

11 • Parasitoids of European butterflies

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SUMMARY

Parasitoids are insects (mainly Hymenoptera and Diptera) whose larvae develop by feeding on the bodies of other arthropods (mainly immature insects) and the adults are free living. They are of immense importance in practically all terrestrial ecosystems because of their impact on the population levels of their hosts. In contrast to the considerable attention paid to European butterflies their parasitoids have received very little scrutiny, and the recognition that some reared parasitoids are in fact hyperparasitoids (parasitoids of parasitoids) has often been lacking in published records. A review of the biology and taxonomy of European butterfly parasitoids is presented, including a simple key to the various parasitoid families that include relevant species, followed by a brief discussion of the authors' current knowledge of their use of butterfly hosts. Quantitative case studies on the butterfly taxa *Iphiclides podalirius*, *Pieris* spp., *Maculinea rebeli*, *Aglais urticae*, *Melitaea* and *Euphydryas* spp. and *Thymelicus lineola* illustrate the range of parasitoid assemblages and the extent to which parasitoids account for butterfly mortality. The needs and difficulties inherent in moving from a simple understanding of what parasitoids are using a host population to a more sophisticated assessment of the impact they may have on the host's population dynamics are outlined. Parasitoids can be expected to have many important effects on the ecology of butterfly species and, on the evolutionary timescale, defence against parasitoids has shaped aspects of the physiology of the immature stages and the behaviour of both larval and adult butterflies. Butterfly researchers are encouraged to help build better knowledge about the host relations and effects of parasitoids. To better understand the place of parasitoids in the lives of butterflies there is still much to be gained from close attention to natural history, careful experimentation and thorough taxonomic investigation.

INTRODUCTION

Parasitism affects the egg, larval and pupal stages of butterflies and its importance as a mortality factor in butterfly

populations is both general and indisputable. Some of the parasitoids involved are extreme specialists but others are more generalist; however, mortality is often high even in the absence of specialists (e.g. Stefanescu *et al.*, 2003b), and almost certainly no European butterfly species altogether escapes.

In view of the considerable attention paid to European butterflies over the years, first by collectors and more recently by conservationists, it is anomalous that we have such poor knowledge of their parasitoids (Shaw, 1990). Apart from a very few, such as pest *Pieris* and *Thymelicus* species, and flagship conservation groups like the *Maculinea* and *Melitaeini* species which have also attracted population ecologists, almost none has been subjected to extensive sampling to investigate parasitism. Such deliberate effort would be needed firstly to establish which parasitoids regularly attack a particular butterfly species, and in which parts of its range, and secondly to investigate the effect these parasitoids have on their host populations.

However, there is a complementary need for parasitoid-based knowledge. Host–parasitoid complexes are not closed systems, and there is no *a priori* way of assessing whether a parasitoid reared from a particular species also uses related hosts, or perhaps unrelated ones occurring in similar environments. Each parasitoid species must be fitted into a continuum between absolute monophagy at one extreme or using the butterfly only marginally as part of a diffuse or differently focused host range at the other. Therefore we need to establish comprehensive knowledge not only of which species attack butterflies, but also of the host associations of each one. This is gradually accruing, at least for common parasitoid species, especially through small-scale rearings involving a large number of host species.

We begin this chapter by explaining why so little is known about parasitoids of butterflies, highlighting the sources of error that undermine the knowledge base (see also Shaw, 1990). Next we summarise the general biology of parasitoids of European butterflies. A simple key, including biological characteristics, links this with the following taxonomically organised section on their life history and host

ranges. The chapter then examines the few existing case studies of parasitoid communities associated with particular butterfly taxa, the contribution of parasitoids to mortality and, to some extent, their potential roles in butterfly population dynamics.

UNDERSTANDING AND IMPROVING OUR KNOWLEDGE

The historical passion for butterfly-collecting was unconvincing to a systematic study of their parasitoids, which were generally seen as a troublesome scourge and too obscure to be interesting. With the more recent decline of butterflies in Western Europe, collecting has decreased, and science-based conservationists have become the more active group. Most effort focuses on getting the 'bottom-up' aspects of the habitat (vegetation composition and quality, thermal properties of sites, etc.) right for the dwindling butterfly population, and (with some notable exceptions) parasitoids and other 'top-down' influences have generally been ignored. However, this is to neglect the strong possibility that the butterfly population will harbour specialist parasitoids even more at risk than their host, that might also play important roles in the host's population dynamics. Thus, it is more enlightened to see the butterfly's conservation in broader terms, including the trophic level above it (Shaw & Hochberg, 2001). Gradually our currently low knowledge might then be enriched by conservation biologists as well as by the scientifically minded enthusiasts who contribute important data on such a wide front.

The difficulty of finding eggs, larvae and especially pupae of most butterfly species in comparison with adults has also kept knowledge on parasitism low. This contrasts strongly with some groups of microlepidoptera whose early stages are the most easily found, resulting in abundant data on the host associations of their parasitoids (e.g. Askew & Shaw, 1974, 1986; Askew, 1994; Shaw & Horstmann, 1997).

One of the most important properties of a parasitoid is how host-specific it is. In practice rather few parasitoids are absolutely host-specific (though locally they may be, if only one of the possible hosts occurs), but rather they usually have a host range that either comprises a group of phylogenetically related hosts or a group of ecologically similar ones, or some balance between the two. It is useful to define *host range* conceptually, such that the host range includes only those species of potential hosts that the parasitoid is usually able to attack successfully, following a pattern of searching behaviour enabling it to encounter them regularly (Shaw,

1994). Thus an abnormal success in developing on a host that is usually rejected (or unsuitable if accepted), or the occasional discovery of a suitable host that is usually absent from the parasitoid's searching environment, will not alter the concept of host range for the parasitoid concerned. Importantly, if host range is expressed in the quantitative terms implied by the definition, then abnormal events and misidentifications will gradually become marginalised.

Many of the parasitoids of European butterflies are univoltine and use univoltine hosts, or are plurivoltine in synchronisation with plurivoltine hosts, or sometimes the parasitoid may be plurivoltine and use a univoltine host generation for successive broods. In all these cases the parasitoid has a potential to be absolutely host-specific, but there are also plurivoltine parasitoids that depend on different host species at different times of year. This complicates the parasitoid's population dynamics enormously, adds another dimension to the concept of host range and places an additional habitat demand because representatives of more than one set of hosts must be present (see also Shaw, 2006). In some cases the alternate hosts of parasitoids of European butterflies are not themselves butterfly species, but other Lepidoptera. Gaining insights into host ranges in these terms is particularly challenging, but of fundamental importance.

Many case studies (e.g. Shaw, 1982, 1990, 1993, 1994, 2002a; Askew & Shaw, 1986; Noyes, 1994) demonstrate that compilations of host-parasitoid records abstracted from the literature are so full of misinformation and ambiguity that they are useless for understanding either the nature or the breadth of host ranges. In particular, misidentifications have been rife, of not only the parasitoid but also the host (often an extraneous insect overlooked during rearing) and, additionally, either the compilations are non-quantitative (giving equal weight to rare and common occurrences) and/or they are corrupted because authors have reiterated host records from already published sources without making it clear that they are not giving new records (thereby leading to multiple scoring: see Shaw, 1993). The only way round these problems is for the focus to shift from literature records to an assessment of extant specimens by competent taxonomists, and for host data for parasitoids to be given in key works, reviews, etc. in quantitative form (as 'host mortalities', scoring gregarious broods as one) based on reared specimens actually seen. Even then, host misidentification may still be a problem, especially if host remains have not been preserved with the adult parasitoid. Ideally, each parasitoid (host mortality) that is reared will have come through rigorous rearing

protocols (see Shaw, 1997), to be preserved with its carefully recovered and assessed host remains and deposited in an active research collection where it will come to the attention of taxonomists. Much can then be understood about realised host ranges (e.g. Shaw, 1994, 2002a; Shaw & Horstmann, 1997) and the extent to which parasitoids of a particular host are engaged in other parasitoid complexes (e.g. Shaw & Aeschlimann, 1994).

Advice on appropriate rearing protocols and preservation techniques can be found in Shaw (1990, 1997) (the latter can also be applied to Tachinidae, with the rider that adults are best killed once their wings have hardened and then direct-pinned) and, for the special techniques needed for preserving Chalcidoidea and other 'microhymenoptera', in Noyes (1982, 1990).

A frequent aim might be to assess the percentage parasitism in a host population, but it is important to understand that this is extremely difficult to do for several reasons (Shaw, 1990). Firstly, parasitised and unparasitised caterpillars often do not behave in the same way, so one category becomes more amenable to whatever sampling method is used; and secondly, parasitised caterpillars often develop at a different rate from unparasitised ones (parasitised hosts are often retarded, though in some cases parasitism speeds the host to its next stage), so that a disproportion of hosts may have left the sampling arena (e.g. as healthy hosts pupate, leaving parasitised ones behind). Indeed, whenever exceptionally high levels of parasitism are recorded in collections of final-instar larvae, these two possibilities should be considered. Further, at whatever time sampling is done, some hosts may have already been killed by parasitoids (and been lost to the sampling process), and some parasitoid attack may not yet have happened. Thus it is usually impractical to sample all stages effectively enough to cover generational parasitism quantitatively.

