus
					fumiferanae
					galleriae
					milleri
					morrisi
					subandinus
					syleptae
				Dolichogenidea	*absona*
					evonymellae
				Pholetesor	*circumscriptus*
				Pseudapanteles	*dignus*
		Cotesiini		*Cotesia*	*congregata*
					euphydryidis
					flavipes
					glomerata
					jucunda
					kariyai
					kazak
					marginiventris
					medicaginis
					melanoscelus
					melitaearum
					ocneriae
					phobetri
					rubecula
					schizurae
					scitula

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
					vestalis
					yakutatensis
				Glyptapanteles	*militaris*
					porthetriae
				Protapanteles	*immunis*
		Microgastrini		*Choeras*	*tedellae*
					tiro
				Microgaster	*hospes*
					tibialis
		Microplitini		*Microplitis*	*alaskensis*
					croceipes
					demolitor
					mediator
					naenia
					ocellatae
					plutellae
					rufiventris
					tuberculifera
	Microtypinae			*Microtypus*	species
					wesmaelii
	Micracinae			*Mirax*	*minuta*
					rufilabris
	Opiinae			*Biosteres*	*arisanus*
					melleus
					vandenboschii
				Diachasmimorpha	*kraussi*
					longicaudata
					tryoni
				Doryctobracon	*areolatus*
					crawfordi
				Fopius	*arisanus*
				Opius	*canaliculatus*

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Opius	*dissitus*
					lectus
					magnus
					rhagoleticola
					striatriventris
				Psyttalia	*incisi*
				Utetes	*anastrephae*
	Braconidae	Orgilini		*Orgilus*	*comptanae*
					lepidus
	Pambolinae	Chremylini		*Cedria*	*paradoxa*
	Rhysipolinae			*Rhysipolis*	*decorator*
					hariolator
					mediator
	Rhyssalinae	Rhyssalini		*Oncophanes*	*americanus*
					laevigatus
	Rogadinae	Clinocentrini		*Clinocentrus*	*gracilpes*
					species
		Rogadini		*Aleiodes*	*circumscriptus*
					gastritor
					nolophanae
					praetor
				Pelecystoma	*harrisinae*
				Rogas	*malacosomatos*
					stigmator
Ichneumonidae	Acaenitinae			*Acaenitus*	*dubiator*
				Phaenolobus	*terebrator*
	Adelognathinae			*Adelognathus*	species
					brevicornis
					granulatus
					laevicollis
					pusillus
	Agriotypinae			*Agriotypus*	*armatus*

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Agriotypus	*changbaishanus*
					chaoi
					gracilis
					himalensis
					jilinensis
					kambaitensis
					lui
					maculiceps
					masneri
					silvestris
					succinctus
					tangi
					townesi
					zhejiangensis
					zhengi
	Anomaloninae	Gravenhorstiini		*Agrypon*	*flaveolatum*
				Parania	*prima*
	Banchinae	Atrophini		*Diradops*	*bethunei*
				Lissonota	*dubia*
		Banchini		*Banchus*	*flavescens*
		Glyptini		*Glypta*	*fumiferanae*
	Campopleginae		*Bathyplectes*	*Bathyplectes*	*anurus*
					contracta
					curculionis
					stenostigma
			Dusona	*Campoletis*	*flavicincta*
					grioti
					sonorensis
				Campoplex	*cursitans*
				Campoplex	*frustranae*
				Campoplex	*punctulatus*
				Diadegma	*chrysostictos*

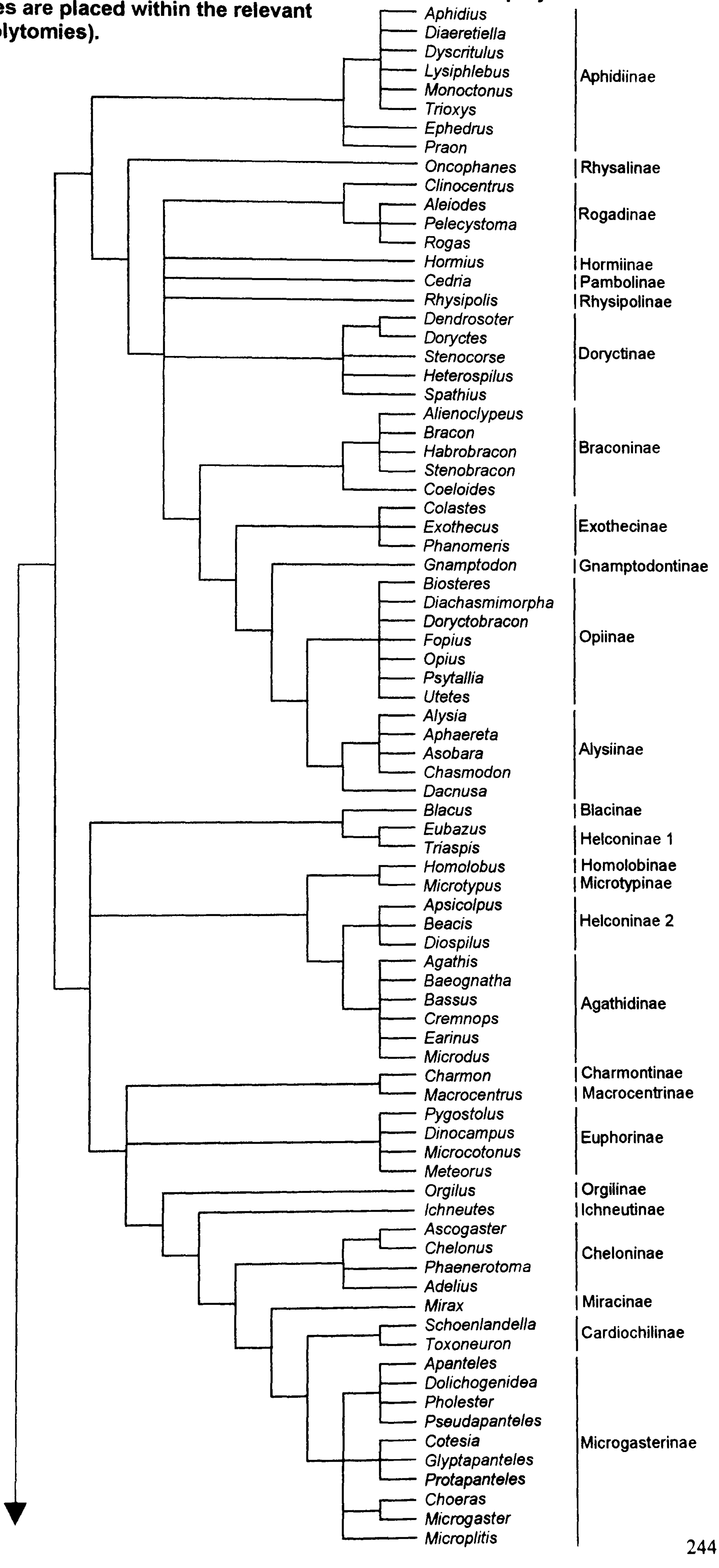
Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Diadegma	*insulare*
					semiclausum
				Dusona	*contumax*
				Eriborus	*terebrans*
					trochanteratus
				Hyposoter	*didymator*
					exiguae
					fugitivus
					horticola
				Lathrostizus	*euurae*
				Phaedroctonus	*moderator*
				Phobocampe	*bicingulata*
					lymantriae
					pallida
				Tranosema	*pedella*
					rostrale
				Venturia	*canescens*
			Gonotypus	*Gonotypus*	*melanostoma*
		Campoplegini		*Sinophorus*	*crassifemur*
					megalodontis
					rhyacioniae
	Collyriinae			*Collyria*	*coxator*
	Cremastinae			*Eiphosoma*	*vitticolle*
				Pristomerus	*rufiabdominalis*
					vulnerator
				Trathala	*flavoorbitalis*
				Trathala	species
	Cryptinae	Cryptini	*Agrothereutina*	*Agrothereutes*	*abbreviatus*
					lanceolatus
					minousubae
					tunetanus
				Gambrus	*ultimus*

Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Hoplocryptus	*signatorius*
			Gabuniina	*Xanthocryptus*	*novozealandicus*
			Mesostenina	*Mesostenus*	*gracilis*
			Sphecophagina	*Sphecophaga*	*vesparum*
		Hemigasterini		*Pleolophus*	*larvicola*
					indistinctus
		Phygadeuontini	*Acrolytina*	*Sozites*	*kerichoensis*
			Endaseina	*Endasys*	*subclavatus*
			Gelina	*Gelis*	*acarorum*
				Gelis	*agilis*
				Gelis	*tenellus*
			Matrina	*Mastrus*	*ridibundus*
			Phygadeuontina	*Phygadeuon*	*elegans*
					exiguus
					wiesmanni
	Ctenopelmatinae	Ctenopelmatini		*Homaspis*	*interruptus*
		Mesoleini		*Lamachus*	*eques*
		Perilissini		*Lathrolestes*	*ensator*
					luteolator
					nigricollis
				Lophyroplectus	*oblongopunctatus*
	Diplazontinae			*Diplazon*	*laetatorius*
					pectoratorius
					tetragonus
					tibiatorius
				Enizemum	*ornatum*
				Syrphophilus	*trinctorius*
	Eucerotinae			*Euceros*	*albitarsus*
					frigidus
	Ichneumoninae	Alomyini		*Diadromus*	*pulchellus*
				Dirophanes	*hariolus*
					maculicornis

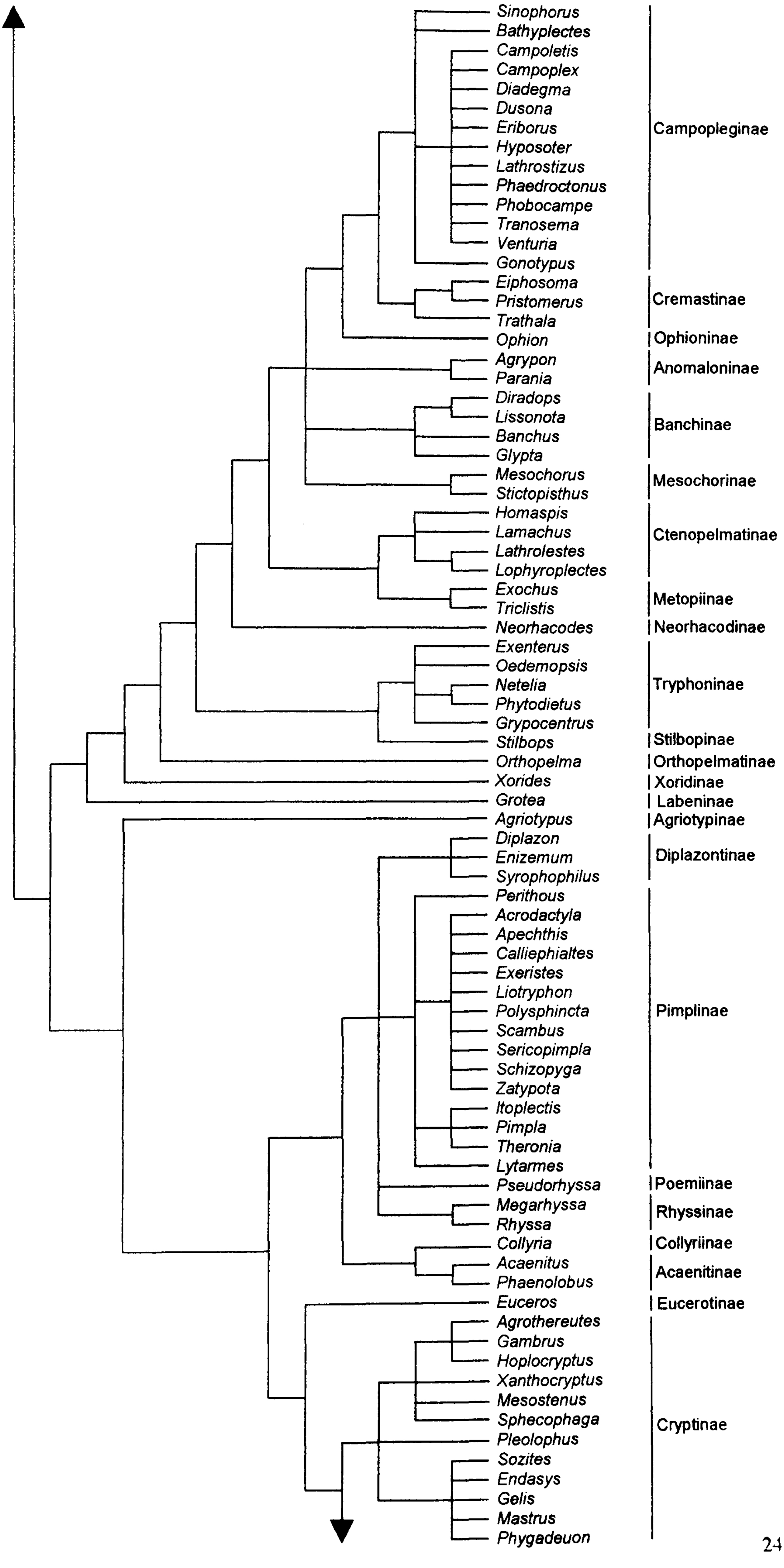
Family	**Subfamily**	**Tribe**	**Group**	**Genus**	**Species**
				Tycherus	*nigridens*
					osculator
		Ichneumonini		*Cratichneumon*	*sublatus*
				Ichneumon	*caloscelis*
					gracilicornis
		Mesoleiini		*Mesoleius*	species
				Olesicampe	*geniculata*
					macellator
					melanogaster
					monticola
	Labeninae	Groteini		*Grotea*	*angunia*
	Mesochorinae			*Mesochorus*	*agilis*
				Stictopisthus	*laticeps*
	Metopiinae			*Exochus*	*nigripalpis tectulum*
				Triclistus	*crassus*
					emarginalus
					podagricus
					species
					xylostellae
	Neorhacodinae			*Neorhacodes*	*enslini*
	Ophioninae			*Ophion*	*flavidus*
					parvulus
	Orthopelmatinae			*Orthopelma*	*mediator*
					species
	Pimplinae			*Lytarmes*	*maculipennis*
		Delomeristini		*Perithous*	*divinator*
		Ephialtini		*Acrodactyla*	*degener*
				Apechthis	*ontario*
				Calliephialtes	*notanda*
				Exeristes	*comstockii*
					roborator
				Liotryphon	*strobilellae*

Family	Subfamily	Tribe	Group	Genus	Species
				Polysphincta	*tuberosa*
				Scambus	*foliae*
					atrocoxalis
					brevicornis
					canadensis
					capitator
					hispae
				Sericopimpla	*sericata*
				Schiizopyga	*frigida*
				Zatypota	*albicoxa*
					bohemani
					percontatoria
		Pimplini		*Itoplectis*	*conquisitor*
					maculator
					naranyae
					quadricingulata
				Pimpla	*turionellae*
				Theronia	*atalantae*
	Poemiinae			*Pseudorhyssa*	*sternata*
	Rhyssinae			*Megarhyssa*	*atrata*
				Rhyssa	*persuasoria*
	Stilbopinae			*Stilbops*	*limneriaeformis*
					ruficornis
					vetulus
	Tryphoninae	Exenterini		*Exenterus*	*abruptorius*
		Oedemopsini		*Oedemopsis*	*scabricula*
		Phytodietini		*Netelia*	*vinulae*
				Phytodietus	*fumiferanae*
		Tryphonini		*Grypocentrus*	*albipes*
					apicalis
		Xoridinae		*Xorides*	*brachylabris*
					corcyrensis

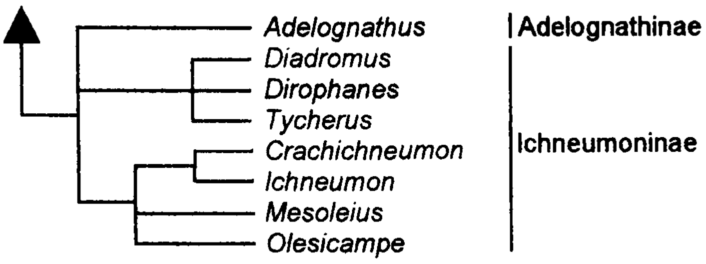
Appendix 7: Part 1. Braconidae – composite (all polytomies are soft polytomies – individual species are placed within the relevant genus as soft polytomies).



Appendix 7: Part 2a. Ichneumonidae – composite cladogram (soft polytomies; species within genus as soft polytomies).



Appendix 7: Part 2b. Ichneumonidae – composite cladogram (soft polytomies; species within genus as soft polytomies).



Appendix 8: Reference list for the Ichneumonoidea data set

1. Aalbersberg, Y.K., van der Westhuizen, M.C. & Hewitt, P.H. 1988. Natural enemies and their impact on *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae) populations. *Bulletin of Entomological Research.* 78: 111-120.

2. AliNiazee, M.T. 1985. Opiine parasitoids (Hymenoptera: Braconidae) of *Rhagoletis pomonella* and *R. zephyria* (Diptera: Tephritidae) in the Willamette Valley, Oregon. *Canadian Entomologist.* 117: 163-166.

3. Allen, D.C. 1972. Insect parasites of the saddled prominent, *Heterocampa guttivitta* (Lepidoptera: Notodontidae), in the northeastern United States. *Canadian Entomologist.* 104: 1609-1622.

4. van Alphen, J.J.M. & Janssen, A.R.M. 1982. Host selection by *Asobara tabida* Nees (Braconidae; Alysiinae) a larval parasitoid of fruit inhabiting *Drosophila* species. II. Host species selection. *Netherlands Journal of Zoology.* 32: 194-214.

5. Altson, A.M. 1920. The life-history and habits of two parasites of blowflies. *Proceedings of the Zoological Society (London).* 1920: 195-243.

6. Aluja, M., Lopez, M. & Sivinski, J. 1998. Ecological evidence for diapause in four native and one exotic species of larval-pupal fruit fly (Diptera: Tephritidae) parasitoids in tropical environments. *Annals of the Entomological Society of America.* 91: 821-833.

7. Alvarado-Rodriguez, B. 1987. Parasites and disease associated with larvae of beet armyworm *Spodoptera exigua* (Lepidoptera: Noctuidae), infesting processing tomatoes in Sinaloa, Mexico. *Florida Entomologist.* 70: 444-449.

8. Antolin, M.F., Ode, P.J. & Strand, M.R. 1995. Variable sex ratios and ovicide in an outbreeding parasitic wasp. *Animal Behaviour.* 49: 589-600.

9. Antolin, M.F. & Strand, M.R. 1992. Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). *Ecological Entomology.* 17: 1-7.

10. Archer, M.E. 1985. Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. *Journal of Animal Ecology.* 54: 473-485.

11. Arthur, A.P. 1966. Associative learning in endoparasitoid *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Canadian Entomologist.* 98: 213-223.

12. Arthur, A.P. & Mason, P.G. 1985. The life-history and immature stages of *Banchus flavescens* (Hymenoptera: Ichneumonidae), a parasitoid of the bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae) in western Canada. *Canadian Entomologist.* 117: 1249-1255.

13. Arthur, A.P. & Mason, P.G. 1986. Life history and immature stages of the parasitoid *Microplitis mediator* (Hymenoptera: Braconidae), reared on the bertha armyworm *Mamestra configurata* (Lepidoptera: Noctuidae). *Canadian Entomologist.* 118: 487-491.