GENERAL PARASITOID BIOLOGY

The following account covers only insect taxa that are fairly regular as parasitoids of European butterflies per se: for fuller accounts see Gauld & Bolton (1988) or a summary in Shaw (1997) for the biology of parasitic Hymenoptera, Shaw & Huddleston (1991) for Braconidae, Herting (1960), Belshaw (1993, 1994) and Stireman *et al.* (2006) for Tachinidae, Shaw & Askew (1976) for parasitism of (British) Lepidoptera as a whole, and classic texts such as Clausen (1940) and Askew (1971) for the biology of wider groups of insect parasitoids. Godfray (1994) and Quicke (1997) give

more evolutionary treatments of different aspects of behaviour and biology.

Parasitoids of butterflies fall into two insect orders, Diptera and Hymenoptera. In both cases the adults are free-living and the larvae develop (whether solitarily or gregariously) by feeding on a single immature host which is killed as a result (cases of survival have occasionally been reported, especially involving Tachinidae). Some other organisms such as Mermithidae (Phylum Nematoda) have life-styles comparable to insect parasitoids (see Eggleton & Gaston, 1990) and may occasionally be associated with European butterflies, but obligate specific relationships are not known and this chapter will not deal with them further.

Several families of Diptera behave as parasitoids but only one, the large family Tachinidae, includes regular and important parasitoids of butterflies (in addition, some species of Bombyliidae are very occasionally reared). All Tachinidae attacking Lepidoptera parasitise the larval stage, though some do not kill the host until it has pupated. They do not have piercing tubular ovipositors as such, and employ a wide variety of strategies to get their larvae into the host.

Many families of Hymenoptera are parasitoids, but relatively few include parasitoids of European butterflies. Only Braconidae and Ichneumonidae (together comprising the superfamily Ichneumonoidea) regularly, and a very few Eulophidae (superfamily Chalcidoidea) rarely, are parasitoids of the larval stage. While Braconidae attacking European butterflies all kill the larval stage, a few Ichneumonidae attack the larval stage but do not complete their development until the host has pupated. Some other Ichneumonidae attack the pupal stage, as do a few Pteromalidae and Chalcididae (both superfamily Chalcidoidea). The eggs are attacked by minute chalcidoids (in several families, especially Trichogrammatidae) and Scelionidae (superfamily Platygastroidea), which complete their development to adulthood within the host egg. Although other access strategies are known, all the Hymenoptera that parasitise European butterflies have tubular piercing ovipositors by means of which the egg is placed either inside or (in rare cases) onto the host directly.

The trophic relationship that a reared parasitoid has to its apparent host may not be as straightforward as it seems. *Primary parasitoids* attack and eventually kill the host itself, but surprisingly often they are themselves subject to attack from *secondary parasitoids*, also known as *hyperparasitoids*, which are parasitoids of the primary parasitoid. Although Tachinidae and Braconidae are all essentially primary

parasitoids, several groups of both Ichneumonidae and Chalcidoidea contain species that function as hyperparasitoids. There are two main categories of hyperparasitoids. *True hyperparasitoids* attack the primary parasitoid while it is still growing inside (or occasionally on the outside of) the host, which is usually still alive at this time (Plate 7a). Thus the searching behaviour of true hyperparasitoids is, at least initially, focused on finding the same hosts as the primary parasitoids it will attack. Virtually all true hyperparasitoids are completely specialised and cannot function as primary parasitoids. Usually the primary parasitoid is not killed until after it has killed the host and made its own apparently normal preparations for pupation, such as spinning a cocoon – from which the adult hyperparasitoid will eventually emerge. *Pseudohyperparasitoids*, on the other hand, attack the primary parasitoid only after it has completed its feeding, by which time the host is dead or moribund. The primary parasitoid will typically be attacked in its cocooned or pupal stage (Plate 7b). Although not sampled by collecting living caterpillars, pseudohyperparasitoids affect host population dynamics by reducing the population of primary parasitoids just as true hyperparasitoids do. Many pseudohyperparasitoids opportunistically use a range of hosts in small cases and cocoons, some of which just happen to be those of primary parasitoids, but others are more specialised. Some parasitoids are capable of functioning as either a primary parasitoid or as a pseudohyperparasitoid of a given host, in which case they are said to be *facultative hyperparasitoids*.

Whether primary or secondary, parasitoids whose larvae feed from the outside of the host are called external parasitoids or *ectoparasitoids*, while those that feed from within the host's body are internal parasitoids or *endoparasitoids*. All tachinids are endoparasitic. Though many parasitic Hymenoptera are ectoparasitic, their frail larvae are in general unsuited to ectoparasitic existence unless they can develop in concealment (exceptions relevant to butterflies occur in Eulophidae). Thus ectoparasitism of butterflies is rare, but might be expected when the host larva is quite deeply endophytic (e.g. some Polyommata). However, many groups of braconids start their life as endoparasitoids but have a final ectophagous phase, and there are just a very few butterfly species (e.g. some Hesperidae and *Vanessa atalanta*) whose larvae rest concealed in retreats that are robust enough to support this.

There is another way to categorise parasitoids by their developmental characteristics than simply as ectoparasitoid or endoparasitoid, which correlates better with certain

parameters such as the potential for breadth of host range (see Haeselbarth, 1979; Askew & Shaw, 1986). In this case the emphasis is on the immediate effect on the host's development. If it is permanently arrested or killed at the time of parasitism, the immature parasitoid need not accommodate to a living host, and is said to be an *idiobiont*. If, on the other hand, the host continues to develop, or move around and look after itself, for at least some time following parasitisation (so that the immature parasitoid has to withstand the various challenges mounted by a living host), the parasitoid is said to be a *koinobiont*. The latter are generally constrained to relatively narrow host ranges, while idiobionts – at least potentially – can use a broader range of hosts found within their searching environment. For example, true hyperparasitoids are all koinobionts, while pseudohyperparasitoids (many of which are facultative hyperparasitoids, thereby having host ranges spanning at least two insect orders) are idiobionts. There is a weak correlation between endoparasitism and koinobiosis on the one hand and ectoparasitism and idiobiosis on the other: importantly, however, when ectoparasitic koinobiosis (rare for parasitoids of European butterflies) or endoparasitic idiobiosis (frequent in parasitoids of butterflies) occur, the host range parameters follow the koinobiosis and idiobiosis dichotomy rather than endoparasitism and ectoparasitism. Tachinidae, however, fit rather uncomfortably into this: they are all endoparasitic koinobionts, yet some have immensely wide host ranges. There are important differences between Tachinidae and parasitic Hymenoptera, regarding both the means of accessing the host and the capacity of Tachinidae to escape the host's encapsulation defences, that seem likely to account for this (see later).

Parasitoids may be *solitary*, when a single individual develops in or on each host, or *gregarious* when a brood of two or more develops from one host. Some Tachinidae parasitising butterflies are strictly solitary, but others typically develop in brood sizes ranging from about one to four. In Hymenoptera, usually a given species is consistently either solitary or gregarious (though for egg parasitoids host size may be a factor) but a few essentially gregarious species of *Cotesia* (Braconidae) parasitise differently sized hosts according to season, and occasionally develop solitarily. In gregarious species there are often several tens of individuals in a brood. The braconid subfamily Microgastrinae furnishes the only gregarious koinobiont endoparasitoids of butterfly larvae, but gregarious idiobiont endoparasitoids of pupae are found in both the ichneumonid subfamily Cryptinae and the chalcidoid family Pteromalidae.

Multiparasitism refers to two species parasitising the same host, and *superparasitism* to more than one oviposition attack from the same parasitoid species. In both situations supernumeraries are usually eliminated, and the first-instar larvae of many species of solitary koinobiont endoparasitoids, in particular, are adapted for fighting competitors.