14. Asaro, C. & Allen, D.C. 1999. Biology of pine false webworm (Hymenoptera: Pamphilidae) during an outbreak. *Canadian Entomologist.* 131: 729-742.

15. Ashley, T.R. 1983. Growth pattern alterations in fall armyworm, *Spodoptera frugiperda*, larvae after parasitization by *Apanteles marginiventris, Campoletis grioti, Chelonus insularis,* and *Eiphosoma vitticole. Florida Entomologist.* 66: 260-266.

16. Ashley, T.R. 1986. Geographical distributions and parasitization levels of the fall armyworm, *Spodoptera frugiperda. Florida Entomologist.* 69: 516-524.

17. Auger, J., Lecomte, C., Paris, J. & Thibout, E. 1989. Identification of leek-moth and diamondback-moth frass volatiles that stimulate the parasitoid, *Diadromus pulchellus*. *Journal of Chemical Ecology*. 15: 1391-1398.

18. Bai, B. & Mackauer, M. 1992. Influence of superparasitism development rate and adult size in a solitary parasitoid wasp, *Aphidius ervi*. *Functional Ecology*. 6: 302-307.

19. Baranowski, R., Glenn, H. & Sivinski, J. 1993. Biological control of the Caribbean fruit fly (Diptera: Tephritidae). *Florida Entomologist*. 76: 245-251.

20. Barker, G.M. & Addison, P.J. 1996. Influence of clavicipitaceous endophyte infection in ryegrass on development of he parasitoid *Microctonus hyperodae* Loan (Hymen.: Brac.) in *Listronotus bonariensis* (Kuschal) (Coleoptera: Curculionidae). *Biological Control*. 7: 281-287.

21. Barlow, N.D. & Goldson, S.L. 1993. A modelling analysis of the successful biological control of *Sitona discoideus* (Coleoptera: Curculionidae) by *Microctonus aethiopoides* (Hymenoptera: Braconidae) in New Zealand. *Journal of Applied Ecology*. 30: 165-178.

22. Barlow, N.D., Moller, H. & Beggs, J.R. 1996. A model for the effect of *Sphecophaga vesparum vesparum* as a biological control agent of the common wasp in New Zealand. *Journal of Applied Ecology*. 33: 31-44.

23. Barratt, B.I.P & Sutherland, M. 2001. Development of teratocytes associated with *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) in natural and novel host species. *Journal of Insect Physiology*. 47: 257-262.

24. Barron, J.R. 1989. Status of the parasite *Agrypon flaveolatum* (Gravenhorst) (Hymenoptera, Ichneumonidae), introduced to control the winter moth in Nova Scotia and British Colombia. *Canadian Entomologist*. 121: 11-26.

25. Barron, J.R. & Bisdee, H.E. 1984. Hymenopterous parasites with lepidopterous and sawfly hosts on *Ionicera* (honeysuckle) in the Ottawa area. *Canadian Entomologist*. 116: 1345-1356.

26. Bartell, D.P. & Pass, B.C. 1980. Morphology, development, and behaviour of the immature stages of the parasite *Bathyplectes anurus* (Hymenoptera: Ichneumonidae). *Canadian Entomologist*. 112: 481-487.

27. Bautista, R.C., Mochizuki, N., Spencer, J.P., Harris, E.J. & Ichimura, D.M. 1999. Mass-rearing of the Tephritid fruit fly parasitoid *Fopius arisanus* (Hymenoptera: Braconidae). *Biological Control*. 15: 137-144.

28. Beckage, N.E. & Riddiford, L.M. 1978. Developmental interactions between the tobacco hornworm *Manduca sexta* and its braconid parasite *Apanteles congregatus*. *Entomologia Experimentalis et Applicata*. 23: 139-151.

29. Begon, M., Sait, S. & Thompson, D.J. 1995. Persistence of a parasitoid-host system: refuges and generation cycles? *Proceedings of the Royal Society of London, Series B*. 260: 131-137.

30. Bellows Jr., T.S. 1982. Simulation models for laboratory populations of *Callosobruchus chiensis* and *C. maculatus*. *Journal of Animal Ecology*. 51: 597-623.

31. Belmont, R.A. & Habeck, D.H. 1983. Parasitoids of *Dioryctria* spp. (Pyralidae: Lepidoptera) coneworms in slash pine seed production areas of North Florida. *Florida Entomologist*. 66: 399-407.

32. Belshaw, R., Grafen, A. & Quicke, D.L.J. 2003. Inferring life history from ovipositor morphology in parasitoid wasps using phylogenetic regression and discriminant analysis. *Zoological Journal of the Linnean Society*. 139: 213-228.

33. Bénédet, F., Bigot, Y., Renault, S., Pouzat, J. & Thibout, E. 1999. Polypeptides of *Acrolepiopsis assectella* cocoon (Lepidoptera: Yponomeutoidea): an external host-acceptance kairomone for the parasitoid *Diadromus pulchellus* (Hymenoptera: Ichneumonidae). *Journal of Insect Physiology*. 45: 375-384.

34. Bénédet, F., Leroy, T., Gauthier, N., Thibaudeau, C., Thibout, E. & Renault, S.2002. Gustatory sensilla sensitive to protein kairomones trigger host acceptance by an endoparasitoid. *Proceedings of the Royal Entomological Society of London, Series B*. 269; 1879-1886.

35. Benjamin, D.M. & Demba, W.M. 1968. Notes on the biology of three parasites of the eggs of *Entypotrachelus meyeri* Kolbe and *E. micans* (Hust. (Col., Curculionidae) laid on tea and *Cinchona*. *Bulletin of Entomological Research*. 59: 473-478.

36. Bennett, A.M.R. 2001. Phylogeny of Agriotypinae (Hymenoptera: Ichneumonidae), with comments on the subfamily relationships of the basal Ichneumonidae. *Systematic Entomology*. 26: 329-356.

37. Bennett, F.D. 1960. Parasites of *Ancylostomia stercorea* (Zell.) (Pyralidae, Lepidoptera) a pod borer attacking a pigeon pea in Trinidad. *Bulletin of Entomological Research*. 50 : 737-757.

38. Benrey, B., Callejas, A., Rios, L., Oyama, K. & Denno, R.F. 1998. The effects of domestication of *Brassica* and *Phaseolus* on the interaction between polyphagous insects and parasitoids. *Biological Control*. 11; 130-140.

39. Benson, J.F. 1973. Intraspecific competition in the population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae). *Journal of Animal Ecology*. 42: 105-124.

40. Bezemer, T.M. & Mills, N.J. 2001. Host density responses of *Mastrus ridibundus*, a parasitoid of the codling moth, *Cydia pomonella*. *Biological Control*. 22: 169-175.

41. Bezemer, T.M. & Mills, N.J. 2002. Clutch size decisions of a gregarious parasitoid under laboratory conditions. *Journal of Animal Ecology*. 66: 1119-1128.

42. Bigot, Y., Hamelin, M.-H. & Periquet, G. 1990. Heterochromatin condensation and evolution of unique satellite-DNA families in two parasitic wasp species: *Diadromus pulchellus* and *Eupelmus vuilleti* (Hymenoptera). *Molecular Biology and Evolution*. 7: 351-364.

43. Bigot, Y., Rabouille, A., Doury, G., Sizaret, P.-Y., Delbost, F., Hamelin, M.-H. & Periquet, G. 1997. Biological and molecular features of the relationships between *Diadromus pulchellus* ascovirus, a parasitoid hymenopteran wasp (*Diadromus pulchellus*) and its lepidopteran host, *Acrolepiopsis assectella*. *Journal of General Virology*. 78: 1149-1163.

44. Bigot, Y., Rabouille, A., Sizaret, P.-Y., Hamelin, M.-H. & Periquet, G. 1997. Particle and genomic characteristics of a new member of the *Ascoviridae*: *Diadromus pulchellus* ascovirus. *Journal of General Virology*. 78: 1139-1147.

45. Billany, D.J., Winter, T.G. & Gauld, I.D. 1985. *Olesicampe monticola* (Hedwig) (Hymenoptera: Ichneumonidae) redescribed together with notes on its biology as a parasite of *Cephalcia lariciphila* (Watchl) (Hymenoptera: Pamphilidae). *Bulletin of Entomological Research*. 75: 267-274.

46. Bin, F., Wäckers, F., Romani, R. & Isidoro, N. 1999. Tyloids in *Pimpla turionellae* (L.) are release structures of male antennal glands involved in courtship behaviour (Hymenoptera: Ichneumonidae). *International Journal of Insect Morphology*. 28: 61-68.

47. Blackbum, T.W. 1990. Comparative and experimental studies of animal life histories. Dphil Thesis, University of Oxford, Oxford.

48. Blackburn, T.M. 1991. A comparative examination of life-span and fecundity in parasitoid Hymenoptera. *Journal of Animal Ecology.* 60: 151-164.

49. Brockerhoff, E.G. & Kenis, M. 1996. Parasitoids associated with *Cydia strobilella* (L.) (Lepidoptera: Tortricidae) in Europe, and considerations for their use for biological control in North America. *Biological Control.* 6: 202-214.

50. Brodeur, J. & Vet, L.E.M. 1994. Usurpation of host behaviour by a parasitic wasp. *Animal Behaviour.* 48: 187-192.

51. Bryan, D.E., Jackson, C.G., Patana, R. & Neemann, E.G. 1971. Field cage and laboratory studies with *Bracon kirkpatricki*, a parasite of the pink bollworm. *Journal of Economic Entomology.* 64: 1236-1241.

52. Büchi, R. 2002. Mortality of pollen beetle (*Meligethes* spp.) larvae due to predators and parasitoids in rape fields and the effect of conservation strips. *Agriculture, Ecosystems and Environment.* 90: 253-263.

53. Büyükgüzel, K. 2001. DNA gyrase inhibitors: novobiocin enhances the survival of *Pimpla turionellae* (Hymenoptera: Ichneumonidae) larvae reared on an artificial diet but other antibiotics do not. *Journal of Applied Entomology.* 125: 583-587.

54. Büyükgüzel, K. 2001. Positive effects of some gyrase inhibitors on survival and development of *Pimpla turionellae* (Hymenoptera: Ichneumonidae) larvae reared on an artificial diet. *Journal of Economic Entomology.* 94: 21-26.

55. Campbell, B.C. & Duffey, S.S. 1981. Alleviation of α-Tomatine-induced toxicity to the parasitoid, *Hyposoter exiguae*, by phytosterols in the diet of the host, *Heliothis zea*. *Journal of Chemical Ecology.* 7: 927-946.

56. Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia.* 114: 236-242.

57. Cassini, J.R. 1985. Biology of *Simyria henrici* (Lepidoptera: Noctuidae) in south-west Florida. *Florida Entomologist.* 68: 645-652.

58. Chau, A. & Mackauer, M. 1999. Self-superparasitism in the solitary parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): proximate mechanisms. *Canadian Entomologist.* 131: 769-777.

59. Chiri, A.A. & Legner, E.F. 1986. Response of three *Chelonus* (Hymenoptera: Braconidae) species to kairomones in scales of six Lepidoptera. *Canadian Entomologist.* 118: 329-333.

60. Chow, F.J. & Mackauer, M. 1984. Inter- and intraspecific larval competition in *Aphidius smithi* and *Praon pequodorum* (Hymenoptera: Aphidiidae). *Canadian Entomologist.* 116: 1097-1107.

61. Chow, F.J. & Mackauer, M. 1986. Host discrimination and larval competition in the aphid parasite *Ephedrus californicus*. *Entomologia Experimentalis et Applicata.* 41: 243-254.

62. Chow, A. & Mackauer, M. 1991. Patterns of host selection by four species of aphidiid (Hymenoptera) parasitoids: influence of host switching. *Ecological Entomology.* 16: 403-410.

63. Chow, A. & Mackauer, M. 1999. Altered dispersal behaviour in parasitized aphids: parasitoid-mediated or pathology? *Ecological Entomology.* 24: 276-283.

64. Chow, A. & Mackauer, M. 1999. Host handling and specificity of the hyperparasitoid wasp, *Dendrocerus carpenteri* (Curtis) (Hym., Megaspilidae): importance of host age and species. *Journal of Applied Entomology.* 123: 83-91.

65. Cloutier, C., Duperron, J., Tertuliano, M. & McNeil, J.N. 2000. Host instar, body size and fitness in the koinobiotic parasitoid *Aphidius nigripes. Entomologia Experimentalis et Applicata.* 97: 29-40.

66. Cohen, M.B. & Mackauer, M. 1987. Intrinsic rate of increase and temperature coefficients of the aphid parasite *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae). *Canadian Entomologist.* 119: 231-237.

67. Cole, E.J. & Streams, F.A. 1970. Insects emerging from brown slime fluxes in southern new England. *Canadian Entomologist.* 102: 321-333.

68. Colfer, R.G. & Rosenheim, J.A. 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia.* 126: 292-304.

69. Collins, D.W. 1996. The separation of *Liriomyza huidobrensis* (Diptera; Agromyzidae) from related indigenous and non-indigenous species encountered in the United Kingdom using cellulose acetate electrophoresis. *Annals of Applied Biology.* 128: 387-398.

70. Cornelius, S.J. & Godfray, H.C.J. 1984. Natural parasitism of the chrysanthemum leaf-miner *Chromatomyia syngenesiae* H. (Diptera: Agromyzidae). *Entomophaga.* 29: 341-345.

71. Cossentine, J.E. & Jensen, L.B. 1995. *Orthosia hibisci* Guenée (Lepidoptera: Noctuidae): indigenous parasitoids and the impact of *Earinus limitarius* (Say) (Hymenoptera: Ichneumonidae) on its host feeding activity. *Canadian Entomologist.* 127: 473-477.

72. Craig, T.P., Itami, J.K. & Price, P.W. 1990. The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. *Ecology.* 71: 1471-1482.

73. Cronin, J.T. & Gill, D.E. 1989. The influence of host distribution, sex, and size on the level of parasitism by *Itoplectis conquisitor* (Hymenoptera: Ichneumonidae). *Ecological Entomology.* 14: 163-173.

74. Cross, W.H., McGovern, W.L. & Mitchell, H.C. 1969. Biology of *Bracon kirkpatricki* and field releases for control of the boll weevil. *Journal of Economic Entomology.* 62: 448-454.

75. Cruz, Y.P. 1986. The defender role of the precocious larvae of *Copidosomopsis tanytmemus* Caltagirone (Encyrtidae, Hymenoptera). *Journal of Experimental Zoology.* 237: 309-318.

76. Danks, H.V. 1970. Biology of some stem-nesting aculeate Hymenoptera. *Transactions of the Royal Entomological Society of London.* 122: 323-399.

77. Dasch, C.E. 1964. Ichneumon-flies of America north of Mexico 5. Subfamily Diplazontinae. *Memoirs of the American Entomological Institute.* 3: 1-304.

78. Davies, N.W. & Madden, J.L. 1985. Mandibular gland secretions of two parasitoid wasps (Hymenoptera: Ichneumonidae). *Journal of Chemical Ecology.* 11: 1115-1127.

79. Davis, A.J., Varley, M.E., Baker, R.H.A. & Hardy, I.C.W. 1996. Parasitoids of *Drosophila* in the British Isles. *The Entomologist.* 115: 1-13.

80. Day, W.H. 1969. Biological notes on *Dibrachys cavus*, a secondary parasite attacking parasites (*Bathyplectes* spp.) of he alfalfa weevil in the eastern United States. *Journal of Economic Entomology.* 62: 1225-1226.

81. Dean, G.J. 1983. Survival of some aphid (Hemiptera: Aphididae) predators with special reference to their parasites in England. *Bulletin of Entomological Research.* 73: 469-480.

82. De Moraes, C.M., Cortesero, A.M., Stapel, J.O. & Lewis, W.J. 1999. Intrinsic and extrinsic competitive interactions between two larval parasitoids of *Heliothis virescens*. *Ecological Entomology*. 24: 402-410.

83. Doganlar, M. & Beirne, B.P. 1980. Parasites of *Phyllonorycter elmaella* (Lepidoptera: Gracilariidae) on apple in the Vancouver district, British Columbia. *Canadian Entomologist*. 112: 314.

84. Dowden, P.R. 1941. Parasites of the birch leaf-mining sawfly (*Phyllotoma nemorata*). *Technical Bulletin of United States Department of Agriculture Washington D.C.* 757: 1-55.

85. Dowell, R. 1978. Ovary structure and reproductive biologies of larval parasitoids of the alfalfa weevil (Coleoptera: Curculionidae). *Canadian Entomologist*. 110: 507-512.

86. van Driesche, R.G., Childs, R., Casagrande, R.A. & Tewksbury, L. 1997. Establishment, distribution, and impact in southern New England of *Lathrolestes nigricollis* (Thomson) (Hymenoptera: Ichneumonidae), an introduced parasitoid of the birch leafminer, *Fenusa pusilla* (Lepeletier) (Hymenoptera: Tenthredinidae). *Canadian Entomologist*. 129: 601-611.

87. van Driesche, R.G. & Nunn, C. 2002. Establishment of a Chinese strain of *Cotesia rubecula* (Hymenoptera: Braconidae) in the northeastern United States. *Florida Entomologist*. 85: 386-388.

88. Driessen, G. & Bernstein, C. 1999. Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *Journal of Animal Ecology*. 68: 445-459.

89. Driessen, G., Bernstein, C., van Alphen, J.J.M. & Kacelnik, K.A. 1995. A count-down mechanism for host search in the parasitoid *Venturia canescens*. *Journal of Animal Ecology*. 64: 117-125.

90. Duan, J.J., Purcell, M.F. & Messing, R.H. 1997. Ovipositional responses of three opiinae fruit fly parasitoids (Hymenoptera: Braconidae) to gall-forming tephritids (Diptera: Tephritidae). *Biological Control*. 9: 81-88.

91. Duan, J.J., Ahmad, M., Joshi, K. & Messing, R.H. 1997. Evaluation of the impact of the fruit fly parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) on a nontarget Tephritid, *Eutreta xanthochaeta* (Diptera; Tephritidae). *Biological Control*. 8: 58-64.

92. Edwards, O.R. & Hopper, K.R. 1999. Using superparasitism by a stem borer parasitoid to infer a host refuge. *Ecological Entomology*. 24: 7-12.

93. Eggleton, P. 1990. Male reproductive behaviour of the parasitoid wasp *Lytarmes maculipennis* (Hymenoptera: Ichneumonidae). *Ecological Entomology*. 15: 357-360.

94. Eidt, D.C. & Embree, D.G. 1968. Distinguishing larvae and pupae of the winter moth *Operophtera brumata*, and the spruce spanworm *O. bruceata* (Lepidoptera: Geometridae). *Canadian Entomologist*. 100: 536-539.

95. Eisenbach, J. 1996. Three-trophic-level interactions in a cattail hybrid zone. *Oecologia*. 105: 258-265.

96. Ellers, J., Bax, M. & van Alphen, J.J.M. 2001. Seasonal changes in female size and its relation to reproduction in the parasitoid *Asobara tabida*. *Oikos*. 92: 309-314.

97. Ellers, J., van Alphen, J.J.M. & Sevenster, J.G. 1998. A field study of size-fitness relationships in the parasitoid *Asobara tabida*. *Journal of Animal Ecology*. 67: 318-324.