Most primary parasitoids attack their hosts at a fairly precise life-history stage, and can be categorised to reflect this. Thus all *egg parasitoids* oviposit into and kill insect eggs, and (in this strict sense of the term) always emerge as adults from them. *Larval parasitoids* attack and also kill the host in its larval stage; if it is an endoparasitoid the parasitoid larva may leave the host to pupate elsewhere (Ichneumonidae and Braconidae make cocoons; Tachinidae pupate inside their tanned last larval skin, known as a puparium), or in some groups (Rogadinae (Braconidae) and a few Campopleginae (Ichneumonidae)) the parasitoid pupates inside the host's larval skin (hardened, or sometimes strengthened by a clear additional cocoon). As butterflies on the whole pupate either in the open, or at least without the benefit of a strongly enclosing cocoon, the rather large number of groups of ichneumonoid parasitoids that depend strongly on Lepidoptera cocoons (including many koinobionts that finally kill prepupal hosts) do not enter the parasitoid complexes of European butterflies. *Pupal parasitoids* (for European butterflies involving only Ichneumonidae and Chalcidoidea) oviposit in or on host pupae and, if they are endoparasitoids, emerge as adults from them. Idiobionts, by definition, always kill the stage attacked, but some koinobionts invariably kill the host at a stage later than the one attacked. In these cases they are known as *egg-larval parasitoids* or *larva-pupal parasitoids*. Egg-larval parasitism of European butterflies is seldom recorded, but it does occur in some species of the braconid subfamily Microgastrinae, in which it is probably only facultative (see Johansson, 1951), and in at least one species of *Hyposoter* (Ichneumonidae: Campopleginae) (Plate 8a) in which it appears to be obligatory (van Nouhuys & Ehrnsten, 2004). In both cases, however, the host larval embryo is so well advanced by the time it can successfully be attacked that oviposition is essentially into a first-instar larva that has not yet hatched. Larva-pupal parasitism of European butterflies is practised by several Tachinidae and a few groups of Ichneumonidae. In the case of the Ichneumonidae pupation is always inside the host pupa, but while some tachinids form their puparium within the host pupa the majority leave the host beforehand.

In Tachinidae the egg must be fertilised to develop, and the female has no control over the sex of her progeny. In

Hymenoptera, however, an unusual form of sex determination, called haplodiploidy, prevails. In this, unfertilised (haploid) eggs develop and become males (a process known as *arrhenotokous parthenogenesis*) while fertilised (diploid) eggs become females. It is usual for mated female parasitic Hymenoptera to regulate access of the stored sperm to the egg as it passes down the oviduct, and so control its sex. Both the overall sex ratio and, for gregarious species, the sexual composition of broods thus reflect reproductive strategies that have presumably been optimised by natural selection. In the case of solitary idiobionts in particular, female progeny are often invested in the larger-sized hosts attacked and males tend to result from the smaller hosts (see Luck *et al.*, 1992; Godfray, 1994). However, in a good many Hymenoptera species males are practically unknown, and diploid females develop from unfertilised eggs by a process known as *thelytokous parthenogenesis* or thelytoky (thelytoky is sometimes, but not always, mediated by microorganisms: Stouthamer *et al.*, 1992).

Adult parasitoids generally feed, at least on sugars which they can obtain from flowers and honeydew, but also in some cases on protein needed to mature their eggs. Some Hymenoptera use their piercing ovipositors or biting mouthparts to wound and often kill hosts (or sometimes other insects) in order to imbibe haemolymph (Plate 8b). This *host-feeding* is practised by parasitoids attacking all host stages, but it is more often done by idiobionts than koinobionts (see Jervis & Kidd, 1986), and it can cause substantial mortality. Another source of protein is pollen (e.g. Zhang *et al.*, 2004).

TAXONOMIC REVIEW

In this section we will firstly provide a simple key to the families of Hymenoptera and Diptera that include known parasitoids of European butterflies, secondly overview these families in so far as they parasitise butterflies, and thirdly within each parasitoid group attempt to give a list or annotated table of butterfly-parasitoid associations (but only for primary parasitoids) that we believe to be reliable. While all of this is complicated by insufficient knowledge, we hope the first two parts can be done fairly confidently: additions and exceptions will undoubtedly arise, but we believe they will be relatively minor.

Regarding host associations, however, we can give only a skeletal account, best seen as a stimulus for further study. The tables we provide for groups of Hymenoptera are based on specimens we have seen (material in the National

Museums of Scotland (NMS) unless otherwise indicated), or in a few cases those seen by careful taxonomists who have passed reliable information on to us (indicated pers. comm. – but in these cases often with no statement of depository). Records from the literature are included only in the very few cases where we believe both host and parasitoid determinations to be particularly reliable. Thus we deliberately exclude a very large number of literature records which (though they may be correct) we cannot directly confirm or corroborate. This involves several taxa that were described from butterfly hosts; if the circumstances are beyond our assessment we felt it inappropriate to enter them in tables, though we have sometimes mentioned the supposed association in the text.

A parasitoid's name is bracketed if we believe it is only casually and infrequently associated with butterflies. In a few cases we have included at the generic level parasitoids for which we cannot give a specific identity, but only when the association seems regular or is noteworthy for some other reason. Butterfly names (other taxa in the parasitoid's host range are not included) follow Karsholt & Razowski (1996) except as subsequently revised, and are entered in bold if the association is known from at least two separate occasions (rearings from numerous host individuals collected in the same place and year are reckoned as only one occasion). If putting the entry in bold depended on NMS specimens reflecting a single occasion combined with those from another source, a '+' is given in the superscript referencing the latter (as all unattributed records depend on NMS specimens). Most host associations in bold are likely to be at least fairly regular – many of those not in bold will be too, but we cannot say so with such confidence. It is, however, extremely important that the host-parasitoid associations mentioned here are NOT used as a means to identify new material, which must always be done more rigorously.

In addition to columns giving host and parasitoid names, a central column is used to give an informal estimation of host range. This depends partly on data given in the table, but also on wide sources of both positive and negative information which, it rapidly became apparent, could not be accounted or referenced in any consistent or purposeful way. The 'less than' symbol < should be read as 'some, but not all, of the species in' [the taxon following].

This whole section looks at parasitism only qualitatively, and from the viewpoint of the parasitoids. A later section will review the published quantitative studies that exist for particular host species.

Simple key to families of insect parasitoids of European butterflies

This key is restricted to taxa likely to be reared from European butterflies. It does not cover parasitoids of all European Lepidoptera, let alone parasitoids in general. Attempting to use it in a wider context may therefore often lead to mistakes. Further, it does not include all of the groups of Chalcidoidea that might be reared as hyperparasitoids unless they are also likely to arise as primary parasitoids.

1. One pair of membranous wings; antenna inconspicuous, shorter than length of head. (*Host killed as larva or pupa; never making a silken cocoon for pupation*).....Diptera 2
 - Two pairs of membranous wings (or wingless); antenna conspicuous, longer than length of head. (*Host killed as egg, larva or pupa; egg parasitoids can be minute (<0.5 mm) but otherwise from ca. 3–30 mm; primary parasitoids and hyperparasitoids*).....Hymenoptera 3
2. Body bristly; legs relatively short, robust and with strong bristles; antenna 3-segmented; colour of wing membrane usually uniform; pupation (usually outside the host remains) in an ovoid immobile puparium formed from the hardened and darkened last larval skin (in which the paired posterior spiracles remain discernible). (*Host killed as larva or pupa; 6–12 mm; solitary or in small broods; always primary parasitoids*).....Tachinidae
 - Body at least partly furry; legs long, slender and with fine bristles; antenna with more than 3 segments; wing membrane usually partly darkened (at least near costal margin); pupa exarate, conspicuously spiny, mobile. (*Host usually killed as pupa, inside which the parasitoid pupates; 6–15 mm; solitary; primary parasitoids or sometimes hyperparasitoids*)Bombyliidae
 - [Other families of Diptera may be saprophagous on the moribund or dead bodies of butterfly larvae or pupae; especially Phoridae, pupating in brown boat-shaped puparia, often numerous, adults (ca. 3 mm) run rapidly with jerky movements and often make short flights.]
3. Antenna with more than 13 segments; fore wing venation including closed cells (or wingless); pupation inside or outside host remains, if outside then a cocoon is made. (*Host killed as larva or pupa*).....Ichneumonoidea 4
 - Antenna with at most 13 segments; fore wing venation only near costal margin or absent, lacking clear enclosed cells (if minute and from host egg may be wingless); pupation usually inside host remains (or in primary

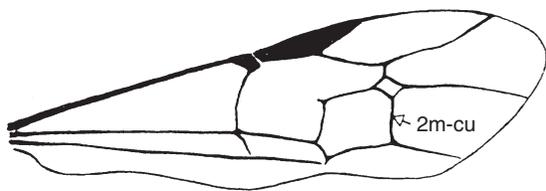


Figure 11.1. Typical fore wing of Ichneumonidae with second recurrent vein (2m-cu) present (except for apterous or brachypterous species).

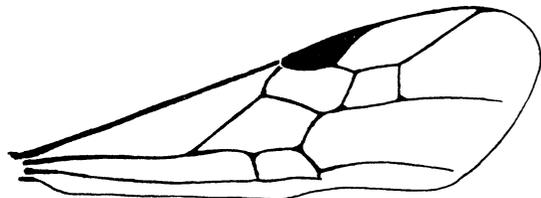


Figure 11.2. Typical fore wing of Braconidae with second recurrent vein (2m-cu) absent (species always fully winged).