98. Elliot, J.M. 1982. The life cycle and spatial distribution of the aquatic parasitoid *Agriotypus armatus* (Hymenoptera: Agriotypidae) and its caddis host *Silo pallipes* (Trichoptera: Goeridae). *Journal of Animal Ecology*. 52: 923-941.

99. Elliot, J.M. 1983. The responses of the aquatic parasitoid *Agriotypus armatus* (Hymenoptera: Agriotypidae) to the spatial distribution and density of its caddis host *Silo pallipes* (Trichoptera: Goeridae). *Journal of Animal Ecology*. 52: 315-330.

100. Elliott, N.C., French, B.W., Reed, D.K., Burd, J.D. & Kindler, S.D. 1994. Host species effects on parasitization by a Syrian population of *Diaeretiella rapae* M'intosh (Hymenoptera: Aphidiidae). *Canadian Entomologist*. 126: 1515-1517.

101. Ellsbury, M.M. & Simpson, R.G. 1978. Biology of *Mesochorus agilis*, an indirect hyperparasite of *Bathyplectes curculionis*. *Annals of the Entomological Society of America*. 71: 865-868.

102. Embree, D.G. 1966. The role of introduced parasites in the control of the winter moth in Nova Scotia. *Canadian Entomologist*. 98: 1159-1168.

103. Eslin, P. & Prévost, G. 1998. Hemocyte load and immune resistance to *Asobara tabida* are correlated in species of the *Drosophila melanogaster* subgroup. *Journal of Insect Physiology*. 44: 807-816.

104. Farid, A., Johnson, J.B., Shafii, B. & Quisenberry, S.S. 1998. Tritrophic studies of Russian wheat aphid, a parasitoid, and resistant and susceptible wheat over three parasitoid generations. *Biological Control*. 12: 1-6.

105. Feder, J.L. 1995. The effects of parasitoids on sympatric host races of *Rhagoletis pomonella* (Diptera; Tephritidae). *Ecology*. 76: 801-813.

106. Ferrari, J., Müller, C.B., Kraaijeveld, A.R. & Godfray, H.C.J. 2001. Clonal variation and covariation in aphid resistance to parasitoids and a pathogen. *Evolution*. 55: 1805-1814.

107. Fischer, R.C. 1959. Life history and ecology of *Horogenes chrysosticos* Gmelin (Hymenoptera: Ichneumonidae), a parasite of *Ephesia sericarium* Scott (Lepidoptera: Phycitidae). *Canadian Journal of Zoology*. 37: 429-446.

108. Fitton, M.G. 1982. The British Acaenitinae (Hymenoptera: Ichneumonidae). *Entomologist's Gazette*. 32: 185-192.

109. Fitton, M.G. 1984. A review of the British Collyriinae, Eucerotinae, Stilbopinae and Neorhacodinae (Hymenoptera: Ichneumonidae). *Entomologist's Gazette*. 32: 185-224.

110. Fitton, M.G., Gauld, I.D. & Shaw, M.R. 1982. The taxonomy and biology of the British Adelognathinae (Hymenoptera: Ichneumonidae). *Journal of Natural History*. 16: 275-283.

111. Fletcher, J.P., Hughes, J.P. & Harvey, I.F. 1994. Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proceedings of the Royal Society of London, Series B*. 258: 163-167.

112. Fox, L.R. & Eisenbach, J. 1992. Contrary choices: possible exploitation of enemy-free space by herbivorous insects in cultivated versus wild crucifers. *Oecologia*. 89: 574-579.

113. Fox, L.R., Letourneau, D.K., Eisenbach, J. & van Nouhuys, S. 1990. Parasitism rates and sex ratios of a parasitoid wasp: effects of herbivore and plant quality. *Oecologia*. 83: 414-419.

114. Freeman, B.L. & Berisford, C.W. 1979. Abundance and parasitic habits of some parasitoids of the Nantucket pine tip moth (Lepidoptera: Tortricidae). *Canadian Entomologist*. 111: 509-514.

115. Fuentes-Contreras, E., Pell, J.K. & Niemeyer, H.M. 1998. Influence of plant resistance at the third trophic level: interactions between parasitoids and entomopathogenic fungi of cereal aphids. *Oecologia*. 117: 426-432.

116. Fuentes-Contreras, J.E., Powell, W., Wadhams, L.J., Pickett, J.A. & Niemeyer, H.M. 1996. Influence of wheat and oat cultivars on the development of the cereal aphid parasitoid *Aphidius rhopalosiphi* and the generalist aphid parasitoid *Ephedrus plagiator*. *Annals of Applied Biology*. 128: 181-187.

117. Fuester, R.W., Taylor, P.B., Day, W.H., Hendrickson, R.M.Jr. & Blumenthal, E.M. 1984. Introduction of exotic parasites for biological control of the birch leafminer (Hymenoptera: Tenthredinidae) in the middle Atlantic states. *Journal of Economic Entomology*. 77: 1565-1570.

118. Furlong, M.J. & Pell, J.K. 1996. Interactions between the fungal entomopathogen *Zoophthora radicans* Brefeld (Entomophthorales) and two hymenopteran parasitoids attacking the diamondback moth, *Plutella xylostella* L. *Journal of Invertebrate Pathology*. 68: 15-21.

119. Gaines, D.N. & Kok, L.T. 1999. Impact of hyperparasitoids on *Cotesia glomerata* in southwestern Virginia. *Biological Control*. 14: 19-28.

120. Gauld, I.D. 1980. A synopsis of the Anomaloninae (Hymenoptera: Ichneumonidae) of sub-Saharan Africa with special reference to species of potential economic importance. *Bulletin of Entomological Research*. 70: 33-41.

121. Geervliet, J.B.F., Verdel, H., Snellen, M.S.W., Schaub, J., Dicke, M. & Vet, L.E.M. 2000. Coexistence and niche segregation by field populations of the parasitoids *Cotesia glomerata* and *Cotesia rubecula* in the Netherlands: predicting field performance from laboratory data. *Oecologia*. 124: 55-63.

122. Georgiev, G. 2001. Notes on the biology and ecology of the parasitoids of the poplar clearwing moth, *Paranthrene tabaniformis* (Rott.) (Lep., Sesiidae) in Bulgaria. I. *Apanteles evonymellae* (Bouché, 1934) (Hym., Braconidae). *Journal of Applied Entomology*. 125: 141-145.

123. Georgiev, G. 2002. Notes on the biology and ecology of the parasitoids of the poplar clearwing moth, *Paranthrene tabaniformis* (Rott.) (Lep., Sesiidae) in Bulgaria. II. *Eriborus terebrans* (Gravenhorst, 1826) (Hym., Ichneumonidae). *Journal of Applied Entomology*. 125: 141-145.

124. Georgiev, G. 2001. Bioecological characteristics of two *Pristomerus* (Hymenoptera: Ichneumonidae) species as parasitoids of poplar borer insects in Bulgaria. In: *Proceedings of third Balkan scientific conference "Study, conservation and utilisation of forest resources" Vol. III* (T. Naydenova, ed.), pp. 101-110.

125. Gibbons, J.R.H. 1979. A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. *American Naturalist*. 114: 719-741.

126. Gillespie, D.R. & Finlayson, T. 1981. Final-instar larvae of native hymenopterous and dipterous parasites of *Operophtera* species (Lepidoptera: Geometridae) in British Columbia. *Canadian Entomologist*. 113: 45-55.

127. Giron, A.R. 1978. Notes on the biology and diapause inducement of the hyperparasitoid *Gelis tenellus*. *Annals of the Entomological Society of America*. 71: 827-829.

128. Glen, D.M. 1982. Effects of natural enemies on a population of codling moth *Cydria pomonella*. *Annals of Applied Biology*. 101: 199-201.

129. Godfray. H.C.J. 1987. The evolution of clutch sizes in parasitic wasps. *American Naturalist*. 129: 221-233.

130. Godfray, H.C.J. & Hassell, M.P. 1991. Encapsulation and host-parasitoid population biology. In *Parasite-host associations, coexistence or conflict?* (C.A. Toft, A. Aeschlimann & L. Bolis, eds) Oxford Science Publications, New York. pp. 131-147.

131. Godfray, H.C.J., Agassiz, D.J.L., Nash, D.R. & Lawton, J.H. 1995. The recruitment of parasitoid species to two invading herbivores. *Journal of Animal Ecology.* 64: 393-402.

132. Goldson, S.L., Phillips, C.B., McNeill, M.R. & Barlow, N.D. 1997. The potential of parasitoid strains in biological control: observations to date on *Microctonus* spp. intraspecific variation in New Zealand. *Agriculture, Ecosystems and Environment.* 64: 115-124.

133. Goldson, S.L., Proffitt, J.R. & McNeill, M.R. 1990. Seasonal biology and ecology in New Zealand of *Microctonus aethiopoides* (Hymenoptera: Braconidae), a parasitoid of *Sitona* spp. (Coleoptera: Curculionidae), with special emphasis on atypical behaviour. *Journal of Applied Ecology.* 27: 703-722.

134. Gonzáles, W.L., Funentes-Contreras, E. & Niemeyer, H.M. 2002. host plant and natural enemy impact on cereal aphid competition in a seasonal environment. *Oikos.* 96: 481-491.

135. Gordon, D.M., Nisbet, R.M., DeRoos, A., Gurney, W.S.C. & Stewart, R.K. 1991. Discrete generations in host-parasitoid models with contrasting life-styles. *Journal of Animal Ecology.* 60: 295-308.

136. Goudegnon, A.E., Kirk, A.A., Schiffers, B. & Bordat, D. 2000. Comparative effects of deltamethrin and neem kernal solution treatments on diamondback moth and *Cotesia plutellae* (Hym., Braconidae) parasitoid populations in the Contonou peri-urban area in Benin. *Journal of Applied Entomology.* 124: 141-144.

137. Grabenweger, G. & Lethmayer, C. 1999. Occurrence and phenology of parasitic Chalcidoidea on the horse chestnut leafminer, *Cameraria ohridella* Deschka and Dimic (Lepidoptera: Gracillaridae). *Journal of Applied Entomology.* 123: 257-260.

138. Grbic, M. & Strand, M.R. 1998. Shifts in the life history of parasitic wasps correlate with pronounced alterations in early development. *Proceedings in the National Academy of Science, USA.* 95: 1097-1101.

139. Green, D.M., Kraaijeveld, A.R. & Godfray, H.C.J. 2000. Evolutionary interactions between *Drosophila melanogaster* and its parasitoid *Asobara tabida. Heredity.* 85: 450-458.

140. Gross, H.R. & Pair, S.D. 1991. Seasonal distribution, response to host development stage, and screened-cage performance of *Archytas marmoratus* (Diptera: Tachinidae) and *Ophion flavidus* (Hymenoptera: Ichneumonidae) on *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist.* 74: 237-245.

141. Gu, H., Wang, Q. & Dorn, S. 2003. Superparasitism in *Cotesia glomerata*: a response of hosts and consequences for parasitoids. *Ecological Entomology.* 28: 422-431.

142. Guerrieri, E., Pennacchio, F. & Tremblay, E. 1997. Effect of adult experience on in-flight orientation to plant and plant-host complex volatiles in *Aphidius ervi* Haliday (Hym., Brac.). *Biological Control.* 10: 159-165.

143. Hagley, E.A.C., Biggs, A.R., Timbers, G.E. & Coutu-Sundy, J. 1993. Effect of age of the puparium of the apple maggot, *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae), on parasitism by *Phygadeuon wiesmanni* Sachtl. (Hymenoptera: Ichneumonidae). *Canadian Entomologist.* 125: 721-724.

144. Hajek, A.E. & Dahlsten, D.L. 1985. Insect and mite associates of *Scolytus multistriatus* (Coleoptera; Scolytidae) in California. *Canadian Entomologist.* 117: 409-421.

145. Hamel, D.R. 1977. The effects of *Bacillus thuringiensis* on parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and the spruce coneworm *Dioryctria reniculelloides* (Lepidoptera: Pyralidae), in Montana. *Canadian Entomologist.* 109: 1409-1415.

146. Hamel, D.R. 1977. The effects of *Bacillus thuringiensis* on parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), and the spruce coneworm, *Dioryctria reniculelloides* (Lepidoptera: Pyralidae), in Montana. *Canadian Entomologist.* 109: 1409-1415.

147. Hanson, P.E. & Gauld, I.D. 1995. The Hymenoptera of Costa Rica. Oxford University Press, Oxford.

148. Hanula, J.L. & Berisford, C.W. 1984. Seasonal flight activity of the smaller European elm bark beetle, *Scolytus multistriatus* (Coleoptera: Scolytidae), and associates in Georgia. *Canadian Entomologist.* 116: 1251-1258.

149. Harcourt, D.G. 1990. Displacement of *Bathyplectes curculionis* (Thoms.) (Hymenoptera: Ichneumonidae) by *B. anurus* (Thoms.) in eastern Ontario populations of the alfalfa weevil, *Hypera postica* (Gyll.) (Coleoptera: Curculionidae). *Canadian Entomologist.* 122: 641-645.

150. Hardy, I.C.W. & Blackburn, T.M. 1991. Brood guarding in a bethylid wasp. *Ecological Entomology.* 16: 55-62.

151. Harvey, J.A. 1996. *Venturia canescens* parasitizing *Galleria mellonella* and *Anagasta kuehniella*: is the parasitoid a conformer or regulator? *Journal of Insect Physiology.* 42: 1017-1025.

152. Harvey, J.A. 2000. Dynamic effects of parasitism by an endoparasitoid wasp on the development of two host species: implications for host quality and parasitoid fitness. *Ecological Entomology.* 25: 267-278.

153. Harvey, J.A., Kadash, K. & Strand, M.R. 2000. Differences in larval feeding behaviour correlate with altered developmental strategies in two parasitic wasps: implications for the size-fitness hypothesis. *Oikos.* 88: 621-629.

154. Harvey, J.A. & Strand, M.R. 2002. The developmental strategies of endoparasitoid wasps vary with host feeding ecology. *Ecology.* 83: 2439-2451.

155. Harvey, J.A. & Thompson, D.J. 1995. Developmental interactions between the solitary endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and two of its hosts, *Plodia interpunctella* and *Corcyra cephalonica* (Lepidoptera: Pyralidae). *European Journal of Entomology.* 92: 427-435.

156. Hasan, S. & Waspshere A.J. 1977. Biology and host specificity of the *Chondrilla* crown moth, *Oporopsamma wertheimsteini* (Rebel) (Lepidoptera: Tortricidae). *Bulletin of Entomological Research.* 67: 619-625.

157. Haseeb, M. & Amano, H. 2002. Effects of contact, oral and persistent toxicity of selected pesticides on *Cotesia plutellae* (Hym., Braconidae), a potential parasitoid of *Plutella xylostella* (Lep., Plutellidae). *Journal of Applied Entomology.* 126: 8-13.

158. Hassell, M.P. & Anderson, R.M. 1984. Host susceptibility as a component in host-parasitoid systems. *Journal of Animal Ecology.* 53: 611-621.

159. Hawkins, B.A. 1994. Pattern and process in host-parasitoid interactions. Cambridge University Press.

160. Hayakawa, D.L., Grafius, E. & Stehr, F.W. 1990. Effects of temperature of longevity, reproduction, and development of the asparagus aphid (Homoptera: Aphididae) and the

parasitoid *Diaeretiella rapae* (Hymenoptera: Braconidae). *Environmental Entomology*. 19: 890-897.

161. Heatwole, H. & Davis, D.M. 1965. Ecology of three sympatric species of parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). *Ecology*. 46: 140-150.

162. Hegazi, E.M. & Khafagi, W.E. 1999. Effect of mating status and age of *Microplitis rufiventris* (Hym., Braconidae) females on the growth pattern and number of their teratocytes. *Journal of Applied Entomology*. 123: 417-422.

163. Hegazi, E.M. & Khafagi, W.E. 2001. Growth patterns of *Microplitis rufiventris* (Hym., Braconidae) teratocytes in *Spodoptera littoralis* (Lep., Noctuidae) larvae treated with a chitin synthesis inhibitor. *Journal of Applied Entomology*. 125: 79-84.

164. Hemerik, L. & Harvey, J.A. 1999. Flexible larval development and the timing of destructive feeding by a solitary endoparasitoid: an optimal foraging problem in evolutionary perspective. *Ecological Entomology*. 24: 308-315.

165. Henter, H.J. 1995. The potential for coevolution in a host-parasitoid system. II. Genetic variation within a population of wasps in the ability to parasitize an aphid host. *Evolution*. 49: 439-445.

166. Hertel, G.D. & Benjamin, D.M. 1979. Biology of the pine webworm in Florida slash pine plantations. *Annals of the Entomological Society of America*. 72: 816-819.

167. Herz, A. & Heitland, W. 1999. Larval parasitism of a forest pest, the common pine sawfly *Diprion pini* (L.) (Hym., Diprionidae), during an endemic density phase. *Journal of Applied Entomology*. 123: 129-137.

168. Heyerdahl, R.H. & Dutcher, J.D. 1985. Hymenopterous parasitoids of Pecan leafminers. *Journal of Entomological Science*. 20: 411-421.

169. Hildebrands, A., Thieme, T. & Vidal, S. 2000. Which factors govern the host preference of aphid parasitoids when offered host races of an aphid species. In: *Hymenoptera: evolution, biodiversity and biological control*. (A. Austin & M. Dowton, eds.). CSIRO Publishing. pp. 359-370.

170. Hilton, D.F.J. 1982. The biology of *Endothenia daeckeana* (Lepidoptera: Olethreutidae), an inhabitant of the ovaries of the northern pitcher plant, *Sarracenia P. purpurea* (Sarraceniaceae). *Canadian Entomologist*. 114: 269-274.

171. Hoang, A. 2002. Physiological consequences of immune response by *Drosophila melanogaster* (Diptera: Drosophilidae) against the parasitoid *Asobara tabida* (Hymenoptera: Braconidae). *Journal of Evolutionary Biology*. 15: 537-543.

172. Hoch, G., Zubrik, M., Novotny, J. & Schopf, A. 2001. The natural enemy complex of the gypsy moth, *Lymantria dispar* (Lep., Lymantriidae) in different phases of its population dynamics in eastern Austria and Slovakia – a comparative study. *Journal of Applied Entomology*. 125: 217-227.

173. Hoffmeister, T. 1992. Factors determining the structure and diversity of parasitoid complexes in tephritid fruit flies. *Oecologia*. 89: 288-297.

174. Hogg, D.B., Anderson, R.E. & Pitre, H.N. 1982. Early-season parasitization of fall armyworm (Lepidoptera: Noctuidae) larvae in Mississippi. *Florida Entomologist*. 65: 584-585.

175. Honda, T. & Kainoh, Y. 1998. Age-related fecundity and learning ability of the egg-larval parasitoid *Ascogaster reticulatus* Watanabe (Hymen.: Braconidae). *Biological Control*. 13: 177-181.

176. Hopper, K.R., Aidara, S., Agret, S., Cabal, J., Coutinot, D., Dabire, R., Lesieux, C., Kirk, G., Reichert, S., Tronchetti, F. & Vidal, J. 1995. Natural enemy impact on the abundance of *Diuraphis noxia* (Homoptera: Aphididae) in wheat in southern France. *Environmental Entomology.* 24: 402-408.

177. Hopper, K.R., Powell, J.E. & King, E.G. 1991. Spatial density dependence in parasitism of *Heliothis virescens* (Lepidoptera: Noctuidae) by *Microplitis croceipes* (Hymenoptera: Braconidae) in the field. *Environmental Entomology.* 20: 292-302.