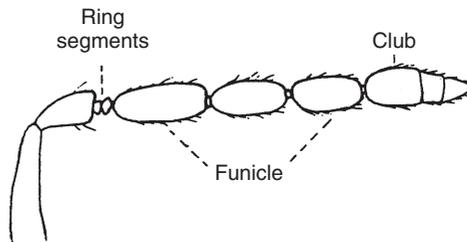


Figure 11.3. Stylised antenna of Chalcidoidea (ring segments are present in all except Encyrtidae). Scelionidae (Platygastridae) are broadly similar but lack ring segments.

- parasitoid cocoon if a hyperparasitoid) and usually no cocoon made [some Chalcidoidea pupate naked or under a slight net outside the host as small obtect pupae].....5
4. Occasionally apterous or brachypterous, otherwise fore wing with second recurrent vein (2m-cu) present (Fig. 11.1) [disposition of other veins, especially costad of this, variable]. (*Host killed as larva (then pupates in cocoon which can be inside or away from host's skin) or pupa (then pupates inside it). Almost always solitary (one gregarious species attacks pupae). As well as primary parasitism, both true hyperparasitism and pseudohyperparasitism occur*).....Ichneumonidae
- Always fully winged and fore wing with second recurrent vein (2m-cu) absent (Fig. 11.2) [otherwise venation, especially costad of this area, variable]. (*Always primary parasitoids, killing host in larval stage. Either a mummy is made from the host body, inside which the parasitoid pupates (Rogadinae: Aleiodes), or one or more cocoons are formed externally to the host. Gregarious development frequent (in Microgasterinae)*).....Braconidae
5. Parasitoids of the egg stage. (*Small to minute, emerging as adults from the host egg*).....6
- Parasitoids of other stages.....Chalcidoidea 9
6. Metasoma (= the most posterior of the 3 clear body divisions) with some parallel longitudinal grooves towards base; female ovipositor apical (but concealed); antenna without minute ring segments (see Fig. 11.3) following

- the second segment (pedicel); pronotum extends back to meet tegulae. (*Usually black*).....
- Scelionidae (Platygastridae)
- Metasoma without basal longitudinal grooves; female ovipositor issuing before apex of metasoma (discernable ventrally if concealed); antenna usually with ring segments (Fig. 11.3); pronotum separated from tegulae. (*Often pale coloured or metallic*).....
- Chalcidoidea 7
- [There are more groups that might possibly be reared from butterfly eggs than are covered by the following couplets to the most regularly found taxa.]
7. Tarsi with 3 segments; if fully winged then fore wing with lines of hairs radiating from the wing base; antenna with not more than 2 funicle segments. (*Body relatively pale, non-metallic, weakly sclerotised; particularly small (0.3–1.2 mm) and often gregarious*).....Trichogrammatidae
- Tarsi with 5 segments; if fully winged then fore wing lacking radiating lines of hairs; antenna with 6 or 7 funicle segments. (*Body more or less dark and at least partly metallic*).....8
8. Antenna with 1 ring segment and 7 funicle segments (or 5 very short ones, totalling less than half the length of the strongly elongate club, in male of *A. bifasciatus*); female fore wing strongly banded (even if brachypterous), in male usually hyaline.....Eupelmidae (*Anastatus*)
- Antenna with no ring segments and 6 funicle segments; wings hyaline and antennal club much shorter than funicle in both sexes.....Encyrtidae (*Ooencyrtus*)
9. Hind femur swollen, extensively toothed on lower (posterior) margin; hind tibia markedly curved to same profile. (*Moderately large (ca. 4–8 mm) solitary parasitoids of pupae; also (usually smaller) pseudohyperparasitoids ex Ichneumonoidea cocoons; black with yellow (occasionally red) leg markings; very heavily sculptured (except metasoma)*).....Chalcididae (*Brachymeria*)

- Hind femur and tibia unmodified. (*Usually smaller, ca. 2–4 mm; usually at least partly metallic greenish or bronze*)10
10. Antenna with 5 or 6 funicle segments; tarsi with 5 segments; front tibial spur well developed and distinctly curved. (*Gregarious parasitoids of pupae; also pseudohyperparasitoids ex Ichneumonoidea cocoons*). [N B Several of the chalcidoid families not known as primary parasitoids of butterflies that do behave as pseudohyperparasitoids will run here (e.g. Eurytomidae, Eupelmidae)]Pteromalidae
- Antenna with 2–4 funicle segments; tarsi with 4 segments; front tibial spur weak, practically straight. (*Primary ectoparasitoids attacking the larval stage (especially as gregarious koinobionts of exposed hosts, but possibly also as idiobionts of concealed ones) do occur, but not commonly. More often seen as solitary or gregarious true hyperparasitoids, and also pseudohyperparasitoids, ex Ichneumonoidea cocoons*)Eulophidae

Hymenoptera

ICHNEUMONOIDEA

This superfamily comprises just two extant families, Ichneumonidae and Braconidae, both of which are very large and diverse.

Ichneumonidae

The overwhelming majority of ichneumonids parasitise the larvae or pupae of holometabolous insects, though a few attack spiders and their egg sacs. About 35 subfamilies of Ichneumonidae occur in Europe but, although 14 contain at least some parasitoids of Lepidoptera, only five include parasitoids of butterflies. Species of two other subfamilies are obligatory true hyperparasitoids, and one of these (Mesochorinae, containing the very large genus *Mesochorus*; Plate 7a) is regularly associated with butterflies. These are solitary with respect to each primary parasitoid attacked, though often several in a gregarious brood can be affected. They are most often reared through endoparasitic koinobiont Ichneumonoidea attacking the host in its larval stage. Ichneumonid pseudohyperparasitoids are found in the subfamilies Cryptinae and Pimplinae, and indeed most of the involvement of Cryptinae with butterflies is through a few common genera that regularly behave as pseudohyperparasitoids. Literature on species of

Ichneumonidae is traceable via Yu & Horstmann (1997) and current versions of Taxapad (see www.taxapad.com).

Subfamily Anomaloninae

All species of this relatively small subfamily are solitary koinobiont larva–pupal endoparasitoids, mostly of Lepidoptera. No genus specialises on butterflies, but most of the few species concerned are specialists with narrow host ranges.

Parasitoid	Suggested host range	Supporting host records
<i>Agrypon anomelas</i> (Gravenhorst)	<Lycaenidae	<i>Neozephyrus quercus</i> ¹ ; <i>Polyommatus coridon</i> ²
<i>Agrypon delarvatum</i> (Gravenhorst)	<Satyrinae + <Hesperiinae	<i>Thymelicus lineola</i> ³ ; <i>Lasiommata maera</i> ; <i>Coenonympha</i> sp.
<i>Agrypon flexorium</i> (Thunberg)	Broad	<i>Callophrys rubi</i>
<i>Agrypon polyxena</i> (Szépligeti)	<Parnassiinae	<i>Zerynthia rumina</i> ; <i>Z. polyxena</i> ; <i>Archon apollinus</i>
<i>Clypeocampulum</i> sp. nov. ⁴	<i>Anthocharis euphenoides</i>	<i>Anthocharis euphenoides</i>
<i>Erigorus apollinis</i> Kriechbaumer	<i>Parnassius</i>	<i>Parnassius apollo</i> ⁵
<i>Erigorus foersteri</i> (Mocsáry)	<Satyrinae	<i>Pyronia tithonus</i> ; <i>Aphantopus hyperantus</i>
<i>Erigorus melanops</i> (Foerster)	<Satyrinae + <low-feeding Noctuidae	<i>Maniola jurtina</i> ; <i>Melanargia galathea</i>
<i>Heteropelma grossator</i> Shestakov (= <i>parargis</i> Heinrich)	<i>Lasiommata</i>	<i>Lasiommata maera</i> ⁵

Species in NMS have been either determined or checked by H. Schnee.

Notes: 1. BMNH. 2. Horstmann *et al.* (1997). 3. Carl (1968). 4. To be described by H. Schnee. 5. H. Schnee, pers. comm.