178. Horne, P.A. 1990. The influence of introduced parasitoids on the potato moth, *Phthorimaea operculella* (Lepidoptera; Gelechiidae) in Victoria, Australia. *Bulletin of Entomological Research.* 80: 159-163.

179. Hotchkin, P.G. & Kaya, H.K. 1983. Interactions between two baculoviruses and several insect parasites. *Canadian Entomologist.* 115: 841-846.

180. House, H.L. 1978. An artificial host: encapsulated synthetic medium for *in vitro* oviposition and rearing the endoparasitoid *Itoplectis conquisitor* (Hymenoptera: Ichneumonidae). *Canadian Entomologist.* 110: 331-334.

181. House, H.L. 1980. Artificial diets for the adult parasitoid *Itoplectis conquisitor* (Hymenoptera: Ichneumonidae). *Canadian Entomologist.* 112: 315-320.

182. Howard, F.W. & Solia, M.A. 1989. Distribution, life history, and host plant relationships of mahogany webworm, *Macalla thyrsisalis* (Lepidoptera: Pyralidae). *Florida Entomologist.* 72: 469-481.

183. Hower, A.A. & Davis, G.A. 1984. Selectivity of insecticides that kill the potato leafhopper (Homoptera: Cicadellidae) and alfalfa weevil (Coleoptera: Curculionidae) and protect the parasite *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae). *Journal of Economic Entomology.* 77: 1601-1607.

184. Hu, G.Y., Mitchell, E.R., Sieglaff, D.H. & Okine, J.S. 1998. Field production of two species of parasitoids of the diamondback moth (Lepidoptera: Plutellidae). *Florida Entomologist.* 81: 526-534.

185. Huddleston, T. & Gauld, I. 1988. Parasitic wasps (Ichneumonoidea) in British light-traps. *The Entomologist.* 107: 134-154.

186. Huddleston, T. & Walker, A.K. 1988. *Cardiochiles* (Hymenoptera: Braconidae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. *Bulletin of Entomological Research.* 78: 435-461.

187. Hufbauer, R.A. 2001. Pea aphid-parasitoid interactions: have parasitoids adapted to differential resistance? *Ecology.* 82: 717-725.

188. Hufbauer, R.A. 2002. Aphid population dynamics: does resistance to parasitism influence population size? *Ecological Entomology.* 27: 25-32.

189. Hufbauer, R.A. 2002. Evidence for nonadaptive evolution in parasitoid virulence following a biological control introduction. *Ecological Applications.* 12: 66-78.

190. Hughes, R.D., Woolcock, L.T., Roberts, J.A. & Hughes, M.A. 1987. Biological control of the spotted alfalfa aphid, *Therioaphis trifoli* F. *maculata*, on Lucerne crops in Australia, by the introduced parasitic hymenopteran *Trioxys complanatus*. *Journal of Applied Entomology.* 24: 515-537.

191. Humble, L.M. 1985. Final-instar of native pupal parasites and hyperparasites of *Operophtera* species (Lepidoptera: Geometridae) on southern Vancouver. *Canadian Entomologist*. 117; 525-534.

192. Hurlbutt, B. 1987. Sexual size, dimorphism in parasitoid wasps. *Biological Journal of the Linnean Society*. 30: 63-89.

193. Idris, A.B. & Grafius, E. 1993. Field studies on the effect of pesticides on the diamondback moth (Lepidoptera: Plutellidae) and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Journal of Economic Entomology*. 86: 1196-1202.

194. Idris, A.B. & Grafius, E. 1993. Pesticides affect immature stages of *Diadegma insulare* (Hymenoptera: Ichneumonidae), and its host, the diamondback moth (Lepidoptera; Plutellidae). *Journal of Economic Entomology*. 86: 1203-1212.

195. Idris, A.B. & Graius, E. 1995. Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth (Lepidoptera; Yponomeutidae). *Environmental Entomology*. 24: 1726-1735.

196. Idris, A.B. & Grafius, E. 1998. Diurnal flight activity of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of the diamondback moth (Lepidoptera; Plutellidae), in the field. *Environmental Entomology*. 27: 406-414.

197. Ives, A.R., Schooler, S.S., Jagar, V.J., Knuteson, S.E., Grbic, M. & Settle, W.H. 1999. Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. *American Naturalist*. 154: 652-673.

198. Ives, A.R. & Settle, W.H. 1996. The failure of a parasitoid to persist with a superabundant host: the importance of the numerical response. *Oikos*. 75: 269-278.

199. Iwao, K., Nakamura, S. & Ohsaki, N. 2001. Plant-based host preference and larval competition of the tachinid parasitoid *Epicampocera succincta*. *Population Ecology*. 43: 149-155.

200. Jackson, D.M., Tingle, F.C. & Mitchell, E.R. 1984. Survey of *Heliothis* species larvae found on Florida beggarweed and postharvest tobacco in Florida. *Florida Entomologist*. 67: 130-141.

201. Janssen, A. 1989. Optimal host selection by *Drosophila* parasitoids in the field. *Functional Ecology*. 3: 469-479.

202. Jervis, M.A. & Kidd, N.A.C. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biological Review*. 61: 395-434.

203. Johnson, J.A., Valero, K.A., Hannel, M.M. & gill, R.F. 2000. Seasonal occurrence of postharvest dried fruit insects and their parasitoids in a culled fig warehouse. *Journal of Economic Entomology*. 93: 1380-1390.

204. Johnson, J.W. 1987. A revision of the species of *Praon* Haliday in North America north of Mexico (Hymenoptera: Aphidiidae). *Canadian Entomologist*. 119: 999-1025.

205. Kadono-Okuda, K., Weyda, F. & Okuda, T. 1998. *Dinocampus* (=*Perilitus*) *coccinella* teratocyte-specific polypeptide: its accumulative property, localization and characterization. *Journal of Insect Physiology*. 44: 1073-1080.

206. Kean, J.M. & Barlow, N.D. 2001. A spatial model for the successful biological control of *Sitona discoideus* by *Microctonus aethiopoides*. *Journal of Applied Ecology*. 38: 162-169.

207. Kerrich, G.J. 1968. Description of an ichneumonid (Hym.) that preys on egg-masses of weevils harmful to tea culture in Kenya. *Bulletin of Entomological Research*. 59: 469-472.

208. Khafagi, W.E., Hegazi, E.M. & Showail, S. 1999. Prediction studies on number of teratocytes and eggs of *Microplitis rufiventris* Kok. (Hym., Braconidae) parasitoid in superparasitized host larvae. *Journal of Applied Entomology*. 123: 37-40.

209. Kingsley, P.C., Bryan, M.D., Day, W.H., Burger, T.L., Dysart, R.J. & Schwalbe, C.P. 1993. Alfalfa weevil (Coleoptera: Curculionidae) biological control: spreading the benefits. *Environmental Entomology*. 22: 1234-1250.

210. Kobayashi, A. & Shimada, M. 2000. Field sex ratio of a braconid parasitoid wasp, *Heterospilus prosopidis* (Hymenoptera: Braconidae), in the southwestern United States: concordance with host-quality. *Annals of the Entomological Society of America*. 93: 819-824.

211.. Kolarov, J., Ozbek, H. & Coruh, S. 2002. New and little known Acaenitinae (Hymenoptera: Ichneumonidae) from Turkey. *Turkiye Entomoloji Dergisi*. 26: 277-281.

212. Koptur, S. & Lawton, J.H. 1988. Interactions among vetches bearing extrafloral nectarines, their biotic protective agents, and herbivores. *Ecology*. 69: 278-283.

213. Kouamé, K.L. & Mackauer, M. 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. *Oecologia*. 88: 197-203.

214. Koziol, M. 2000. Cono- and seminiphagous insects of Norway spruce *Picea abies* (L.) Karst. and their parasitoids in lower and upper montane zone of the Tatra National Park in Poland. *Journal of Applied Entomology*. 124: 259-266.

215. Kraaijeveld, A.R. 1999. Kleptoparasitism as an explanation for paradoxical oviposition decisions of the parasitoid *Asobara tabida*. *Journal of Evolutionary Biology. Asobara tabida12: 129-133.*

216. Kraaijeveld, A.R. & van der Wel, N.N. 1994. Geographic variation in reproductive success of the parasitoid *Asobara tabida* in larvae of several *Drosophila* species. *Ecological Entomology*. 19: 221-229.

217. Kring, T.J. & Kring, J.B. 1988. Aphid fecundity, reproductive longevity, and parasite development in the *Schizaphis graminum* (Rondani) (Homoptera: Aphididae) – *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) system. *Canadian Entomologist*. 120: 1079-1083.

218. Kristofferson, A.B., Lingjaerde, O.C., Stenseth, N.C. & Shimada, M. 2001. Non-parametric modelling of non-linear density dependence: a three-species host-parasitoid system. *Journal of Animal Ecology*. 70: 808-819.

219. Kudon, L.H. & Berisford, C.W. 1981. Identification of host origin of parasites of bark beetles (Coleoptera: Scolytidae) by fatty acid composition. *Canadian Entomologist*. 113: 205-212.

220. Kuhar, T.P., Youngman, R.R. & Laub, C.A. 2000. Alfalfa weevil (Coleoptera: Curculionidae) population dynamics and mortality factors in Virginia. *Environmental Entomology*. 29: 1295-1304.

221. La Mana, M.L. & Miller, J.C. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*. 6: 232-237.

222. Lei, G.-C., Vikbergs, V., Nieminen, M. & Kuussaari, M. 1997. The parasitoid complex attacking the Glanville fritillary *Melitaea cinxia* (Lep.: Nymphalidae), an endangered butterfly. *Journal of Natural History.* 31: 635-648.

223. Le Masurier, A.D. 1991. Effect of host size on clutch size in *Cotesia glomerata*. *Journal of Animal Ecology.* 60: 107-118.

224. Lewis, W.J. & Nordlund, D.A. 1980. Employment of parasitoids and predators for fall armyworm control. *Florida Entomologist.* 63: 433-532.

225. Li, S., Fitzpatrick, S.M., Troubridge, J.T., Sharkey, M.J., Barron, J.R. & O'Hara, J.E. 1999. Parasitoids reared from the obliquebanded leafroller (Lepidoptera: Tortricidae) infesting raspberries. *Canadian Entomologist.* 131: 399-404.

226. Li, Y., Dickens, J.C. & Steiner, W.W. 1992. Antennal olfactory responsiveness of *Microplitis croceipes* (Hymenoptera: Braconidae) to cotton plant volatiles. *Journal of Chemical Ecology.* 18: 1761-1773.

227. Lindquist, O.H. 1973. Notes on the biology of the larch needleworm, *Zeiraphera improbana* (Lepidoptera: Olethreutidae), in Ontario. *Canadian Entomologist.* 105: 1129-1131.

228. Longhurst, C. & Baker, R. 1981. Host location in *Olesicampe monticola*, a parasite of larvae of larch sawfly *Cephalcia lariciphila*. *Journal of Chemical Ecology.* 7: 203-208.

229. Lopez, M., Aluja, M. & Sivinski, J. 1999. Hymenopterous larval-pupal and pupal parasitoids of *Anastrepha* flies (Diptera: Tephritidae) in Mexico. *Biological Control.* 15: 119-129.

230. Luff, M.L. 1976. The biology of *Microctonus caudatus* (Thomson), a braconid parasite of the ground beetle *Harpalus rufipes* (Degeer). *Ecological Entomology.* 1: 111-116.

231. Lyons, D.B. 1999. Phenology of the native parasitoid *Sinophorus megalodontis* (Hymenoptera: Ichneumonidae) relative to its introduced host, the pine false webworm (Hymenoptera: Pamphilidae). *Canadian Entomologist.* 131: 787-800.

232. Lysyk, T.J. & Nealis, V.G. 1988. Temperature requirements for development of the jack pine budworm (Lepidoptera: Tortricidae) and two of its parasitoids (Hymenoptera). *Journal of Economic Entomology.* 81: 1045-1051.

233. Mackauer, M. 1996. Sexual size dimorphism in solitary parasitoid wasps: influence of host quality. *Oikos.* 76: 265-272.

234. Mackauer, M. & Kambhampati, S. 1984. Reproduction and longevity of cabbage aphid, *Brevicoryne brassicae* (Homoptera; Aphididae), parasitized by *Diaeretiella rapae* (Hymenoptera: Aphidiidae). *Canadian Entomologist.* 116: 1605-1610.

235. Mackauer, M. & Michaud, J.P. 1996. Host choice by aphidiid parasitoids (Hymenoptera: Aphidiidae): host recognition, host quality, and host value. *Canadian Entomologist.* 128: 959-980.

236. Mackauer, M., Sequeira, R. & Otto, M. 1997. Growth and development in parasitoid wasps; adaptation to variable host resources. In: *Vertical food web interactions: evolutionary patterns and driving forces* (K. Dettner, G. Bauer & W. Vajlkl, eds.). Ecological Studies Vol. 130. Springer, Berlin, New York. pp. 191-203.

237. MacPhee, A.W. 1967. The winter moth, *Operophtera brumata* (L.) (Lepidoptera: Geometridae), a new pest attacking apple orchards in Nova Scotia, and its coldhardiness. *Canadian Entomologist.* 99: 829-834.

238. MacPhee, A., Newton, A., & McRae, K.B. 1988. Population studies on the winter moth *Operophtera brumata* (L.) (Lepidoptera: Geometridae) in apple orchards in Nova Scotia. *Canadian Entomologist*. 120: 73-83.

239. Maltais, J, Régnière, J., Cloutier, C., Hébert, C. & Perry, D.F. 1989. Seasonal biology of *Meteorus trachynotus* Vier. (Hymenoptera: Braconidae) and its overwintering host *Choristoneura rosaceana* (Harr.) (Lepidoptera: Tortricidae). *Canadian Entomologist*. 121: 745-756.

240. Manojlovic, B., Zabel, A., Kostic, M. & Stankovic, S. 2000. Effect of nutrition of parasites with nectar of melliferous plants on parasitism of the elm bark beetles (Coleoptera: Scolytidae). *Journal of Applied Entomology*. 124: 155-161.

241. Marino, P.C. & Cornell, H.V. 1992. Adult movement of the native holly leafminer, *Phytomyza ilicicola* Loew (Diptera: Agromyzidae): consequences for host choice within and between habitats. *Oecologia*. 92: 76-82.

242. Markovic, C. & Stojanovic, A. 2003. Significance of parasitoids in the reduction of oak bark beetle *Scolytus intricatus* Ratzeburg (Col., Scolytidae) in Serbia. *Journal of Applied Entomology*. 127: 23-28.

243. Martínez-Castillo, M., Leyra, J.L., Cibrián-Tovar, J. & Bujanos-Muñiz, R. 2002. Parasitoid diversity and impact on populations of the diamondback moth *Plutella xylostella* (L.) on *Brassica* crops in central Mexico. *Biocontrol*. 47: 23-31.

244. Mason, P.G., Erlandson, M.A., Elliot, R.H. & Harris, B.J. 2002. Potential impact of spinosad on parasitoids of *Mamestra configurata* (Lepidoptera: Noctuidae). *Canadian Entomologist*. 134: 59-68.

245. Mason, W.R.M. 1978. Ichneumonoid parasites (Hymenoptera) accidentally introduced into Canada. *Canadian Entomologist*. 110: 603-608.

246. Mason, W.R.M. 1978. A synopsis of the nearctic Braconini, with revisions of nearctic species of *Coeloides* and *Mysoma* (Hymenoptera: Braconidae). *Canadian Entomologist*. 110: 721-768.

247. Mason, W.R.M. 1979. A new *Rogas* (Hymenoptera: Braconidae) parasite of ten caterpillars (*Malacosoma* spp. Lepidoptera: Lasciocampidae) in Canada. *Canadian Entomologist*. 111: 783-786.

248. Mayhew, P.J. & van Alphen, J.J.M. 1999. Gregarious development in alysiine parasitoids evolved through a reduction in larval aggression. *Journal of Animal Behaviour*. 58: 131-141.

249. Mayhew, P.J. & Blackburn, T.M. 1999. Does development mode organise life-history traits in the parasitoid Hymenoptera? *Journal of Animal Ecology*. 68: 906-916.

250. McNeill, M.R. 2000. Effect of container type on suitability of the pathogen *Serratia marcescens* – *Microctonus hyperodae* (Hym., Braconidae) association to indicate parasitoid oviposition attempts. *Journal of Applied Entomology*. 124: 93-98.

251. Meyer, W.L. & Knight Jr., R. 1998. A new host record for the Caribbean fruit fly (Diptera: Tephritidae). *Florida Entomologist*. 81: 235-237.

252. Miller, J.C. 1980. Niche relationships among parasitic insects occurring in a temporary habitat. *Ecology*. 61: 270-275.

253. Miller, J.C. 1982. Life history of insect parasites involved in successful multiparasitism. *Oecologia*. 54: 8-9.

254. Milne, W.M. & Bishop. A.L. 1987. The role of predators and parasites in the natural regulation of Lucerne aphids in Eastern Australia. *Journal of Applied Ecology*. 24: 893-905.

255. Mirchev, P., Georgiev, G. & Tsankov, G. 2001. Studies on the parasitoids of *Gelechia senticetella* (Stgr.) (Lepidoptera: Gelechiidae) in Bulgaria. *Anzeiger fuer Schaedlingskunde*. 74: 94-96.

256. Mitchell, E.R. 1984. Damage of sunflower by the southern armyworm (Lepidoptera: Noctuidae). *Florida Entomologist*. 67: 273-277.

257. Mitchell, E.R., Hu, G.Y. & Okine, J.S. 1997. Diamondback moth (Lepidoptera: Plutellidae) infestation and parasitism by *Diadegma insulare* (Hymenoptera: Ichneumonidae) in collards and adjacent cabbage fields. *Florida Entomologist*. 80: 54-62.

258. Mitchell, E.R., Tingle, F.C., Navasero-Ward, R.C. & Kehat, M. 1997. Diamondback moth (Lepidoptera: Plutellidae): parasitism by *Cotesia plutellae* (Hymenoptera: Braconidae) in cabbage. *Florida Entomologist*. 80: 477-489.

259. Molau, U., Eriksen, B. & Knudsen, J.T. 1989. Predispersal seed predation in *Bartsia alpina*. *Oecologia*. 81: 181-185.

260. Moore, D. 1983. Hymenopterous parasitoids of stem-boring Diptera (e.g. *Oscinella frit* (L.)) in perennial ryegrass (*Lolium perenne*) in Britain. *Bulletin of Entomological Research*. 73: 601-608.

261. Moore, D., Clements, R.O. & Ridout, M.S. 1986. Effects of pasture establishment and renovation techniques on the hymenopterous parasitoids of *Oscinella frit* L. and other stem-boring Diptera in ryegrass. *Journal of Applied Ecology*. 23: 871-881.

262. Morrill, W.L., Kushnak, G.D. & Gabor, J.W. 1998. Parasitism of the wheat stem sawfly (Hymen.: Cephidae) in Montana. *Biological Control*. 12: 159-163.

263. Morris, R.C.J., Müller, C.B. & Godfray, H.C.J. 2001. Field experiments testing for apparent competition between primary parasitoids mediated by secondary parasitoids. *Journal of Animal Ecology*. 70: 301-309.

264. Müller, C.B., Adriaanse, I.C.T., Belshaw, R. & Godfray, H.C.J. 1999. the structure of an aphid-parasitoid community. *Journal of Animal Ecology*. 68: 346-370.

265. Münster-Swendsen, M. 1985. A simulation study of primary-, clepto- and hyperparasitism in *Epinotia tedella* (Lepidoptera: Tortricidae). *Journal of Animal Ecology*. 54: 683-695.

266. Murray, D.A., Kriegel, R.D., Johnson, J.W. & Howitt, A.J. 1996. Natural enemies of cranberry fruitworm, *Acrobasis vacinii*, (Lepidoptera: Pyralidae) in Michigan highbush blueberries. *Great Lakes Entomologist*. 29: 81-86.

267. Nakai, M. & Kunimi, Y. 1998. Effects of the timing of entomopoxvirus administration to the smaller tea tortrix, *Adoxophyes* sp. (Lepid.: Tort.) on the survival of the endoparasitoid, *Ascogaster reticulatus* (Hym.: Braconidae). *Biological Control*. 13: 63-69.

268. Nealis, V. 1987. The number of instars in jack pine budworm, *Choristoneura pinus pinus* Free. (Lepidoptera: Tortricidae), and the effect of parasitism on head capsule width and development time. *Canadian Entomologist*. 119: 773-777.

269. Nealis, V.G. 1991. Parasitism in sustained and collapsing populations of the jack pine budworm, *Choristoneura pinus pinus* Free. (Lepidoptera: Tortricidae), in Ontario. *Canadian Entomologist*. 123: 1065-1075.

270. Nealis, V. & van Frankenhuuyzen, K. 1990. Interactions between *Bacillus thuringiensis* Berliner and *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae), a parasitoid of the spruce budworm, *Choristoneura occidentalis* (Clem.) (Lepidoptera: Tortricidae). *Canadian Entomologist*. 122: 585-594.

271. Nealis, V. & Fraser, S. 1988. Rate of development, reproduction, and mass-rearing of *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae) under controlled conditions. *Canadian Entomologist*. 120: 197-204.

272. Nealis, V.G. & Lysyk, T.J. 1988. Sampling overwintering jack pine budworm, *Choristoneura pinus pinus* Free. (Lepidoptera: Tortricidae), and two of its parasitoids (Hymenoptera). *Canadian Entomologist*. 120: 1101-1111.

273. Nealis, V. & Régnière, J. 1987. The influence of parasitism by *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae) on spring dispersal and changes in the distribution of larvae of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist*. 119: 141-146.

274. Nemeye, P.S., Moore, D. & Prior, C. 1990. Potential of the parasitoid *Heterospilus prosopidis* (Hymenoptera: Braconidae) as a vector of plant-pathogenic *Colletotrichum* species. *Annals of Applied Biology*. 116: 11-19.

275. Nénon, J.-P., Kacem, N. & Le Lannic, J. 1997. Structure, sensory equipment, and secretions of the ovipositor in a giant species of Hymenoptera: *Megarhyssa atrata* F. (Ichneumonidae, Pimplinae). *Canadian Entomologist*. 129: 789-799.

276. Ngi-Song, A.J. & Overholt, W.A. 1997. Host location and acceptance by *Cotesia flavipes* Cameron and *C. sesamiae* (Cameron) (Hymenoptera: Braconidae), parasitoids of African gramineous stemborers: role of frass and other host cues. *Biological Control*. 9: 136-142.

277. Niwa, C.G. 1988. Parasites and predators associated with the ponderosa pine tip moth, *Rhyacionia zozana* (Kearfott) (Lepidoptera: Tortricidae), in California and Oregon. *Canadian Entomologist*. 120: 881-886.

278. Niwa, C.G., Stelzer, M.J. & Beckwith, R.C. 1987. Effects of *Bacillus thuringiensis* on parasitoids of western spruce budworm (Lepidoptera: Tortricidae). *Journal of Economic Entomology*. 80: 750-753.

279. Nixon, G.E.J. 1970. A revision of the N.W. European species of *Microplitis* Förster (Hymenoptera: Braconidae). *Bulletin of the British Museum of Natural History (Entomology)*. 25: 1-30.

280. Nixon, G.E.J. 1986. A revision of the European Agathidinae (Hymenoptera: Braconidae). *Bulletin of the British Museum of Natural History (Entomology)*. 52: 183-242.

281. van Nouhuys, S. & Hanski, I. 2000. Apparent competition between parasitoids mediated by a shared hyperparasitoid. *Ecology Letters*. 3: 82-84.

282. van Nouhuys, S. & Via, S. 1999. Natural selection a genetic differentiation of behaviour between parasitoids from wild and cultivated habitats. *Heredity*. 83: 127-137. 1999.

283. van Nouhuys, S. & Via, S. 1999. Natural selection a genetic differentiation of behaviour between parasitoids from wild and cultivated habitats. *Heredity*. 83: 127-137. 1999.

284. Nussbaumer, C., Stradner, A. & Schopf, A. 2002. Effects of parasitization or injection of parasitoid-derived factors from the endoparasitic wasp *Glyptapanteles porthetriae* (Hym., Braconidae) on the development of the larval host, *Lymantria dispar* (Lep., Lymantriidae). *Journal of Applied Entomology*. 126: 1-7.

285. Obrycki, J.J., Ormond, A.M., Gabriel, A.D. & Orr, C.J. 1993. Larval and pupal parasitism of the strawberry leafroller (Lepidoptera; Tortricidae). *Environmental Entomology*. 22: 679-683.

286. Ode, P.J., Antolin, M.F. & Strand, M.R. 1995. Brood-mate avoidance in the parasitic wasp *Bracon hebetor*. *Animal Behaviour*. 49: 1239-1248.

287. Ode, P.J., Antolin, M.F. & Strand, M.R. 1996. Sex allocation and sexual asymmetries in intra-brood competition in the parasitic wasp *Bracon hebetor*. *Journal of Animal Ecology*. 65: 690-700.

288. Odebiyi, J.A. 1982. Parasites of the corn leafroller, *Sylepta derogata* (F.) (Lepidoptera: Pyralidae), in south-western Nigeria. *Bulletin of Entomological Research*. 72: 329-333.

289. Ohsaki, N. & Sato, Y. 1994. Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. *Ecology*. 75: 59-68.

290. Ohsaki, N. & Sato, Y. 1999. The role of parasitoids in evolution of habitat and larval food plant preference by three *Pieris* butterflies. *Researches on Population Ecology*. 41: 107-119.

291. Okine, J.S., Mitchell, E.R. & Hu, G.Y. 1996. Low temperature effect on viability of *Diadegma insulare* (Hymenoptera: Ichneumonidae) pupae and effect of this parasitoid on feeding rate of diamondback moth larvae (Lepidoptera: Plutellidae). *Florida Entomologist*. 79: 503-509.

292. Olson, A.C., Ives, A.R. & Gross, K. 2000. Spatially aggregated parasitism on pea aphids, *Acyrthosiphon pisum*, caused by random foraging behaviour of the parasitoid *Aphidius ervi*. *Oikos*. 91: 66-76.

293. Ostaff, D.P. & Quiring, D.T. 1994. Seasonal distribution of adult eclosion, oviposition, and parasitism and predation of eggs of the spruce budworm moth, *Zeiraphera canadensis* (Lepidoptera: Tortricidae). *Canadian Entomologist*. 126: 995-1006.

294. Otten, H., Wäckers, F., Battini, M. & Dorn, S. 2001. Efficiency of vibrational sounding in the parasitoid *Pimpla* is affected by female size. *Animal Behaviour*. 61: 671-677.

295. Otto, M. & Mackauer, M. 1998. The developmental strategy of an idiobiont ectoparasitoid, *Dendrocerus carpenteri*: influence of variations in host quality on offspring growth and fitness. *Oecologia*. 117: 353-364.

296. Otto, C. & Svensson, B.S. 1980. Parasitism by *Agriotypus armatus* (Walker) (Hymenoptera: Agriotypidae) in relation to aggregation of its host *Silo pallipes* (F.) (Trichoptera: Goeridae). *Entomologist's Gazette. 31: 199-201.*

297. Outreman, Y., Le Ralec, A., Wajnberg, E. & Pierre, J.S. 2001. Can imperfect host discrimination explain partial patch exploitation in parasitoids. *Ecological Entomology*. 26: 271-280.

298. Özalp, P. & Emre, I. 2001. The effects of carbohydrates upon the survival and reproduction of adult female *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae). *Journal of Applied Entomology*. 125: 177-180.

299. Papp, J. 1996. Braconid wasps from Cape Verde Islands (Hymenoptera, Braconidae) 1. Cheloninae, Exothecinae, Homolobinae, Microgasterinae, Rogadinae. *Boletim do Museu Municipal do Funchal*. 0(48): 197-216.

300. Parr, J.C., Pass, B.C. & Nordin, G.L. 1993. Compatibility of *Zoophthora phytonomi* (Enthomphthorales: Entomophthoraceae) and *Bathyplectes anurus* (Hymenoptera: Ichneumonidae) in Kentucky alfalfa fields. *Environmental Entomology*. 22: 674-678.

301. Pavuk, D.M. & Barrett, G.W. 1993. influence of successional and grassy corridors on parasitism of *Plathypena scabra* (F.) (Lepidoptera: Noctuidae) larvae in soybean agroecosystems. *Environmental Entomology.* 22: 541-546.

302. Periquet, G., Hedderwick, M.P., El Agoze, M. & Poirié, M. 1993. Sex determination in the hymenopteran *Diadromus pulchellus* (Ichneumonidae): validation of the one-locus multi-allele model. *Heredity.* 70: 420-427.

303. Pexton, J.J. & Mayhew, P.J. 2002. Siblicide and life-history evolution in parasitoids. *Behavioural Ecology.* 13: 690-695.

304. Pike, K.S., Stary, P., Miler, T., Allison, D., Graf, G., Boydston, L., Miller, R. & Gillespie, R. 1999. Host range and habitats of the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae) in Washington State. *Environmental Entomology.* 28: 61-71.

305. Pivnick, K.A. 1993. Diapause initiation and pupation site selection of the braconid parasitoid *Microplitis mediator* (Haliday): a case of manipulation of host behaviour. *Canadian Entomologist.* 125: 825-830.

306. Powell, J.E. 1988. Development of *Heliothis virescens* (Lepidoptera: Noctuidae) larvae after parasitization by *Microplitis croceipes* and *Microplitis demolitor* (Hymenoptera: Braconidae). *Florida Entomologist.* 71: 370-374.

307. Prévost, Y.H. 2002. Seasonal feeding patterns of insects in cones of tamarack, *Larix laricina* (Du Roi) K. Koch (Pinaceae). *Forest Ecology and Management.* 168; 101-109.

308. Price, P.W. 1972. Parasitoids utilizing the same host: adaptive nature of differences in size and form. *Ecology.* 53: 190-195.

309. Price, P.W. 1975. Evolutionary strategies of parasitic insects and mites. Plenum Press, New York.

310. Prokopy, R.J. & Webster, R.P. 1978. Oviposition-deterring pheromone of *Rhagoletis pomonella*, a kairomone for its parasitoid *Opius lectus. Journal of Chemical Ecology.* 4: 481-494.

311. Pschorn-Walcher, H. 1987. Interspecific competition between the principal larval parasitoids of the pine sawfly, *Neodiprion sertifer* (Geoff) (Hymenoptera: Diprionidae). *Oecologia.* 73: 621-625.

312. Pschorn-Walcher, H. & Altenhofer, E. 1939. The parasitoid community of leaf-mining sawflies (Fenusini and Heterarthrini): a comparative analysis. *Zoologischer Anzeiger.* 222: 37-57.

313. Pungerl, N.B. 1984. Host preferences of *Aphidius* (Hymenoptera: Aphidiidae) populations parasitizing pea and cereal aphids (Hemiptera: Aphididae). *Bulletin of Entomological Research.* 74: 153-161.

314. Purcell, M.F., Duan, J.J. & Messing, R.H. 1997. Response of three hymenopteran parasitoids introduced for fruit fly control to a gall-forming Tephritid, *Procecidochares alani* (Diptera: Tephridae). *Biological Control.* 9: 193-200.

315. Putnam, L.G. 1968. Experiments in the quantitative relations between *Diadegma insularis* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae) with their host *Plutella maculipennis* (Lepidoptera: Plutellidae). *Canadian Entomologist.* 100: 11-16.

316. Quednau, F.W. 1990. Introduction, permanent establishment, and dispersal in eastern Canada of *Olesicampe geniculatae* Quednau & Lim (Hymenoptera: Ichneumonidae), an

important biological control agent of the mountain ash sawfly, *Pristiphora geniculata* (Hartig) (Hymenoptera: Tenthredinidae). *Canadian Entomologist*. 122: 921-934.

317. Quednau, F.W. & Lim, K.P. 1983. *Olesicampe geniculatae*, a new palaerctic ichneumonid parasite of *Pristiphora geniculata* (Hymenoptera: Tenthredinidae). *Canadian Entomologist*. 115: 109-113.

318. Quicke, D.L.J. 1997. Parasitic wasps. Chapman & Hall.

319. Quimio, G.M. & Walter, G.H. 2001. Host preference and host suitability in an egg-pupal fruit fly parasitoid, *Fopius arisanus* (Sonan) (Hym., Braconidae). *Journal of Applied Entomology*. 125: 135-140.

320. Randall, M.G.M. 1982. The ectoparasitization of *Coleophora alticolella* (Lepidoptera) in relation to its altitudinal distribution. *Ecological Entomology*. 7: 177-185.

321. Read, D.P., Feeny, P.P. & Root, R.B. 1970. Habitat selection by the aphid parasite *Diaeretiella rapae* (Hymenoptera: Braconidae) and hyperparasite *Charips brassicae* (Hymenoptera; Cynipidae). *Canadian Entomologist*. 102: 1567-1578.

322. Renault, S., Petit, A., Bénédet, F., Bigot, S. & Bigot, Y. 2002. Effects of *Diadromus pulchellus* ascovirus, DpAV-4, on the hemocytic encapsulation response and capsule melanization of the leek-moth pupa, *Acrolepiopsis assectella*. *Journal of Insect Physiology*. 48: 297-302.

323. Reznik, S.Y., Chernoguz, D.G. & Zinovjeva, K.B. 1992. Host searching, oviposition preferences and optimal synchronisation in *Alysia manducator* (Hymenoptera: Braconidae), a parasitoid of the blowfly, *Calliphora vicina*. *Oikos*. 65: 81-88.

324. Riggin, T.M., Espelie, K.E., Wiseman, B.R. & Isenhour, D.J. 1993. Distribution of fall armyworm (Lepidoptera: Noctuidae) parasitoids on five corn genotypes in south Georgia. *Florida Entomologist*. 76: 292-302.

325. Rotheray, G.E. 1981. Host searching and oviposition behaviour of some parasitoids of aphidophagous Syrphidae. *Ecological entomology*. 6: 79-87.

326. Rotheray, G.E. 1984. Host relations, life cycles and multi-parasitism in some parasitoids of aphidophagous Syrphidae (Diptera). *Ecological entomology*. 9: 303-310.

327. Rothman, L.D. & Darling, D.C. 1990. Parasitoids of the goldenrod gall moth: effects of scale on spatial density dependence. *Oecologia*. 83: 1-6.

328. Rouleux-Bonnin, F., Renault, S., Rabouille, A., Periquet, G. & Bigot, Y. 1999. Free serosal cells originating from the embryo of the wasp *Diadromus pulchellus* in the pupal body of parasitized leek-moth, *Acrolepiosis assectella*. Are these cells teratocyte-like? *Journal of Insect Physiology*. 45: 479-484.

329. Ru, N. & Workman, R.B. 1979. Seasonal abundance and parasites of the imported cabbageworm, diamondback moth, and cabbage webworm in north-east Florida. *Florida Entomologist*. 62: 68-69.

330. Rungrojwanich, K. & Walter, G.H. 2000. The Australian fruit fly parasitoid *Diachasmimorpha kraussi* (Fullaway): life history, ovipositional patterns, distribution and hosts (Hymenoptera: Braconidae: Opiinae). *Pan-Pacific Entomologist*. 76: 1-11.

331. Sandlan, K. 1979. Sex ratio regulation in *Coccygomimus turionella* Linnaeus (Hymenoptera: Ichneumonidae) and its ecological implications. *Ecological Entomology*. 4: 365-378.

332. Schaupp, W.C., Volney, W.J.A. & Waters, W.E. 1991. Parasitoids of endemic and epidemic populations of *Choristoneura occidentalis* Freeman and *Choristoneura retiniana* (Walsingham) (Lepidoptera: Tortricidae) in Southern Oregon. *Canadian Entomologist*. 123: 1095-1102.

333. Schellhorn, N.A., Kuhman, T.R., Olson, A.C. & Ives, A.R. 2002. Competition between native and introduced parasitoids of aphids: nontarget effects and biological control. *Ecology*. 83: 2745-2757.

334. Schmid, J.M. 1981. Distribution of western spruce budworm (Lepidoptera: Tortricidae) insect parasites in the crowns of host trees. *Canadian Entomologist*. 113: 1101-1106.

335. Schooler, S.S., Ives, A.R. & Harmon, J. 1996. Hyperparasitoid aggregation in response to variation in *Aphidius ervi* host density at three spatial scales. *Ecological Entomology*. 21: 249-258.

336. Sequeira, R. & Mackauer, M. 1992. Nutritional ecology of an insect host-parasitoid association: the pea aphid *Aphidius ervi* system. *Ecology*. 73: 183-189.

337. Sequeira, R. & Mackauer, M. 1993. The nutritional ecology of a parasitoid wasp, *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae. *Canadian Entomologist*. 125: 423-430.

338. Shaltiel, L. & Ayal, Y. 1998. The use of kairomones for foraging decisions by an aphid parasitoid in small host aggregations. *Ecological Entomology*. 23: 319-329.

339. Sharkey, M.J. 1985. Notes on the genera *Bassus* Fabricius and *Agathis* Latreille, with a description of *Bassus arthurellus* n. sp. (Hymenoptera: Braconidae). *Canadian Entomologist*. 117: 1497-1502.

340. Shaw, M.R. 1983. On(e) evolution of endoparasitism: the biology of some genera of Rogadinae (Braconidae). *Contributions of the American Entomological Institute*. 20: 307-328.

341. Shaw, M.R. 1988. *Meteorus brevicauda* Thomson (Hymenoptera: Braconidae) reared from larvae of *Zeugophora subspinosa* (Fabricius) (Coleoptera: Chrysomelidae). *Entomologist's Gazette*. 39: 205-206.

342. Shaw, M.R. 1989. A host record for *Stilbops limneriaeformis* Schmiedeknecht (Hymenoptera: Ichneumonidae, Stilbopinae) in Scotland. *Entomologist's Gazette*. 40: 5-6.

343. Shaw, M.R. & Wahl, D.B. 1989. The biology egg and larvae of *Acaenitus dubitator* Panzer (Hymenoptera: Ichneumonidae: Acaenitinae). *Systematic Entomology*. 14: 117-125.

344. Shaw, M.R. 1992. *Microtypus wesmaelii* Ratzeburg (Hymenoptera: Braconidae, Microtypinae), a species and subfamily new to Britain. *Entomologist's Gazette*. 43: 289-291.