Subfamily Campopleginae

All species in this large subfamily are koinobiont larval (very rarely larva–pupal or egg–larval) endoparasitoids. Most are solitary parasitoids of Lepidoptera, but a few genera attack other holometabolous orders. In Europe parasitoid species specialised to butterflies are known in several genera but *Benjaminia* is the only genus that apparently wholly specialises on butterflies. All *Benjaminia* probably parasitise Melitaeini but, while several Nearctic species have been reared, reliable host data exist for only one European and one other of the eight Palearctic species (Wahl, 1989). Species of *Benjaminia* and most of the *Hyposoter* (Plate 8a) species that attack butterflies pupate inside the host's skin (a blotched cocoon shows through in some), killing it about an instar before full growth or in some cases as an advanced final-instar larva. *Casinarina* and *Phobocampe* species also generally kill the host before full growth, but in these cases the cocoon is spun outside the host remains. Some genera (*Campoplex*, *Diadegma*, *Enytus* and *Sinophorus*) specialise

on concealed hosts that are usually killed as prepupae, and there are apparent specialists (*D. aculeatum* and *Sinophorus* sp. indet.) on concealed butterflies. Otherwise, rearings of these genera from butterflies probably represent abnormal (if sometimes repeated) events; for example, several species that usually attack concealed microlepidoptera larvae occasionally develop in small larvae of *Vanessa atalanta*, presumably attacked because of its similar resting position. Mostly the Campopleginae that attack butterflies overwinter as early-instar larvae inside host larvae and they spin their cocoons, which are often bird-dropping mimics, firmly attached to vegetation: the cocoons, which are very prone to pseudohyperparasitism, then produce adults quickly. *Phobocampe*, however, make unattached hard ovoid cocoons, which the parasitoid larva within can cause to 'jump' in response to heat and light until the cocoon finds a secluded place. Although often plurivoltine so that emergence from the cocoon can be rapid, these *Phobocampe* species spend the winter as a cocooned stage.

Parasitoid	Suggested host range	Supporting host records seen
<i>Alcina orbitale</i> (Gravenhorst)	> <i>Zygaena</i> ¹	<i>Hipparchia semele</i> ; <i>H. statilinus</i> ; <i>Arethusana arethusa</i>
<i>Benjaminia fumigator</i> Aubert	<i>Melitaea didyma</i>	<i>Melitaea didyma</i>
(<i>Campoletis annulata</i> (Gravenhorst)) ²	Includes <i>Autographa gamma</i> ³	<i>Maniola jurtina</i>
(<i>Campoplex lyratus</i> (Thomson)) ²	<Microlepidoptera	<i>Vanessa atalanta</i> ⁴
(<i>Campoplex tumidulus</i> Gravenhorst (= <i>rufinator</i> Aubert)) ²	<Microlepidoptera	<i>Vanessa atalanta</i> ^{4,5}
<i>Casinarina petiolaris</i> (Gravenhorst)	Coenonymphini	<i>Coenonympha tullia</i> ; <i>C. pamphilus</i>
<i>Diadegma aculeatum</i> (Bridgman)	<i>Cupido</i>	<i>Cupido minimus</i>
(<i>Diadegma</i> sp.) ⁶	?	<i>Celastrina argiolus</i> ⁵
(<i>Enytus apostatus</i> (Gravenhorst)) ²	<Microlepidoptera	<i>Celastrina argiolus</i> ^{4,5} ; <i>Vanessa atalanta</i> ⁴
<i>Hyposoter ebeninus</i> (Gravenhorst) ²	<Pyrginae; <Pierinae ⁷	<i>Carcharodus alceae</i> ; <i>Anthocharis cardamines</i> ; <i>Euchloe belemia</i> ; <i>E. crameri</i> ; <i>E. simplonia</i> ; <i>E. ausonia</i> ; <i>E. insularis</i> ; <i>Pieris brassicae</i> ; <i>P. rapae</i> ^{3,8} ; <i>P. napi</i> ; <i>Pontia daplidice</i>
<i>Hyposoter ebenitor</i> Aubert ²	<Pierinae	<i>Euchloe ausonia</i> ; <i>Pontia daplidice</i> ; <i>P. chloridice</i> ; <i>P. edusa</i> ⁸

<i>Hyposoter horticola</i> (Gravenhorst) ²	<Melitaea	<i>Melitaea cinxia</i> ; <i>M. aurelia</i>
<i>Hyposoter notatus</i> (Gravenhorst)	<Polyommataini	<i>Cupido osiris</i> ; <i>C. lorquini</i> ; <i>Scolitantides orion</i> ⁹ ; <i>Plebejus hesperica</i> ; <i>Aricia eumedon</i> ⁹ ; <i>A. agestis</i> ; <i>A. artaxerxes</i> ; <i>Polyommatus icarus</i> ; <i>P. abdon</i> ; <i>P. hispana</i> ⁹ ; <i>P. albicans</i> ; <i>P. fabressei</i> ; <i>P. ?ripartii</i> ; <i>P. ?aroaniensis</i>
<i>Hyposoter placidus</i> (Desvignes)	Lycanini	<i>Lycaena phlaeas</i> ; <i>L. helle</i> ; <i>L. dispar</i> ; <i>L. hippothoe</i>
<i>Hyposoter rhodocerae</i> (Rondani) ²	<i>Gonepteryx</i>	<i>Gonepteryx rhamni</i> ; <i>G. cleopatra</i>
<i>Hyposoter caudator</i> Horstmann	<Polyommataini	<i>Plebejus pyrenaica</i> ; <i>Polyommatus dorylas</i> ³
<i>Hyposoter</i> sp.	<Maniolini	<i>Pyronia tithonus</i> ; <i>Maniola jurtina</i>
<i>Phobocampe confusa</i> (Thomson)	<Nymphalini	<i>Inachis io</i> ; <i>Aglais urticae</i> ; <i>Polygonia c-album</i> ⁴ ; <i>Araschnia levana</i> ; <i>Nymphalis polychloros</i> ⁴
(<i>Phobocampe crassiuscula</i> (Gravenhorst)) ²	Broad	<i>Limenitis camilla</i> ⁴
<i>Phobocampe tempestiva</i> (Holmgren) ²	Broad	<i>Limenitis camilla</i>
<i>Phobocampe quercus</i> Horstmann	Theclini	<i>Thecla betulae</i> ⁸ ; <i>Neozephyrus quercus</i>
<i>Sinophorus</i> sp.	<Pyrginae	<i>Carcharodus alceae</i> ; <i>C. baeticus</i> ; <i>Muschampia proto</i>
(<i>Sinophorus turionus</i> (Ratzeburg)) ²	Includes <i>Ostrinia</i> <i>nubilalis</i> ³	<i>Vanessa atalanta</i> ⁴

Single rearings of unidentified parasitoids have been excluded from the table.

Notes: 1. *Alcima orbitale* is a regular genus-specific parasitoid of *Zygaena* in most parts of Europe; only in Spain have we seen it from a range of other hosts. 2. Determined by K. Horstmann. 3. K. Horstmann, pers. comm. 4. Infrequent host. 5. Only two rearings (separate occasions) from this extremely commonly reared host. 6. The condition of the specimens prevents a certain determination (K. Horstmann, pers. comm.). 7. Such a disparate host range suggests the possibility of two parasitoid species. 8. BMNH. 9. Horstmann *et al.* (1997).

Subfamily Cryptinae

This large subfamily has a wide host range, focused on cocoons or similar structures including Diptera puparia. Most species are solitary idiobionts, though both gregarious development and (separately) larva-pupal koinobiosis occur. Relatively few genera and species are associated with Lepidoptera and, as butterflies do not make cocoons, there are few Cryptinae that parasitise them. *Blapsidotes vicinus* (Gravenhorst) is a moderately common gregarious idiobiont endoparasitoid of exposed butterfly pupae. Brood sizes of up to a few tens have been seen from *Pieris rapae*, *Vanessa atalanta*, *Polygonia c-album* and *Euphydryas desfontainii*. We have seen a single *Agrothereutes parvulus* (Habermehl) reared from a pupa of *Euphydryas aurinia*, and Horstmann *et al.* (1997) record a single *Polytribax rufipes* (Gravenhorst) parasitising the pupa of *Polyommatus coridon*, but it is doubtful that these species regularly attack butterflies. The same applies to

several species of *Gelis* that occasionally parasitise Lepidoptera pupae including those of butterflies (see Schwarz & Shaw, 1999). The genus *Ischnus* includes species that specialise on Lepidoptera pupae, but again no regular association with butterflies is evident. However, many genera of small Cryptinae (e.g. *Acrolyta*, *Bathythrix*, *Gelis* and *Lysibia*) include pseudohyperparasitoids that regularly attack the cocoons of primary parasitoids of butterflies (Plate 7b). Some species are highly polyphagous but others are more specialised, for example on cocoons of Microgastrinae, though none is exclusively associated with butterflies (see Schwarz & Shaw, 1999, 2000, in prep.).

Subfamily Ichneumoninae

The entire subfamily, which is large, attacks Lepidoptera as solitary endoparasitoids. With very few exceptions (not concerning butterflies), all species emerge as adults from

the host pupa. Rather few genera include species that parasitise butterflies, but some that do are specialised to them at the generic level (e.g. *Hoplismenus*, *Psilomastax*, *Trogus*), as is the entire tribe Listrodromini (genera *Anisobas*, *Listrodromus* and *Neotypus* in the table) which are larva-pupal parasitoids of Lycaenidae. *Listrodromus nyctemerus*, at least in Britain, appears to be responsible for cyclical population crashes in its host, *Celastrina argiolus* (Revels, 1994, 2006). Larva-pupal parasitism is frequent in the subfamily, but a majority of species attack hosts either as prepupae or as freshly turned pupae, apparently tracking semiochemicals associated with this moult (Hinz, 1983). Many ichneumonines (particularly in the genus *Ichneumon*) pass the winter as adult females, and most others do so within host pupae. However *Psilomastax pyramidalis* attacks young hosts and overwinters inside the diapausing host larva which is still small (Dell &

Burckhardt, 2004). The related genus *Trogus* (Plate 9a) can attack old or young larval hosts facultatively, and similarly delays larval development beyond its first instar until the host has pupated (Prota, 1963).

Several species of *Hoplismenus* and *Ichneumon* other than those tabulated have been recorded in the literature as parasitoids of butterflies (especially Nymphalidae). The determinations of tabulated *Anisobas*, *Ichneumon*, *Neotypus* and *Thyrateles* species have been either made or checked by K. Horstmann. The taxon given as *I. eumerus* (Plate 9b) might be an aggregate of two species (one from *M. rebeli* and the other from both *M. alcon* and *M. teleius*), but if so it is unclear at present which is the true *I. eumerus* (K. Horstmann, pers. comm.). The taxon listed as *I. gracilicornis* might also be an aggregate (Hilpert, 1992). Data on experimental hosts of *Ichneumon* species are given by Hinz & Horstmann (2007).

Parasitoid	Suggested host range	Supporting host records
<i>Anisobas brombacheri</i> Heinrich (= <i>martinae</i> Riedel)	<i>Glaucopsyche alexis</i>	<i>Glaucopsyche alexis</i> ¹
<i>Anisobas cephalotes</i> Kriechbaumer	<i>Iolana iolas</i>	<i>Iolana iolas</i>
<i>Anisobas cingulatus</i> Horstmann (= <i>cingulatorius</i> (Gravenhorst), preocc.)	<Polyommataini	<i>Plebejus argus</i> ; <i>Aricia agestis</i> ; <i>Polyommatus coridon</i> ; <i>P. hispana</i> ¹
<i>Anisobas hostilis</i> (Gravenhorst)	<i>Neozephyrus quercus</i>	<i>Neozephyrus quercus</i> ¹
<i>Anisobas platystylus</i> (Thomson)	<i>Callophrys rubi</i>	<i>Callophrys rubi</i> ¹
<i>Anisobas rebellis</i> Wesmael (= <i>jugorum</i> Heinrich)	<i>Lycaena</i>	<i>Lycaena phlaeas</i> ¹ ; <i>L. dispar</i> ¹ ; <i>L. virgaureae</i> ¹ ; <i>Lycaena</i> sp.
<i>Anisobas seyrigi</i> Heinrich (<i>Cratichneumon fabricator</i> (Fabricius))	> <i>Glaucopsyche melanops</i> ² ?Broad	<i>Glaucopsyche melanops</i> <i>Neozephyrus quercus</i>
<i>Hoplismenus axillatorius</i> (Thunberg) (= <i>albifrons</i> Gravenhorst)	Coenonymphini	<i>Coenonympha tullia</i> ; <i>C. pamphilus</i>
<i>Hoplismenus terrificus</i> Wesmael	?	<i>Polygonia c-album</i> ³
<i>Ichneumon albiornatus</i> Tischbein	<i>Limenitis</i>	<i>Limenitis populi</i> ⁴ ; <i>L. camilla</i> ⁴
<i>Ichneumon berninae</i> (Habermehl)	Includes high altitude Arctiidae ⁴	<i>Boloria pales</i> ⁴
<i>Ichneumon caloscelis</i> Wesmael	<Satyrinae	<i>Pyronia tithonus</i> ; <i>Maniola jurtina</i> ; <i>Hipparchia semele</i>
<i>Ichneumon cessator</i> Müller	Nymphalini	<i>Aglais urticae</i> ; <i>Nymphalis antiopa</i> ⁴
<i>Ichneumon cinxiae</i> Kriechbaumer	<Melitaeini	<i>Melitaea cinxia</i> ; <i>M. britomartis</i> ; <i>M. athalia</i>
<i>Ichneumon cynthiae</i> Kriechbaumer	<i>Euphydryas cynthia</i>	<i>Euphydryas cynthia</i> ⁴
<i>Ichneumon eumerus</i> Wesmael agg.	< <i>Maculinea</i>	<i>Maculinea teleius</i> ⁴ ; <i>M. alcon</i> ⁴ ; <i>Maculinea rebeli</i> ⁴
<i>Ichneumon exilicornis</i> Wesmael	<Polyommataini	<i>Plebejus argus</i> ⁴ ; <i>Polyommatus ?amandus</i> ⁵ ; <i>P. coridon</i> ⁺⁴ ; <i>P. admetus</i> ; <i>P. ripartii</i> ⁵ ; <i>P. nephohiptamenos</i> ⁵

<i>Ichneumon fulvicornis</i> Gravenhorst	<Maculinea	<i>Maculinea teleius</i> ^{4,6}
<i>Ichneumon gracilicornis</i> Gravenhorst	<Nymphalidae	? <i>Brenthis ino</i> ; <i>Euphydryas aurinia</i> ⁴ ; <i>Melitaea cinxia</i> ; <i>M. didyma</i> ; <i>M. diamina</i> ⁴ ; <i>M. athalia</i> ; <i>Maniola jurtina</i>
<i>Ichneumon macilentus</i> (Tischbein)	High-altitude Nymphalinae	<i>Boloria pales</i> ⁴ ; <i>Euphydryas cynthia</i> ⁴
<i>Ichneumon novemalbus</i> Kriechbaumer	<Satyrinae	<i>Melanargia lachesis</i>
<i>Ichneumon obliteratus</i> Wesmael	<i>Euphydryas cynthia</i>	<i>Euphydryas cynthia</i> ⁴
<i>Ichneumon occidentis</i> Hilpert	Includes high-altitude Geometridae and Arctiidae ⁴	<i>Boloria pales</i> ⁴ ; <i>Euphydryas cynthia</i> ⁴
<i>Ichneumon ?quadrialbatus</i> Gravenhorst ⁷	?	<i>Colias crocea</i>
<i>Ichneumon quinquealbatus</i> Kriechbaumer	?	<i>Boloria eunomia</i>
<i>Ichneumon sculpturatus</i> Holmgren	?	<i>Lycaena tityrus</i> ⁴
<i>Ichneumon silaceus</i> Gravenhorst	< <i>Boloria</i>	<i>Boloria selene</i> ; <i>B. pales</i> ⁴
<i>Ichneumon stenocerus</i> Thomson	?	<i>Euphydryas aurinia</i>
<i>Ichneumon vorax</i> Geoffroy	<i>Apatura</i>	<i>Apatura iris</i> ⁴
<i>Ichneumon</i> sp. ⁷	?	<i>Euphydryas iduna</i>
<i>Ichneumon</i> sp. ⁷	<Melitaeini	<i>Euphydryas maturna</i>
<i>Listrodromus nyctemerus</i> (Gravenhorst)	<i>Celastrina argiolus</i>	<i>Celastrina argiolus</i>
<i>Neotypus coreensis</i> Uchida	<Maculinea	<i>Maculinea arion</i> ⁸
<i>Neotypus intermedius</i> Mocsáry	<Polyommagini	<i>Lampides boeticus</i> ⁹
<i>Neotypus melanocephalus</i> (Gmelin) (= <i>pusillus</i> Gregor)	<Maculinea	<i>Maculinea teleius</i> ¹⁰ ; <i>M. nausithous</i> ¹⁰
<i>Neotypus nobilitator</i> (Gravenhorst)	<i>Cupido</i>	<i>Cupido minimus</i>
<i>Psilomastax pyramidalis</i> Tischbein	<i>Apatura</i>	<i>Apatura ilia</i> ; <i>A. iris</i>
<i>Syspasis scutellator</i> (Gravenhorst)	<i>Thymelicus</i>	<i>Thymelicus lineola</i> ^{8,11}
<i>Thyrateles camelinus</i> (Wesmael)	Nymphalini	<i>Vanessa cardui</i> ; <i>Nymphalis antiopa</i>
<i>Thyrateles haereticus</i> (Wesmael)	Nymphalini	<i>Inachis io</i>
<i>Trogus lapidator</i> (Fabricius)	<i>Papilio</i>	<i>Papilio machaon</i>
<i>Trogus violaceus</i> (Mocsáry)	<i>Papilio</i> ¹²	<i>Papilio machaon</i> ; <i>P. hospiton</i>
<i>Virgichneumon callicerus</i> (Gravenhorst)	<Lycaenidae	<i>Callophrys rubi</i> ⁸ ; <i>Polyommatus bellargus</i> ; <i>Polyommatus</i> sp.
<i>Virgichneumon tergenus</i> (Gravenhorst)	<Lycaenidae	<i>Satyrrium w-album</i> ; <i>S. pruni</i> ⁸ ; <i>S. esculi</i> ; <i>Plebejus argus</i> ; <i>Polyommatus icarus</i> ⁺¹³ ; <i>P. hispana</i> ¹³