345. Shaw, M.R. 1994. Parasitoid host ranges. In: *Parasitoid community ecology* (B.A. Hawkins & N. Sheehan, eds.), Oxford University Press. pp. 111-114.

346. Shaw, M.R. & Askew, R.R. 1976. Ichneumonoidea (Hymenoptera) parasitic upon leaf-mining insects of the orders Lepidoptera, Hymenoptera, and Coleoptera. *Ecological Entomology*. 1: 127-133.

347. Shenefelt, R.D. 1970. Braconidae 3. Agathidinae. *Hymenopterum catalogues*, Pars 6: 306-428.

348. Shenefelt, R.D. 1972. Braconidae 4. Microgasterinae *Apanteles*. *Hymenopterum catalogues*, Pars 7: 429-668.

349. Shiotsu, Y. & Arakawa, R. 1982. One host-one parasitoid system: seasonal life cycles of *Pryeria sinica* (Lepidoptera) and *Agrothereutes minousubae* (Hymenoptera). *Researches on Population Ecology*. 24: 43-57.

350. Shorthouse, J.D. & Leggo, J.L. 2002. Immature stages of the galler *Diplolepis triforma* (Hymenoptera: Cynipidae) with comments on the role of its prepupa. *Canadian Entomologist*. 134: 433-446.

351. Sieglaff, D.H., Mitchell, E.R.. & Hu, G.Y. 1998. Evaluation of rearing methods for *Diadegma insulare* (Hymenoptera: Ichneumonidae), an endoparasitoid of the diamondback moth (Lepidoptera: Plutellidae). *Florida Entomologist*. 81: 578-582.

352. Sigsgaard, L. 2002. A survey of aphids and aphid parasitoids in cereal fields in Denmark, and the parasitoids role in biological control. *Journal of Applied Entomology*. 126: 101-107.

353. Singh, R. & Srivastava, P.N. 1990. Host specificity and seasonal distribution of *Alloxysta pleuralis*, a Cynipoid hyperparasitoid of aphids in India. *Ecological Entomology*. 15: 215-224.

354. Sirot, E. 1996. The pay-off from superparasitism in the solitary parasitoid *Venturia canescens*. *Ecological Entomology*. 21: 305-307.

355. Sivapragasam, A. & Chua, T.H. 1997. Natural enemies for the cabbage webworm, *Hellula undalis* (Fabr.) (Lepidoptera: Pyralidae) in Malaysia. *Researches on Population Ecology*. 39: 3-10.

356. Sivinski, J., Aluja, M. & Holler, T. 1999. The distributions of the Caribbean fruit fly, *Anastrepha suspensa* (Tephritidae) and its parasitoids (Hymenoptera: Braconidae) within the canopies of host trees. *Florida Entomologist*. 82: 72-81.

357. Sivinski, J., Aluja, M., Holler, T. & Eitam, A. 1998. Phenological comparison of two Braconid parasitoids of the Caribbean fruit fly (Diptera: Tephritidae). *Environmental Entomology*. 27: 360-365.

358. Sivinski, J.M., Calkins, C.O., Baranowski, R., Harris, D., Brambila, J., Diaz, J., Burns, R.E., Holler, T. & Dodson, G. 1996. Suppression of a Caribbean fruit fly (*Anastrepha suspensa* (Loew) Diptera: Tephritidae) population through augmented releases of the parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). *Biological Control*. 6: 177-185.

359. Smith, D.B. & Sears, M.K. 1984. Life history of *Plutella porrectella*, a relative of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Canadian Entomologist*. 116: 913-917.

360. Spradberry, J.P. 1968. The biology of *Pseudorhyssa sternata* Merrill (Hymenoptera: Ichneumonidae), a cleptoparasite of Siricid woodwasps. *Bulletin of Entomological Research*. 59: 291-297.

361. Spradberry, J.P. & Kirk, A.A. 1978. Aspects of the ecology of siricid woodwasps (Hymenoptera: Sircidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research*. 68: 341-359.

362. Stadler, B. & Mackauer, M. 1996. Influence of plant quality on interactions between the aphid parasitoid *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae) and its host, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphidiidae). *Canadian Entomologist*. 128: 27-39.

363. Stairs, G.R. 1983. Oviposition by *Glypta fumiferanae* (Hymenoptera: Ichneumonidae) in *Choristoneura fumiferana* (Lepidoptera: Tortricidae) larvae and the effect of honey on their fecundity and survival. *Canadian Entomologist*. 115: 689-692.

364. Stark, J.D., Vargas, R.I. & Thalman, R.K. 1991. Diversity and abundance of oriental fruit fly parasitoids (Hymenoptera: Braconidae) in guava orchards in Kauai, Hawaii. *Journal of Economic Entomology.* 84: 1460-1467.

365. Stark, J.D., Vargas, R.I. & Walsh, W.A. 1994. Temporal synchrony and patterns in an exotic host-parasitoid community. *Oecologia.* 100: 196-199.

366. Stamp, N.E. 1981. Behaviour of parasitized aposematic caterpillars: advantageous to the parasitoid of the host? *American Naturalist.* 118: 715-725.

367. Stary, P. 1993. The fate of released parasitoids (Hymenoptera: Braconidae, Aphidiinae) for biological control of aphids in Chile. *Bulletin of Entomological Research.* 83: 633-639.

368. Stary, P. 1999. Parasitoids and biocontrol of Russian wheat aphid, *Diuraphis noxia* (Kurdj.) expanding in central Europe. *Journal of Applied Entomology.* 123: 273-279.

369. Stephenson, A.G. 1982. The role of the extrafloral nectarines of *Catalpa speciosa* in limiting herbivory and increasing fruit production. *Ecology.* 63: 663-669.

370. Stille, B. 1984. The effect of host plant and parasitoids on the reproductive success of the parthenogenetic gall wasp *Diplolepis rosae* (Hymenoptera: Cynipidae). *Oecologia.* 63: 364-369.

371. Stireman III, J.O. & Singer, M.S. 2002. Spatial and temporal variation in the parasitoid assemblage of an exophytic polyphagous caterpillar. *Ecological Entomology.* 27: 588-600.

372. Stuart, M.K. & Greenstone, M.H. 1997. Immunological detection of hymenopteran parasitism in *Helicoverpa zea* and *Heliothis virescens. Biological Control.* 8: 197-202.

373. Sugimoto, T., Minkenberg, O.P.J.M., Takabayashi, J., Dicke, M. & van Lenteren, J.C. 1990. Foraging for patchily-distributed lea mines by the parasitic wasp, *Dacnusa sibirica. Researches on Population Ecology.* 32: 381-389.

374. Sugonyaev, E.S. 1994. Cotton pest management: Part 5. A commonwealth of independent states perspective. *Annual Review of Entomology.* 39: 579-592.

375. Sulanç, M. & Emrei, I. 2000. Effects of B group vitamins and choline chloride on the development and protein synthesis in the male larvae of *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae). *Journal of Applied Entomology.* 124: 151-153.

376. Surgeoner, G.A. & Wallner, W.E. 1978. Foliage consumption by the variable oak leaf caterpillar, *Heterocampa manteo* (Lepidoptera: Notodontidae), its use in defoliation predictions. *Canadian Entomologist.* 110: 241-244.

377. Synder, W.E. & Ives, A.R. 2001. Generalist predators disrupt biological control by a specialist parasitoid. *Ecology.* 82: 705-716.

378. Tahhan, O. & van Emden, H.F. 1989. Biology of *Bruchus dentipes* Baudi (Coleoptera: Bruchidae) on *Vicia faba* and a method to obtain gravid females during the imaginal quiescence period. *Bulletin of Entomological Research.* 79: 201-210.

379. Takabayashi, J., Sato, Y., Horikoshi, M., Yamaoka, R., Yano, S., Ohsaki, N. & Dicke, M.
380. 1998. Plant effects on parasitoid foraging: differences between two tritrophic systems. *Biological Control.* 11: 97-103.

381. Teder, T., Tanhuanpää, M., Ruohamäki, K., Kaitaniemi, P. & Henriksson, J. 2000. Temporal and spatial variation of larval parasitism in non-outbreaking populations of a folivorous moth. *Oecologia.* 123: 516-524.

382. Thaler, J.S. 2002. Effect of jasmonate-induced plant responses on the natural enemies of herbivores. *Journal of Animal Ecology.* 71: 141-150.

383. Thompson, L.C. & Kulman, H.M. 1980. Parasites of the yellowhead spruce sawfly, *Pikonema alaskensis* (Hymenoptera: Tenthredinidae), in Maine and Nova Scotia. *Canadian Entomologist.* 112: 25-29.

384. Thompson, L.C., Kulman, H.M. & Hellenthal, R.A. 1979. Parasitism of the larch sawfly by *Bessa harveyi* (Diptera: Tachinidae). *Annals of the Entomological Society of America.* 72: 468-471.

385. Thompson, S.N. 1982. Immediate effects of parasitization by the insect parasite, *Hyposoter exiguae* on the nutritional physiology of its host, *Trichoplusia ni. Journal of Parasitology.* 68: 936-941.

386. Tillman, P.G. & Laster, M.L. 1995. Parasitization of *Heliothis virescens* and *Heliothis virescens-H. subflexa* backcross (Lepidoptera: Noctuidae) by *Microplitis croceipes* (Hymenoptera: Braconidae). *Environmental Entomology.* 24: 409-411.

387. Tillman, P.G. & Powell, J.E. 1991. Developmental time in relation to temperature for *Microplitis croceipes, M. demolitor, Cotesia kazak* (Hymenoptera: Braconidae), and *Hyposoter didymator* (Hymenoptera: Ichneumonidae), Endoparasitoids of the tobacco budworm (Lepidoptera: Noctuidae). *Environmental Entomology.* 20: 61-64.

388. Tingle, F.C., Mitchell, E.R. & heath, R.R. 1989. Mating and oviposition by *Cotesia* (=*Apanteles*) *marginiventris* (Hymenoptera: Braconidae) in presence of synthetic pheromone of *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Journal of Chemical Ecology.* 15: 2045-2050.

389. Tipping, P.W. 1993. Field studies with *Cassida rubiginosa* (Coleoptera: Chrysomelidae) in Canada thistle. *Environmental Entomology.* 22: 1402-1407.

390. Toft, R.J., Malham, J.P. & Beggs, J.R. 1999. Mortality and emergence pattern of overwintering cocoons of the wasp parasitoid *Sphecophaga vesparum vesparum* (Hymenoptera: Ichneumonidae) in New Zealand. *Environmental Entomology.* 28: 9-13.

391. Tuda, M. 1996. Temporal / spatial structure and the dynamic property of laboratory host-parasitoid systems. *Researches in Population Ecology.*38: 133-140.

392. Tuda, M. 1998. Evolutionary character changes and population responses in an insect host-parasitoid experimental system. *Researches in Population Ecology.* 40: 293-299.

393. Turnock, W.J. 1988. Density, parasitism, and disease incidence of larvae of the bertha armyworm, *Mamestra configurata* Walker (Lepidoptera: Noctuidae), in Manitoba., 1973-1986. *Canadian Entomologist.* 120: 401-413.

394. Turnock, W.J. & Bilodeau, R.J. 1984. Survival of pupae of *Mamestra configurata* (Lepidoptera: Noctuidae) and two of its parasites in untilled and tilled soil. *Canadian Entomologist.* 116: 257-267.

395. Uçkan, F. & Gülel, A. 2002. Age-related fecundity and sex ratio variation in *Apanteles galleriae* (Hym., Braconidae) and host effect on fecundity and sex ratio of its hyperparasitoid *Dibrachys boarmiae* (Hym., Pteromalidae). *Journal of Applied Entomology.* 126: 534-537.

396. Ueno, T. 1994. Self-recognition by the parasite wasp *Itoplectis naranyae* (Hymenoptera: Ichneumonidae). *Oikos.* 70: 333-339.

397. Ueno, T. 1999. Adult size and reproduction in the ectoparasitoid *Agrothereutes lanceolatus* Walker (Hym., Ichneumonidae). *Journal of Applied Entomology.* 123: 357-361.

398. Ueno, T. 2000. Host concealment: a determinant for host acceptance and feeding in an ectoparasitoid wasp. *Oikos*. 89: 223-230.

399. Vakenti, J.M., Cossentine, J.E., Cooper, B.E., Sharkey, M.J., Yoshimoto, C.M. & Jensen, L.B.M. 2001. Host-plant range and parasitoids of obliquebanded and three-lined leafrollers (Lepidoptera: Tortricidae). *Canadian Entomologist*. 133: 139-146.

400. Vaughn, T.T. & Antolin, M.F. 1998. Population genetics of an opportunistic parasitoid in an agricultural landscape. *Heredity*. 80: 152-162.

401. Vet, L.E.M. & van Alphen, J.J.M. 1985. A comparative functional approach to he host detection behaviour of parasitic wasps. 1. A qualitative study on Eucoilidae and Alysiinae. *Oikos*. 44: 478-486.

402. Vet, L.E.M., Datema, A., Janssen, A. & Snellen, H. 1994. Clutch size in a larval-pupal endoparasitoid: consequences for fitness. *Journal of Animal Ecology*. 63: 807-815.

403. Vet, L.E.M. & Janse, C.J. 1984. Fitness of two sibling species of *Asobara* (Braconidae: Alysiinae), larval parasitoids of Drosophilidae in different microhabitats. *Ecological Entomology*. 9: 345-354.

404. Vet, L.E.M., Lewis, W.J. & Cardé, R.T. 1992. Parasitoid foraging and learning. In: *Natural selection: domains, levels and challenges*. (G.C. Williams, ed.) Oxford University Press, New York. pp. 65-101.

405. Vincent, C., Rancourt, B., Sarazin, M. & Kulhmann, U. 2001. Releases and first recovery of *Lathrolestes ensator* (Hymenoptera: Ichneumonidae) in North America, a parasitoid of *Hoplocampa testudinae* (Hymenoptera: Tenthredinidae). *Canadian Entomologist*. 133: 147-149.

406. Vinson, S.B. 1975. Biochemical coevolution between parasitoids and their hosts. In: *Evolutionary strategies of parasitic insects and mites*. (P.W. Price, ed.). Plenum Press, New York. pp. 14-48.

407. Visser, M.E. 1994. The importance of being large: the relationship between size and fitness in females of the parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). *Journal of Animal Ecology*. 63: 963-978.

408. Visser, M.E. & Rosenheim, J.A. 1998. The influence of competition between foragers on clutch size decisions in insect parasitoids. *Biological Control*. 11: 169-174.

409. Völkl, W. & Mackauer, M. 2000. Oviposition behaviour of Aphidiine wasps (Hymenoptera: Braconidae, Aphidiinae): morphological adaptations and evolutionary trends. *Canadian Entomologist*. 132: 197-212.

410. Vos, M., Hemerik, L. & Vet, L.E.M. 1998. Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. *Journal of Animal Ecology*. 67: 774-783.

411. Wäckers, F.L., Mitter, E. & Dorn, S. 1998. Vibrational sounding by a pupal parasitoid *Pimpla* (*Coccygomimus*) *turionellae*: an additional solution to the reliability-detectability problem. *Biological Control*. 11: 141-146.

412. Wang, Q. & Shi, G. 2001. Host preference and sex allocation of three hymenopteran parasitoid species (Ichneumonidae and Braconidae) of a longicorn pest, *Oemona hita* (Fabr.) (Col., Cerambycidae). *Journal of Applied Entomology*. 125: 463-467.

413. Wardle, A.R. 1990. Learning of host microhabitat colour by *Exeristes roborator* (F.) (Hymenoptera: Ichneumonidae). *Animal Behaviour*. 39: 914-923.

414. Wardle, A.R. & Borden, J.H. 1985. Age-dependent associative learning by *Exeristes roborator* (F.) (Hymenoptera: Ichneumonidae). *Canadian Entomologist*. 117: 605-616.

415. Wei, H., Goyer, R.A. & Lenhard, G. 1998. Abundance of parasitoids of *Archips argyrospila* (Lepidoptera: Tortricidae) in Louisiana. *Environmental Entomology*. 27: 726-730.

416. Went, D.F. 1982. Egg activation and parthenogenetic reproduction in insects. *Biological Review*. 57: 319-344.

417. West, R.J. & Kenis, M. 1997. Screening four exotic parasitoids as potential controls for the eastern hemlock looper, *Lambdina fiscellaria fiscellaria* (Guenée) (Lepidoptera: Geometridae). *Canadian Entomologist*. 129: 831-841.

418. West, R.J., Dixon, P.L., Quednau, F.W., Lim K.P. & Hiscock, K. 1994. Establishment of *Olesicampe geniculatae* Quednau & Lim (Hymenoptera: Ichneumonidae) to control the mountain ash sawfly, *Pristiphora geniculata* (Hartig) (Hymenoptera: Tenthredinidae), in Newfoundland. *Canadian Entomologist*. 126: 7-11.

419. West, R.J., Kenis, M., Butt, G.W. & Bennett, S.M. 1999. Parasitoid complex of *Zeiraphera Canadensis* (Lepidoptera: Tortricidae) and evaluation of *Tycherus osculator* (Hymenoptera: Ichneumonidae) as a biological control agent. *Canadian Entomologist*. 131: 465-474.

420. Wharton, R.A. 1977. New World *Aphaereta* species (Hymenoptera: Braconidae: Alysiinae), with a discussion of terminology used in the Tribe Alysiini. *Annals of the Entomological Society of America*. 70: 782-803.

421. Wharton, R.A. 2000. Can braconid classification be reconstructed to facilitate portrayal of relationships? In: *Hymenoptera: Evolution, biodiversity and biological control* (A. Austin & M. Dowton, eds.), CSIRO Publishing. pp. 143-153.

422. Wylie, H.G. 1977. Observations on *Mercia ampelus* (Diptera: Tachinidae), an occasional parasite of the bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae), in western Canada. *Canadian Entomologist*. 109: 1023-1024.

423. Wylie, H.G. & Ayre, G.L. 1979. Hosts of *Banchus flavescens* (Hymenoptera: Ichneumonidae) and *Athrycia cinerea* (Diptera: Tachinidae) in Manitoba. *Canadian Entomologist*. 111: 747-748.

424. Wylie, H.G. & Bucher, G.E. 1977. The bertha armyworm, *Mamestra configurata* (Lepidoptera: Noctuidae). Mortality of immature stages on the rape crop, 1972-1975. *Canadian Entomologist*. 109: 823-837.

425. Xu, J., Shelton, A.M. & Cheng, X. 2001. Comparison of *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Microplitis plutellae* (Hymenoptera: Braconidae) as biological control agents of *Plutella xylostella* (Lepidoptera: Plutellidae): field parasitism, insecticide susceptibility, and host-searching. *Journal of Economic Entomology*. 92: 14-20.

426. Yates, M.G. 1984. The biology of the oak bark beetle, *Scolytus intricatus* (Ratzeburg) (Coleoptera: Scolytidae) in southern England. *Bulletin of Entomological Research*. 74: 569-579.

427. Yokami, R.K. & Tang, Y.Q. 1996. A survey of parasitoids of brown citrus aphid (Homoptera; Aphididae) in Puerto Rico. *Biological Control*. 6: 222-225.

428. Zaviezo, T. & Mills, N. 2001. The response of *Hyssopus pallidus* to hosts previously parasitized by *Ascogaster quadridentata*: heterospecific discrimination and host quality. *Ecological Entomology*. 26: 91-99.