Notes: 1. Horstmann (2007). 2. The parasitoid is more widely distributed than this host (Horstmann, 2007). 3. HNSalzburg (K. Horstmann, pers. comm.). 4. Hinz & Horstmann (2007). 5. Possibly a separate species from Greece; females are identical to *I. exilicornis* from central Europe, but in the males the tyloids differ slightly and the 2nd and 3rd gastral tergites are darker (K. Horstmann, pers. comm.). 6. The only certainly identified host is *M. teleius*, but it has been reared many times from co-occurring pupae of *M. teleius* or *M. nausithous*, which are morphologically indistinguishable. 7. The specimen(s) are male and determination is therefore uncertain. 8. BMNH. 9. Selfa *et al.* (1994). 10. K. Horstmann, pers. comm. 11. Carl (1968). 12. *T. violaceus*, a regular parasitoid of *P. hospiton*, is confined to Corsica and Sardinia where it also parasitises the much less frequently collected *P. machaon*. Wahl & Sime (2006) do not regard it as a species distinct from *T. lapidator*. 13. Horstmann *et al.* (1997).

Subfamily Pimplinae

Host associations and modes of development in this medium-sized subfamily are exceptionally wide. Only one rather limited tribe (Pimplini) of solitary idiobiont endoparasitoids of (mostly) Lepidoptera pupae attacks butterflies regularly. Most records involve the genera *Pimpla* (Plate 10a) and *Apechthis*, the latter being particularly adapted to oviposit in oblong pupae with overlapping sclerites through having a hooked ovipositor tip (Cole, 1959). One species in each of these genera is very regularly (but not exclusively) reared from butterfly pupae. Host range in Pimplini, most of which are plurivoltine, depends mostly on searching behaviour, host recognition (some, for example, prefer cocooned hosts, or those concealed in stems) and size suitability – in general, females will be reared from the large end of the host-size spectrum used. Another genus, *Itopectis* (Plate 8b), is more often a primary parasitoid of semi-concealed or cocooned smallish moth pupae, but some could be expected to use small species of butterflies occasionally. *Itopectis* species are also regularly pseudohyperparasitoids, and often reared from Campopleginae cocoons in particular, including those deriving from butterflies. A further species, *Theronia atalantae* (Poda), is regularly reared from largish Lepidoptera pupae including those of butterflies, but it seems to be an obligatory secondary parasitoid. Among idiobiont ectoparasitic Pimplinae, *Scambus signatus* (Pfeffer) (tribe Ephialtini) regularly

develops as a solitary parasitoid of Tortricidae feeding in Fabaceae pods, and would be expected also to attack lycaenid larvae in the same situations; however, we have seen no reared specimens.

Braconidae

As a family, Braconidae has a wider insect host range than Ichneumonidae (Gauld, 1988), being associated also with some groups of hemimetabolous insects and in some cases attacking the adult stage of long-lived insects, though not Lepidoptera (Shaw & Huddleston, 1991). About 33 subfamilies of Braconidae occur in Europe, of which 22 include parasitoids of Lepidoptera. Species attacking macrolepidoptera are found in 11 of these, but there are substantial numbers of species doing it in only two, Microgastrinae and Rogadinae. Only these two and a few species of *Meteorus* (Euphorinae), and under exceptional circumstances possibly Braconinae, parasitise butterflies in Europe. However, many species of Microgastrinae (especially some *Cotesia*; Plates 10b and 11) specialise on butterflies and are among their most conspicuous natural enemies. No group of Braconidae functions as hyperparasitoids. The failure of many subfamilies of Braconidae to have radiated into parasitising butterflies, with their (typically) exophytic feeding biology and usually weakly concealed pupation habits, is biological rather than accidental. Many braconid taxa are either ectoparasitic idiobionts or (very often) have a

Parasitoid	Suggested host range	Supporting host records
<i>Apechthis compunctor</i> (Linnaeus)	Broad (often medium/large butterflies)	<i>Pieris brassicae</i> ; <i>Colias crocea</i> ; <i>Lycaena dispar</i> ; <i>Satyrrium pruni</i> ; <i>Boloria titania</i> ; <i>Vanessa atalanta</i> ; <i>Inachis io</i> ; <i>Aglais urticae</i> ; <i>Nymphalis antiopa</i> ; <i>Euphydryas maturna</i> ; <i>E. desfontainii</i> ; <i>E. aurinia</i>
<i>Apechthis quadridentata</i> (Thomson)	Broad (especially Tortricidae, but butterflies possibly important over the winter)	<i>Pieris napi</i> ; <i>Pararge aegeria</i> ¹
(<i>Itopectis maculator</i> (Fabricius))	Broad (seldom small/medium butterflies)	<i>Satyrrium w-album</i>
<i>Pimpla aethiops</i> Curtis	?Large fenland Lepidoptera ²	<i>Papilio machaon</i> ²
<i>Pimpla rufipes</i> (Miller) (= <i>instigator</i> (Fabricius), preocc.)	Broad (often medium/large butterflies)	<i>Papilio machaon</i> ; <i>Pieris brassicae</i> ; <i>P. rapae</i> ; <i>P. napi</i> ; <i>Colias crocea</i> ; <i>Lycaena dispar</i> ; <i>Vanessa atalanta</i> ; <i>Euphydryas aurinia</i> ; <i>Charaxes jasius</i>
(<i>Pimpla turionellae</i> (Linnaeus))	Broad (seldom small/medium butterflies)	<i>Pieris rapae</i> ; <i>Satyrrium w-album</i>

Notes: 1. Cole (1967), as *A. resinator*, who considered it to be an important winter host. 2. Based on old British material in BMNH, but *P. aethiops* appears now to be extinct in Britain (Fitton *et al.*, 1988).

larval existence that starts as a koinobiont endoparasitoid but ends with an ectoparasitic final instar (Shaw & Huddleston, 1991). In both cases, concealed hosts – and/or physically well-protected host pupation sites, such as tough or subterranean cocoons – are a vital requirement for the parasitoid. This reality is clearly demonstrated by the kind of butterfly hosts suitable for the genus *Microgaster* (see later), and it also explains why genera such as *Cotesia* (which is fully endoparasitic), rather than some others in the subfamily Microgastrinae, have been such successful colonists of butterflies as a host group. The current version of Taxapad (see www.taxapad.com) includes a treatment of the literature on species of Braconidae.

Subfamily Braconinae

Except for the small non-European subtribe Aspidobraconina (which includes endoparasitoids in butterfly pupae: van Achterberg, 1984), all species of the large subfamily Braconinae are believed to be idiobiont ectoparasitoids and they attack a wide range of concealed holometabolous insects, usually as well-grown larvae. Although we have not seen reared specimens, it seems probable that some species of the large genus *Bracon* (most of which are gregarious) could facultatively attack butterflies that live endophytically as late-instar larvae, for example in the seed pods of Fabaceae, or as miners. While these habits are essentially restricted to a few Lycaenidae, other possible hosts could be Hesperiididae resting in strongly constructed retreats.

Subfamily Euphorinae

This diverse medium-sized subfamily contains koinobiont endoparasitoids of the adult stages of various insects (though not Lepidoptera), but also includes a group (dominated by the genus *Meteorus* and previously classified as a separate subfamily, Meteorinae) which parasitises larval Coleoptera and Lepidoptera. One, *Meteorus colon* (Haliday), is a regular parasitoid of *Limenitis camilla* in Britain (Shaw, 1981) though it also uses other hosts. Two others are occasionally reared from butterflies: we have seen *M. pulchricornis* (Wesmael) from *Iphiclides podalirius*, *Thecla betulae* and *Charaxes jasius*; and *M. versicolor* (Wesmael) from *Callophrys rubi* and *Maniola jurtina*, although both are much commoner from other macrolepidoptera. All the foregoing are solitary species that suspend their cocoons from the foodplant on a thread.

Subfamily Microgastrinae

This is one of the largest subfamilies of Braconidae and is practically restricted to Lepidoptera (though one species has

been reared from terrestrial Trichoptera: van Achterberg, 2002). All are koinobiont endoparasitoids, killing the larval stage of the host, and many are gregarious. Several species of the very large genus *Cotesia* (which used to come under the old generic concept of '*Apanteles*') parasitise butterflies, usually having narrow host ranges. Some of the smaller genera also contain specialist parasitoids of butterflies, though the occasional use of butterflies as part of more diffuse host ranges is more often seen. Egg-larval parasitism sometimes occurs, and various modifications of host behaviour have been noted, including the selection of particular resting sites before the parasitoid larva egresses.