429. Zijp, J.P. & Blommers, L.H.M. 2002. Apple sawfly *Hoplocampa testudinae* (Hymenoptera, Tenthredinidae) and its parasitoid *Lathrolestes ensator* in Dutch apple orchards (Hymenoptera, Ichneumonidae, Ctenopelmatinae). *Journal of Applied Entomology*. 126: 265-274.

430. Zijp, J.P. & Blommers, L.H.M. 2002. Impact of the parasitoid *Lathrolestes ensator* (Hymenoptera, Ichneumonidae, Ctenopelmatinae) as antagonist of apple sawfly *Hoplocampa testudinae* (Hymenoptera, Tenthredinidae). *Journal of Applied Entomology*. 126: 366-377.

431. Zolubas, P., Gedminas, A. & Shields, K. 2001. Gypsy moth parasitoids in the declining outbreak in Lithuania. *Journal of Applied Entomology*. 125: 229-234.

References

Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evolutionary Ecology Research*. 1: 895-909.

Anderson, W.W. & King, C.E. 1970. Age-specific selection. *Proceedings of the National Academy of Sciences, USA*. 66: 780-786.

Archie, J. 1989a. A randomization test for phylogenetic information in systematic data. *Systematic Zoology*. 38: 239-252.

Archie, J. 1989b. Homoplasy excess ratios: new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. *Systematic Zoology*. 38: 253-269.

Arnaud, P.H. Jr. 1978. *A host parasite catalog of North American Tachinidae (Diptera)*. USDA miscellaneous publication no. 1319. USDA, Washington, D.C.

Arnold, S.J. 1992. Constraints on phenotypic evolution. *The American Naturalist*. 140: S85-S107.

Askew, R.R. 1975. The organisation of chalcid-dominated parasitoid communities centred upon endophytic hosts. In: *Evolutionary strategies of parasitoids* (P.W. Price, ed.), pp. 130-153. Plenum, New York.

Askew, R.R. 1994. Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? In: *Parasitoid community ecology* (B.A. Hawkins & W. Sheehan, eds.), pp. 177-202. Oxford University Press, Oxford.

Askew, R.R. & Shaw, M.R. 1974. An account of the Chalcidoidea (Hymenoptera) parasitizing leaf-mining insects of deciduous trees in Britain. *Biological Journal of the Linnean Society*. 6: 289-335.

Askew, R.R. & Shaw, M.R. 1986. Parasitoid communities: their size, structure and development. In: *Insect parasitoids* (J. Waage & D. Greathead, eds.), pp. 225-264. Academic Press, London.

Baker, G. L. 1976. The biology of *Pristocera rufa* Kieffer (Hymenoptera: Bethylidae), a parasite of *Pantorhytes szentvanyi* Marshall (Coleoptera: Curculionidae) in Papua New Guinea. *Journal of the Australian Entomological Society*. 15: 153-160.

Basibuyuk, H.H. & Quicke, D.L.J. 1995. Morphology of the antenna cleaner in the Hymenoptera with particular reference to non-aculeate families (Insecta). *Zoologica Scripta* 24: 157-177.

Belshaw, R. & Quicke, D.L.J. 2002. Robustness of ancestral state estimates: evolution of life history strategy in Ichneumonoid parasitoids. *Systematic Biology*. 51: 450-477.

Belshaw, R., Fitton, M., Herniou, E., Gimeno, C. & Quicke, D.L.J. 1998. A phylogenetic reconstruction of the Ichneumonoidea (Hymenoptera) based on the D2 variable region of 28S ribosomal RNA. *Systematic Entomology*. 23: 109-123.

Belshaw, R., Grafen, A. & Quicke, D.L.J. 2003. Inferring life history from ovipositor morphology in parasitoid wasps using phylogenetic regression and discriminant analysis. *Zoological Journal of the Linnean Society*. 139: 213-228.

Bennett, P. and Owens, I. 2002. *Evolutionary ecology of birds: life histories, mating systems and extinction*. Oxford University Press, Oxford.

Benton, M.J. 1998. Molecular and morphological phylogenetics of mammals: congruence with stratigraphic data. *Molecular Phylogenetics & Evolution*. 9: 398-407.

Bernays, E.A. & Chapman, R.F. 1994. *Host-plant selection by phytophagous insects.* Chapman & Hall, New York.

Bjorklund, M. 1997. Variation in growth rate in the blue tit (*Parus caeruleus*). *Journal of Evolutionary Biology*. 10: 139-155.

Blackburn, T.W. 1990. Comparative and experimental studies of animal life histories. Dphil Thesis, University of Oxford, Oxford.

Blackburn, T.M. 1991a. A comparative examination of life-span and fecundity in parasitoid Hymenoptera. *Journal of Animal Ecology*. 60: 151-164.

Blackburn, T.M. 1991b. Evidence for a 'fast-slow' continuum of life-history traits among parasitoid Hymenoptera. *Functional Ecology*. 5: 65-74.

Boivin, G. & van Baaren, J. 2000. The role of larval aggression and mobility in the transition between solitary and gregarious development in parasitoid wasps. *Ecology Letters*. 3: 469-474.

Braby, M.F. 2002. Life history strategies and habitat templates of tropical butterflies in north-eastern Australia. *Evolutionary Ecology*. 16: 399-413.

Brodeur, J., Geervliet, J.B.F. & Vet L.E.M. 1996. The role of host species, age and defensive behaviour on ovipositional decisions in a solitary specialist and gregarious generalist parasitoid (*Cotesia* species). *Entomologia Experimentalis et Applicata*. 81: 125-132.

Brodeur, J., Geervliet, J.B.F. & Vet L.E.M. 1998. Effects of *Pieris* host species on life history parameters in a solitary specialist and gregarious generalist parasitoid (*Cotesia* species). *Entomologia Experimentalis et Applicata*. 86: 145-152.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist*. 124: 255-279.

Brown, W. L . Jr. 1982. Hymenoptera. In: *Synopsis and classification of living organisms* (S.P. Parker, ed.), pp. 652-668. McGraw-Hill, New York.

Calder, W.A. III. 1984. *Size, function and life-history*. Harvard University Press, Cambridge, Massachusetts, USA.

Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. *Proceedings of the Royal Society of London, Series B*. 266: 1221-1225.

Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *Journal of Animal Ecology*. 71: 79-87.

Charlesworth, B. 1990. Optimization models, quantitative genetics and mutation. *Evolution*. 44: 520-538.

Charnov, E.L. 1991. Evolution of life-history variation among female mammals. *Proceedings of the National Academy of Science, USA*. 88: 1134-1137.

Charnov, E.L. 1993. *Life history invariants: some explorations of symmetry in evolutionary ecology*. Oxford University Press, Oxford.

Charnov, E.L. 2000. Evolution of life-history variation among species of altrical birds. *Evolutionary Ecology Research*. 2: 365-373.

Charnov, E.L. 2001. Evolution of mammal life histories. *Evolutionary Ecology Research.* 3: 521-535.

Cheverud, J.M., Dow, M.M. & Leutenegger, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution.* 39: 1335-1351.

Clutton-Brock, T.H. & Harvey, P.H. 1977. Primate ecology and social organisation. *Journal of Zoology.* 183; 1-33.

Crawley, M.J. 1993. *GLIM for ecologists.* Blackwell Scientific Publications, Oxford.

Deevey, E.S. 1947. Life tables for natural populations. *Quarterly Review of Biology.* 22: 283-314.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and adult survival. *Journal of Animal Ecology.* 59: 269-285.

Dowton, M. 1999. Relationships among the cyclostome braconid (Hymenoptera: Braconidae) subfamilies inferred from a mitochondrial tRNA gene arrangement. *Molecular Phylogenetics & Evolution.* 11: 283-287.

Dowton, M. & Austin, A.D. 1998. Phylogenetic relationships among the microgastroid wasps (Hymenoptera: Braconidae): Combined analysis of 16s and 28s rDNA genes, and morphological data. *Molecular Phylogenetics & Evolution.* 10: 354-366.

Dowton, M. & Austin, A.D. 2001. Simultaneous analysis of 16s, 28s, COI and morphology in the Hymenoptera Apocrita - evolutionary transitions among parasitic wasps. *Biological Journal of the Linnean Society.* 74: 87-111.

Dowton, M., Belshaw, R., Austin, A.D. & Quicke, D.L.J. 2002. Simultaneous molecular and morphological analysis of braconid relationships (Insecta: Hymenoptera: Braconidae) indicates independent mt-tRNA inversions within a single wasp family. *Journal of Molecular Evolution.* 54: 210-226.

Edwards, S.V. & Kot, M. 1995. Comparative methods at the species level: geographic variation in morphology and group size in grey-crowned babblers (*Pomatostomus temporalis*). *Evolution.* 49: 1134-1146.

Eggleton, P. & Belshaw, R. 1992. Insect parasitoids: an evolutionary overview. *Proceedings of the Royal Society of London, B.* 337: 1-20.

Ellers, J. 1996. Fat and eggs: an alternative method to measure the trade-off between survival and reproduction in insect parasitoids. *Netherlands Journal of Zoology.* 46: 227-235.

Ellers, J. & van Alphen, J.J.M. 1997. Life history evolution in *Asobara tabida*: plasticity in the allocation of fat reserves to survival and reproduction. *Journal of Evolutionary Biology.* 10: 771-785.

Ellers, J., van Alphen, J.J.M. & Sevenster, J.G. 1998. A field study of size-fitness relationships in the parasitoid *Asobara tabida. Journal of Animal Ecology.* 67: 318-324.

Ellers, J., Driessen, G. & Sevenster, J.G. 2000a. The shape of the trade-off function between egg production and life span in the parasitoid wasp *Asobara tabida. Netherlands Journal of Zoology.* 50: 29-36.

Farris, J.S. 1989. The retention index and rescaled consistency index. *Cladistics.* 2: 14-419.

Felsenstein, J. 1973a. Maximum-likelihood estimation of evolutionary trees from continuous characters. *American Journal of Human Genetics*. 25: 471-492.

Felsenstein, J. 1973b. Maximum-likelihood and minimum-steps methods for estimating evolutionary trees from data on discrete characters. *Systematic Zoology*. 22: 240-249.

Felsenstein, J. 1985. Phylogenies and the comparative method. *The American Naturalist*. 125: 1-15.

Fenster, E.J. & Sorhannus, U. 1991. On the measurement of morphological rates of evolution. A review. *Evolutionary Biology*. 25: 375-410.

Fisher, D.O., Owens, I.P.F. & Johnson, C.N. 2001. The ecological basis of life history variation in marsupials. *Ecology*. 82: 3531-3540.

Flanders, S.E. 1950. Regulation of ovulation and egg disposal in the parasitic Hymenoptera. *Canadian Entomologist*. 101; 467-480.

Foote, M. 1996. Models of morphological diversity. In. *Evolutionary paleobiology* (D. Jablonski, D.H. Erwin & J.H. Lipps, eds.), pp. 62-86. University of Chicago Press, Chicago.

Fox, L.R. & Morrow, P.A. 1981. Specialization: species property or local phenomenon? *Science*. 211: 887-893.

Franco, M. and Silvertown, J. 1997. Life history variation in plants: an exploration of the fast-slow continuum hypothesis. In: *Plant life histories: ecology, phylogeny and evolution* (J. Silvertown, M. Franco & J.L. Harper, eds.), pp. 210-227. Cambridge University Press, Cambridge.

Frank, S.A. 1997. Models of symbiosis. *The American Naturalist*. 150: S80-S99.

Freckleton, R.P., Harvey, P.H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*. 160: 712-726.

Futuyma, D.J. 1976. Food plant specialization and environmental predictability in Lepidoptera. *The American Naturalist*. 110: 285-292.

Futuyma, D.J. 2001. Ecological specialization and generalization. In: *Evolutionary ecology: concepts and case studies* (C.A. Fox, D.A. Roff & D.J. Fairburn, eds.), pp. 177-189. Oxford University Press, Oxford.

Futuyma, D.J. & Moreno, G. 1988. The evolution of ecological specialization. *Annual Review of Ecological Systematics*. 19: 207-292.

Garland, T. Jr., Harvey, P.H. & Ives, A.R. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*. 41: 18-32.

Gaston, K.J. 1990. Patterns in the geographical ranges of species. *Biological Research*. 65: 105-129.

Gaston, K.J. 1991. The magnitude of global insect species richness. *Conservation Biology*. 5: 283-296.

Gaston, K.J. & Blackburn, T.M. 2000. *Pattern and process in macroecology*. Blackwell Science Limited.

Gauld, I.D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology*. 11: 155-161.

Gauld, I.D. 1987. Some factors affecting the composition of tropical ichneumonid faunas.

Biological Journal of the Linnean Society. 30: 299-312.

Gauld, I.D. 1988. Evolutionary patterns of host utilisation by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society*. 57: 137-162.

Gauld, I. & Bolton, B. 1988. *The Hymenoptera*. Oxford University Press.

Gauld, I. & Fitton, M.G. 1987. Sexual dimorphism in Ichneumonidae; a response to Hurlbutt. *Biological Journal of the Linnean Society*. 31: 291-300.

Gauld, I.D., Gaston, K.J. & Janzen, D.H. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the 'nasty' host hypothesis. *Oikos*. 65: 353-357.

Gauthier, N., La Salle, J., Quicke, D.L.J., Godfray, H.C.J. 2000. Phylogeny of Eulophidae (Hymenoptera: Chalcidoidea), with a reclassification of Eulophinae and the recognition that Elasmidae are derived eulophids. *Systematic Entomology*. 25: 521-539.

Gavrilets, S. 1999. Dynamics of clade diversification on the morphological hypercube. *Proceedings of the Royal Society of London*, *Series B*. 266: 817-824.

Gemmill, A.W., Skorping, A. & Read, A.F. 1999. Optimal timing of first reproduction in parasitic nematodes. *Journal of Evolutionary Biology*. 12: 1148-1156.

Gingerich, P.D. 1993. Quantification and comparison of evolutionary rates. *American Journal of Science*. 293A: 453-478.

Gittleman, J.L. 1986. Carnivore brain size, behavioural ecology, and phylogeny. *Journal of Mammals*. 67: 23-36.

Gittleman, J.L. 1993. Carnivore life histories: a re-analysis in the light of new models. In: *Mammals as predators* (N. Dunstone & M.L. Gorman, eds.), pp. 65-86. Oxford University Press, Oxford.

Gittleman, J.L. & Decker, D. 1994. The phylogeny of behaviour. In: *Behaviour and Evolution* (P.J.B. Slater & T.R. Halliday, eds.), pp. 80-105. Cambridge University Press, Cambridge.

Gittleman, J.L., Anderson, C.G., Kot, M. & Luh, H-K. 1996a. Phylogenetic lability and rates of evolution: a comparison of behavioural, morphological and life history traits. In: *Phylogenies and the comparative method in animal behaviour* (E.P. Martins, ed.), pp. 167-206. Oxford University Press.

Godfray, H.C.J. 1987. The evolution of clutch size in parasitic wasps. *The American Naturalist*. 129: 221-233.

Godfray, H.C.J. 1994. *Parasitoids: behavioural and evolutionary ecology*. Princeton University Press, Princeton.

Gonzalez, D., Hagen, K.S., Stary, P., Bishop, G.W., Davis, D.W. & Pike, K.S. 1995. Pea aphid and blue alfalfa aphid. In: *Biological control in the Western United States* (J.R. Nichols, L.A. Andrew, J.W. Beardsley, R.D. Goeden & D.G. Jackson, eds.), pp. 129-135. University of California Division of Agriculture and Natural Resources Publication 3361.

Grafen, A. 1989. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London, Series B*. 326: 119-157.

Greathead, D.J. 1975. Biological control of the bean fly *Ophiomyia phaseoli* (Diptera: Agromyzidae) by *Opius* species (Hymenoptera: Braconidae) in the Hawaiian Islands, USA. *Entomophaga*. 20: 313-316.

Grimaldi, D.A. 1990. A phylogenetic revised classification of genera in the Drosophilidae Diptera. *Bulletin of the American Museum of Natural History*. 197: 1-139.

Gustafsson, L. & Sutherland, W.J. 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature*. 335: 813-815.

Haeselbarth, E. 1979. Zur parasitierung der puppen von fonleule (*Panolis flammea* [Schiff]), kiefernspanner (*Bupalus piniarius* [L.]) und heidelbeerspanner (*Boarmia bistortana* [Goeze]) in bayerischen kiefernwaldern. *Zeitschrift fur Angewandte Entomology*. 87: 186-202; 311-322.

Hamilton, W.D. 1996. *Narrows roads to gene land. I. Evolution of social behaviour.* Freeman, New York.

Hanson, P. E. and Gauld, I. D. 1997. *The Hymenoptera of Costa Rica*. Oxford University Press, Oxford.

Hardy, I.C.W., Griffiths, N.T. & Godfray, H.C.J. 1992. Clutch size in a parasitoid wasp: a manipulation experiment. *Journal of Animal Ecology*. 61: 121-129.

Hardy, I.C.W. and Mayhew, P. J. 1998. Sex ratio, sexual dimorphism and mating structure in bethylid wasps. *Behavioural & Ecological Sociobiology*. 42: 383-395.

Harvey, J.A. & Strand, M.R. 2002. The developmental strategies of endoparasitoid wasps vary with host feeding ecology. *Ecology*. 83: 2439-2451.

Harvey, J.A., Kadesh, K. & Strand, M.R. 2000. Differences in larval feeding behaviour correlate with altered developmental strategies in two parasitic wasps: implications for the size-fitness hypothesis. *Oikos*. 88: 621-629.

Harvey, P.H. & Clutton-Brock, T.H. 1985. Life history variation in primates. *Evolution*. 39: 559-581.

Harvey, P.H. & Mace, G.M. 1982. Comparisons between taxa and adaptive trends: problems of methodology. In *Current problems in sociobiology* (King's College Sociobiology Group, ed.), pp. 343-361. Cambridge University Press.

Harvey, P.H. & Pagel, M.D. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.

Harvey, P.H. & Partridge, L. 1987. Murderous mandibles and black holes in hymenopteran wasps. *Nature*. 326: 128-129.

Harvey, P.H. & Purvis, A. 1999. Understanding the ecological and evolutionary reasons for life history variation: mammals as a case study. In: *Advanced ecological theory: principles and applications* (J.M. McGlade, ed.), pp. 232-248. Blackwell Science.

Harvey, P. H. & Rambaut, A. 2000. Comparative analyses for adaptive radiations. *Philosophical Transactions of the Royal Society of London, Series B*. 355: 1599-1605.

Harvey, P.H. & Zammuto, R.M. 1985. Patterns of mortality and age at 1st reproduction in natural populations of mammals. *Nature*. 315: 319-320.

Hawkins, B.A. 1994. *Pattern and processes in host-parasitoid interactions*. Cambridge University Press.

Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.

Hoffmeister, T. 1992. Factors determining the structure and diversity of parasitoid complexes in tephritid fruit flies. *Oecologia* 89: 288-297.

Hubbard, S.F., Marris, G. Reynolds, A. & Rowe, G.W. 1987. Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *Journal of Animal Ecology*. 56: 387-401.

Hufbauer, R.A. 2002. Evidence for nonadaptive evolution in parasitoid virulence following a biological control introduction. *Ecological Applications*. 12: 66-78.

Huffaker, C.B. & Messenger, P.S. 1976. *Theory and practice of biological control*. Academic Press, New York.

Huxley, J.S. 1932. *Problems of relative growth*. Methuen, London.

Jackson, D.J. 1966. Observations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasite of the eggs of Dytiscidae (Coleoptera) III. The adult life and sex ratio. *Transactions of the Royal Entomological Society, London*. 118: 23-49.

Jaenike, J. 1990. Host specialization in phytophagous insects. *Annual Review of Ecological Systematics*. 21: 243-273.

James, F.C. 1983. Environmental component of morphological differentiation in birds. *Science*. 221: 184-186.

Janz, N. & Nylin, S. 1998. Butterflies and plants: a phylogenetic study. *Evolution*. 52: 486-502.

Janz, N, Nyblom, K. & Nylin, S. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. *Evolution*. 55: 783-796.

Janzen, D.H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution*. 20: 249-275.

Janzen, D.H. 1981. The peak in North American ichneumonid species richness lies between 38^{O} and 42^{O}N. *Ecology*. 62: 532-537.

Janzen, D.H. & Pond, C.M. 1975. A comparison, by sweeping, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. *Transactions of the Royal Entomological Society of London*. 127: 33-50.

Jervis, M. A., Heimpel, G. E., Ferns, P. N., Harvey, J. A. and Kidd, N. A. C. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of "ovigeny". *Journal of Animal Ecology*. 70: 442-458.

King, B.H. 1989. Host-size dependent sex ratios among parasitoid wasps: does host size matter? *Oecologia*. 78: 420-426.

Kouamé, K.L. & Mackauer, M. 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. *Oecologia*. 88: 197-203.

Kozlowski, J. & Gawelczyk, A. T. 2002. Why are species' body size distributions usually skewed to the right? *Functional Ecology*. 16: 419-432.

Kozlowski, J. & Weiner, J. 1996. Interspecific allometries are by-products of body size optimization. *The American Naturalist*. 149: 352-380.

Kraaijeveld, A.R. & Godfray, H.C.J. 1997. Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. *Nature*. 389: 278-280.

Lack, D. 1947. The significance of clutch size. *Ibis*. 89: 302-352.

Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology*. 63: 607-615.

La Salle, J. & Gauld, I.D. 1991. Parasitic Hymenoptera and the biodiversity crisis. *Redia*. 74: 315-334.

Law, R. 1979. Ecological determinants in the evolution of life histories. In: *Population dynamics* (R.M. Anderson, B.D. Turner & L.R. Taylor, eds.), pp. 81-103. Blackwell, Oxford.

Lei, G. & Hanski, I. 1998. Spatial dynamics of two competing specialist parasitoids in a host metapopulation. *Journal of Animal Ecology*. 67: 422-433.

Lessells, C.M. 1986. Brood size in Canada Geese: a manipulation experiment. *Journal of Animal Ecology*. 55: 669-689.

Lessells, C.M. 1991. The evolution of life histories. In: *Behavioural ecology: an evolutionary approach 3rd edition* (J.R. Krebs & N.B. Davies, eds), pp. 32-68. Blackwell Scientific Press, Oxford.

Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton.

Levinton, J. 1988. *Genetics, palaeontology and macroevolution*. Cambridge University Press, Cambridge.

Lorenz, K. 1965. *Evolution and modification of behaviour*. University of Chicago Press, Chicago.

Mackauer, M. & Chau, A. 2001. Adaptive self-superparasitism in a solitary parasitoid wasp: the influence of clutch size on offspring size. *Functional Ecology*. 15: 335-343.

Maddison, D.R. & Maddison, W.P. 2001. *MacClade 4: Analysis of phylogeny and character evolution*. Version 4.03. Sinauer Associates, USA.

Maddison, W.P. & Maddison, D.R. 1992. *MacClade Version 3: analysis of phylogeny and character evolution*. Sinauer Associates, Inc. USA.

Mangel, M. 1987. Oviposition site selection and clutch size in insects. *Journal of Mathematical Biology*. 25: 1-22.

Martin, P. & Bateson, P. 1993. *Measuring behaviour. An introductory guide*. 2nd edition. Cambridge University Press, Cambridge.

Martins E.P. 1994. Estimating the rate of phenotypic evolution from comparative data. *The American Naturalist*. 144: 193-209.

Martins, E.P. & Hansen, T.F. 1996. Statistical analysis of interspecific data. In: *Phylogenies and the comparative method in animal behaviour* (E.P. Martins, ed.), pp. 22-75. Oxford University Press, Oxford.

Le Masurier, A.D. 1987. A comparative study of the relationship between host size and brood size in *Apanteles* spp. (Hymenoptera: Braconidae). *Ecological Entomology*. 12: 383-393.

Mayhew, P.J. 1997. Fitness consequences of ovicide in parasitoid wasps. *Entomologia Applicata et Experimentalis*. 84: 115-126.

Mayhew, P.J. 1998. The evolution of gregariousness in parasitoid wasps. *Proceedings of the Royal Society of London. Series B*. 265: 383-389.

Mayhew, P.J. & van Alphen, J.J.M. 1999. Gregarious development in alysiine parasitoids evolved through a reduction in larval aggression. *Journal of Animal Behaviour.* 58: 131-141.

Mayhew, P.J. & Blackburn, T.M. 1999. Does development mode organise life-history traits in the parasitoid Hymenoptera? *Journal of Animal Ecology.* 68: 906-916.

Mayhew, P.J. & Glaziot, O. 2001. Integrating theory of clutch size and body size evolution for parasitoids. *Oikos.* 92: 372-376.

Mayhew, P.J. & Hardy, I.C.W. 1998. Nonsiblicidal behaviour and the evolution of clutch size in bethylid wasps. *The American Naturalist.* 151: 409-424.

Mayhew, P.J. & Pen, I. 2002. Comparative analysis of sex ratios. In: *Sex ratios: concepts and research methods* (I.C.W. Hardy, ed.), pp. 132-156. Cambridge University Press, Cambridge.

Mayr, E. 1942. *Systematics and the origin of species.* Columbia University Press.

Mayr, E. 1963. *Animal species and evolution.* Harvard University Press, Cambridge.

Mills, N.J. 1992. Parasitoid guilds, life-styles, and host ranges in the parasitoid complexes of tortricoid hosts (Lepidoptera: Tortricidae). *Environmental Entomology.* 21: 320-329.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R. and Godfray, H. C. J. 1999. The structure of an aphid-parasitoid community. *Journal of Animal Ecology.* 68: 346-370.

Ode, P.J. & Rosenheim, J.A. 1988. Sex allocation and the evolutionary transition between solitary and gregarious parasitoid development. *The American Naturalist.* 151: 757-761.

Owens, I.P.F. & Bennett, P.M. 1995. Ancient ecological diversification explains life-history variation among living birds. *Proceedings of the Royal Society of London, Series B.* 261: 227-232.

Pagel, M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta.* 26: 331-348.

Pagel, M. 1999a. Inferring the historical patterns of biological evolution. *Nature.* 401: 877-884.

Pagel, M. 1999b. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology.* 48: 612-622.

Pagel, M.D. & Harvey, P.H. 1989. Comparative methods for examining adaptation depend on evolutionary models. *Folia Primatologica.* 53: 203-220.

Parker, F.D. & Pinnell, R.E. 1973. Effect on food consumption of the imported cabbage worm when parasitised by two species of *Apanteles*. *Environmental Entomology.* 2: 216-219.

Parker, G.A. & Maynard Smith, J. 1990. Optimality theory in evolutionary biology. *Nature.* 348: 27-33.

Partridge, L. & Harvey, P.H. 1988. The ecological context of life history evolution. *Science.* 241: 1449-1455.

Pexton, J.J. & Mayhew, P.J. 2002. Siblicide and life-history evolution in parasitoids. *Behavioural Ecology.* 13: 690-695.

Pianka, E.R. & Parker, W.S. 1975. Age-specific reproductive tactics. *The American Naturalist*. 109: 453-464.

Plotkin, H.C. 1988. Behaviour and evolution. In: *The role of behaviour in evolution* (H.C. Plotkin, ed.), pp. 1-17. MIT Press, Cambridge, Massachusetts.

Price, P.W. 1972. Parasitoids utilizing the same host: adaptive nature of difference in size and form. *Ecology*. 53: 190-195.

Price, P.W. 1973a. Parasitoid strategies and community organisation. *Environmental Entomology*. 2: 623-626.

Price, P.W. 1973b. Reproductive strategies in parasitoid wasps. *The American Naturalist*. 107: 684-693.

Price, P.W. 1974. Strategies for egg production. *Evolution*. 28: 76-84.

Price, P.W. 1975. *Evolutionary strategies of parasitic insects and mites*. Plenum Press, New York.

Price, P.W. 1981. Semiochemicals in evolutionary time. In: *Semiochemicals, their role in pest control* (D.A. Nordlund, R.L. Jones & W.J. Lewis, eds.), pp. 510-523. John Wiley, New York.

Price, T. 1997. Correlated evolution and independent contrasts. *Philosophical Transactions of the Royal Society of London, B*. 352: 519-529.

Prinzing, A., Durka, W., Koltz, S. & Brandl, R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London*, *Series B*. 268: 2383-2389.

Purvis, A. & Harvey, P.H. 1995. Mammal life history evolution: a comparative test of Charnov's model. *Journal of Zoology*. 237: 259-283.

Purvis, A. & Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Computer Applications in Bioscience*. 11: 247-251.

Quicke, D.L.J.1997. *Parasitic wasps*. Chapman and Hall.

Quicke, D.L.J., Fitton, M.G., Notton, D., Broad, G. & Dolphin, K. 2000. Phylogeny of the subfamilies of Ichneumonidae (Hymenoptera): A simultaneous molecular and morphological analysis. In: *Hymenoptera: Evolution, biodiversity and biological control* (A. Austin & M. Dowton, eds.), pp. 74-83. CSIRO publishing.

Read, A.F. & Harvey, P.H. 1989. Reassessment of comparative evidence for Hamilton and Zuk theory on the evolution of secondary sexual characters. *Nature*. 339: 618-620.

Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution*. 43: 223-225.

Ricklefs, R. E. and Starck, J. M. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos*. 77: 167-172.

Ridley, M. 1983. Can classification do without evolution? *New Scientist*. 100: 647-651.

Ridley, M. 1986. *Evolution and classification: the reformation of cladism*. Longman, London.

Roff, D.A. 1994. Optimality modelling and quantitative genetics: a comparison of the two approaches. In: *Quantitative genetic studies of behavioural evolution* (C.R.B. Boake, ed.), pp. 49-66. University of Chicago Press, Chicago.

Rohwer, F.C. 1985. The adaptive significance of clutch size in prairie ducks. *Auk*. 102: 354-361.

Roitberg, B., Sircom, J., Roitberg, C, van Alphen, J. & Mangel, M. 1993. Life expectancy and reproduction. *Nature*. 364: 108.

Ronquist, F. 1999a. Phylogeny of the Hymenoptera (Insects): the state of the art. *Zoologica Scripta*. 28: 3-11.

Ronquist, F. 1999b. Phylogeny, classification and evolution of the Cynipoidea. *Zoologica Scripta*. 28: 139-164.

Rosenheim, J.A. 1993. Single-sex broods and the evolution of nonsiblicidal parasitoid wasps. *The American Naturalist*. 141: 90-104.

Rotheray, G.E. & Barbosa, P. 1984. Host related factors affecting oviposition behaviour in *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae). *Entomologia Experimentalis et Applicata*. 35: 141-145.

Sato, H. 1990. Parasitoid complexes of lepidopteran leafminers on oaks (*Quercus dentata* and *Quercus mongolica*) in Hokkaido, Japan. *Ecological Research*. 5: 1-8.

Schluter. D. 1994. Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. *Ecology*. 74: 699-709.

Schluter, D. 2001. Ecological character displacement. In: *Evolutionary ecology: concepts and case studies* (C.A. Fox, D.A. Roff & D.J. Fairburn, eds.), pp. 177-189. Oxford University Press, Oxford.

Schmidt, J.M. & Smith, J.J.B. 1985. The mechanism by which the parasitoid *Trichogramma minutum* responds to host clusters. *Entomologia Experimentalis et Applicata*. 39: 287-294.

Seehausen, O., Mayhew, P.J. & van Alphen, J.J.M. 1999. Evolution of colour patterns in East African cichlid fish. *Journal of Evolutionary Biology*. 12: 514-534.

Shaw, M.R. 1983. On(e) evolution of endoparasitism: the biology of Rogadinae (Braconidae). *Contributions to the American Entomological Institute*. 20: 307-328.

Shaw, M.R. 1994. Parasitoid host ranges. In: *Parasitoid community ecology* (B.A. Hawkins & W. Sheehan, eds.), pp 111-114. Oxford University Press.

Shaw, M.R. & Huddleston, T. 1991. *Classification and biology of braconid wasps (Hymenoptera: Braconidae)*. Handbooks for the identification of British insects. Vol. 7. Pt II. pp. 46-51. Royal Entomological Society, London.

Shaw, S.R. 1988. Euphorinae phylogeny: the evolution of diversity in host utilisation by parasitoid wasps (Hymenoptera: Braconidae). *Ecological Entomology*. 16: 129-131.

Sheehan, W. & Hawkins, B.A. 1991. Attack strategy as an indicator of host range in metopiine and pimpline Ichneumonidae (Hymenoptera). *Ecological Entomology*. 16: 129-131.

Smith, C.C. & Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *The American Naturalist*. 108: 499-506.

Smith, R.H. 1991. Genetic and phenotypic aspects of life-history evolution in animals. *Advances in Ecological Research*. 21: 63-120.

Sneath, P.H.A. & Sokal, R.R. 1973. *Numerical taxonomy*. W.H. Freeman, San Francisco.

Sokal, R.R. & Rohlf, F.J. 1969. *Biometry*. First edition. Freeman, New York.

Stearns, S.C. 1989. Trade-offs in life-history evolution. *Functional Ecology*. 3: 259-268.

Stearns, S.C. 1992. *The evolution of life-histories*. Oxford University Press. Oxford.

Stevens, G.C. 1989. The latitudinal gradient in geographic range – how so many species coexist in the tropics. *The American Naturalist*. 133: 240-256.

Stireman, J.O. & Singer, M.S. 2003. What determines host range in parasitoids? An analysis of a tachinid parasitoid community. *Oecologia*. 135: 629-638.

Strand, M.R. 2000. Developmental traits and life-history evolution in parasitoids. In: *Parasitoid population biology* (M.E. Hochberg & A.R. Ives, eds.), pp. 139-162. Princeton University Press, Princeton.

Strand, M.R. & Grbic, M. 1997. The life history development of polyembryonic parasitoids. In: *Parasites and pathogens: effects on host hormones and behaviour* (N.E. Beckage, ed.), pp. 37-56. Chapman & Hall.

Strand, M.R. & Obrycki, J.L. 1996. Host specificity of insect parasitoids and predators. *Bioscience*. 46: 422-429.

Streams, F.A. 1971. Encapsulation of insect parasites in superparasitized hosts. *Entomologia Experimentalis et Applicata*. 14: 484-490.

Svensson, E. & Sheldon, B.C. 1998. The social context of life history evolution. *Oikos*. 33: 466-477.

Tatarenkov, A., Kwiatowski, J., Skarecky, D., Barrio, E. & Ayala, F.J. 1999. On the evolution of *Dopa decarboxylase* (*Dbc*) and *Drosophila* systematics. *Journal of Molecular Evolution*. 48: 445- 462.

Thompson, J.N. 1999. The raw material for coevolution. *Oikos*. 84: 5-16.

Vet, L.E.M. & Janse, C.J. 1984. Fitness of 2 sibling species of *Asobara* (Braconidae: Alysiinae) larval parasitoids of Drosophilidae in different microhabitats. *Ecological Entomology*. 9: 345-354.

Vet, L.E.M. & van Opzeeland, K. 1985. Olfactory microhabitat selection in *Leptopilina heterotoma* (Thompson) (Hymenoptera: Eucoilidae), a parasitoid of Drosophilidae. *Netherlands Journal of Zoology*. 35: 497-504.

Vet, L.E.M., Janse, C.J., van Achterberg, C. & van Alphen, J.J.M. 1984. Microhabitat location and niche segregation in two sibling species of drosophilid parasitoids: *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae). *Oceologia*. 61: 182-188.

Vet, L.E.M., Datema, A., Van Welzen, K. & Snellen, H. 1993. Clutch size in a larval-pupal endoparasitoid. 1. Variation across and within host species. *Oecologia*. 95: 410-415.

Waage, J.K. 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: *Insect parasitoids: 13th Symposium of the Royal Entomological Society of London* (J.K. Waage & D.J. Greathead, eds.), pp. 63-96. Academic Press, London.

Waage, J.K. & Godfray, H.C.J. 1985. Reproductive strategies and population ecology of insect parasitoids. In: *Behavioural ecology: ecological consequences of adaptive behaviour* (R.M. Sibly & R.H. Smith, eds.), pp. 449-470. Blackwell Scientific, Oxford.

Wahl, D.B. & Gauld, I.D. 1998. The cladistics and higher classification of the Pimpliformes (Hymenoptera: Ichneumonidae). *Systematic Entomology*. 23: 265-298.

Wcislo, W.T. 1989. Behavioural environments and evolutionary change. *Annual Review of Ecological Systematics*. 20: 137-169.

Wells, A. 1992. The first parasitic Trichoptera. *Ecological Entomology*. 17: 299-302.

West, S. A. and Herre, E. A. 1998. Stabilizing selection and variance in fig wasp sex ratios. *Evolution*. 52: 475-485.

Westoby, M., Leishman, M.R. & Lord, J.M. 1995a. On misinterpreting the phylogenetic correction. *Journal of Ecology*. 83: 531-534.

Westoby, M., Leishman, M.R. & Lord, J.M. 1995b. Further remarks on phylogenetic correction. *Journal of Ecology*. 83: 727-729.

Wharton, R.A. 1977. New World *Aphaereta* species (Hymenoptera: Braconidae: Alysiinae), with a discussion of terminology used in the Tribe Alysiini. *Annals of the Entomological Society of America*. 70: 782-803.

Wharton, R.A.. 1984. *Biology of the Alysiini (Hymenoptera: Braconidae), parasitoids of cyclorrhaphous Diptera*. The Texas agricultural experiment station. Technical monograph II.

Whitfield, J.B. 1992. Phylogeny of the non-aculeate Apocrita and the evolution of parasitism in the Hymenoptera. *Journal of Hymenoptera Research*. 1: 3-14.

Wilson, K. 1989. The evolution of oviposition behaviour in the bruchid *Callosobruchus maculatus*. PhD Thesis, University of Sheffield, UK.

Wimberger, P.H. & de Queiroz, A. 1996. Comparing behavioural and morphological characters as indicators of phylogeny. In: *Phylogenies and the comparative method in animal behaviour* (E.P. Martins, ed.), pp. 206-233. Oxford University Press, Oxford.

Wootton, J.T. 1987. The effects of body mass, phylogeny, habitat and trophic level on mammalian age at first reproduction. *Evolution*. 41: 732-749.

Zaldivar-Riverón, A., Areekul, B., Shaw, M.R. & Quicke, D.L.J. 2004. Comparative morphology of the venom apparatus in the braconid wasp subfamily Rogadinae (Insecta, Hymenoptera, Braconidae) and related taxa. *Zoologica Scripta*. 33(3): 223-237.