Many microgastrines are essentially haemolymph-feeders and leave the host little consumed when they vacate it, allowing it to remain alive for a few days afterwards. In the case of *Pieris brassicae* parasitised by *Cotesia glomerata*, the moribund host sometimes spins a layer of silk across the yellow cocoon mass of its gregarious parasitoid (Brodeur, 1992) – probably an induced behaviour affording protection from generalist predation (as it does not deter pseudohyperparasitoids significantly) rather than an attempt to entrap the *Cotesia*. Some microgastrines, including the genus *Microgaster*, are haemolymph-feeders at first but then erupt from the host to continue their feeding externally, consuming virtually all but the skin of the host (illustrated in Shaw, 2004). This needs the protection of a secluded environment: the fact that the only butterflies regularly parasitised by *Microgaster* species are those, such as Hesperiididae and *Vanessa atalanta*, that rest in retreats like the mainstream hosts of the genus (concealed microlepidoptera larvae) particularly clearly shows the role of life history and behaviour in determining a host's parasitoids.

Several *Cotesia* species that are plurivoltine, notably those associated with Melitaeini (Plate 10b), have successive generations on a single host generation, having progressively larger broods on older hosts. Other plurivoltine *Cotesia* species may use different hosts at different times of year: for example, *C. vestalis* is a solitary parasitoid that overwinters in Satyrinae larvae but attacks *Aglais urticae* and sometimes other Nymphalini in summer, as well as its economically important host, the pluteid *Plutella xylostella* (see Wilkinson, 1939). Similar alternations are presumably needed by several others, for example *C. saltator* and *C. risilis*, which are parasitoids of respectively Anthocharini and *Gonepteryx* species that feed as larvae in early summer. These parasitoids emerge from their cocoons quickly, but the hosts needed subsequently to complete the annual life cycle are unknown. *Cotesia gonepterygis*, another solitary parasitoid of *Gonepteryx*, spins a tough golden cocoon

(invariably on a twig; Plate 11) which persists to emerge the following spring, and consequently this univoltine species needs no other host. Some *Cotesia* species can pass the winter in more than one way (for example *C. glomerata* does so in its cocoons if its late-summer host was a *Pieris* species, or as larvae inside the diapausing larva of *Aporia crataegi*), but no Microgastrinae are believed to hibernate as adults.

Adult Microgastrinae always emerge from the cocoon by cutting a neat circular cap from the anterior end. If a hyperparasitoid develops in the cocoon, however, the adult hyperparasitoid invariably chews its way out, making a much less regular hole, usually subapically. This difference can be used to assess the level of hyperparasitism suffered by Microgastrinae when their cocoons are collected post-emergence.

Parasitoid	Suggested host range	Supporting host records
<i>Cotesia acuminata</i> (Reinhard) agg.*	<Melitaeini	Molecular ¹ and morphological data suggest there are 4 separate species on (a) <i>Euphydryas maturna</i> , (b) <i>Melitaea phoebe</i> , <i>M. telona</i> (c) <i>M. didyma</i> and (d) <i>M. athalia</i>
<i>Cotesia ?amesis</i> (Nixon)* ²	<Polyommagini	<i>Plebejus glandon</i>
<i>Cotesia ancilla</i> (Nixon)*	<i>Colias</i>	<i>Euchloe charlomia</i> ³ ; <i>Colias palaeno</i> ⁴ ; <i>C. crocea</i> ; <i>C. chrysotheme</i> ⁴ ; <i>C. hyale</i> ⁴ ; <i>C. alfajariensis</i>
<i>Cotesia astrarches</i> (Marshall)*	<Polyommagini	<i>Cupido minimus</i> ; <i>Aricia agestis</i> ; <i>A. artaxerxes</i> ; <i>Polyommatus thersites</i>
<i>Cotesia bignellii</i> (Marshall) agg.* ⁵	<i>Euphydryas aurinia</i>	<i>Euphydryas aurinia</i>
<i>Cotesia cuprea</i> (Lyle)*	<i>Lycaena</i> ⁶	<i>Lycaena phlaeas</i> ; <i>L. helle</i> ⁴ ; <i>L. dispar</i> ; <i>L. thersamon</i>
<i>Cotesia cynthiae</i> (Nixon)*	<i>Euphydryas cynthia</i>	<i>Euphydryas cynthia</i> ⁺⁴
<i>Cotesia glabrata</i> (Telenga)*	<Pyrginae	<i>Carcharodus alceae</i> ; <i>C. tripolinus</i> ; <i>Pyrgus cirsii</i>
<i>Cotesia glomerata</i> (Linnaeus)*	<Pierini	<i>Aporia crataegi</i> ; <i>Pieris brassicae</i> ; <i>P. mannii</i> ; <i>P. rapae</i> ; <i>P. napi</i> ; <i>Pontia daplidice</i> ⁴
<i>Cotesia gonepterygis</i> (Marshall)	<i>Gonepteryx</i>	<i>Gonepteryx rhamni</i> ; <i>G. cleopatra</i>
<i>Cotesia inducta</i> (Papp)	<Lycaenidae	<i>Tomares ballus</i> ; <i>Callophrys avis</i> ; <i>Satyrium w-album</i> ; <i>Celastrina argiolus</i> ; <i>Glaucopsyche melanops</i>
<i>Cotesia lycophron</i> (Nixon)*	<Melitaea	<i>Melitaea trivialis</i> ; <i>M. didyma</i>
<i>Cotesia melitaeorum</i> (Wilkinson) agg.*	<Melitaeini	Molecular ⁷ and morphological data suggest that at least 5 species are included; provisionally assessed as on (a) <i>Euphydryas aurinia</i> , (b) <i>E. desfontainii</i> + <i>E. aurinia</i> (Spain), (c) <i>Melitaea cinxia</i> and probably <i>M. diamina</i> , (d) <i>M. trivialis</i> , (e) <i>M. athalia</i> and probably both <i>M. deione</i> and <i>M. parthenoides</i>
<i>Cotesia pieridis</i> (Bouché)*	<i>Aporia crataegi</i>	<i>Aporia crataegi</i>
<i>Cotesia risilis</i> (Nixon)	<i>Gonepteryx</i> ⁸	<i>Gonepteryx rhamni</i> ; <i>G. cleopatra</i>
<i>Cotesia rubecula</i> (Marshall)	< <i>Pieris</i> spp. (not <i>P. brassicae</i>)	<i>Pieris rapae</i>
<i>Cotesia saltator</i> (Thunberg)	<Anthocharini ⁸	<i>Anthocharis cardamines</i> ; <i>A. euphenoides</i> ; <i>Euchloe crameri</i>
<i>Cotesia saltatoria</i> (Balevski)	<Polyommagini	<i>Aricia agestis</i> ; <i>A. artaxerxes</i> ; <i>Polyommatus amandus</i> ; <i>P. icarus</i> ; <i>P. coridon</i> ⁹
<i>Cotesia sibyllarum</i> (Wilkinson)*	< <i>Limenitis</i>	<i>Limenitis camilla</i> ; <i>L. reducta</i>
<i>Cotesia specularis</i> (Szépligeti)*	<Polyommagini (especially in Fabaceae pods)	<i>Lampides boeticus</i> ; <i>Glaucopsyche alexis</i> ; <i>Iolana iolas</i>

<i>Cotesia tenebrosa</i> (Wesmael)*	<Polyommadini	<i>Cupido alcetas</i> ; <i>Plebejus argus</i> ; <i>Aricia morronensis</i> ; <i>Polyommatus icarus</i> ; <i>P. daphnis</i> ; <i>P. bellargus</i> ; <i>P. coridon</i> ; <i>P. albicans</i> ¹⁰ ; <i>P. admetus</i>
<i>Cotesia tetrica</i> (Reinhard)*	<Satyrinae	<i>Lasiommata megera</i> ⁴ ; <i>Maniola jurtina</i> ; <i>Erebia aethiops</i>
<i>Cotesia tibialis</i> (Curtis)*	<Noctuidae; <Satyrinae	<i>Pyronia tithonus</i> ⁴ ; <i>Maniola jurtina</i> ⁴
<i>Cotesia vanessae</i> (Reinhard)* ¹¹	<Nymphalini; <Noctuidae over the winter	<i>Vanessa atalanta</i> ; <i>V. cardui</i> ; <i>Aglais urticae</i>
<i>Cotesia vestalis</i> (Haliday) (= <i>plutellae</i> (Kurdjumov))	<Nymphalini; <Satyrinae; various others include <i>Plutella xylostella</i> ¹²	<i>Vanessa cardui</i> ; <i>Aglais urticae</i> ¹³ ; <i>Nymphalis polychloros</i> ; <i>Maniola jurtina</i> ⁴ ; <i>Hipparchia semele</i>
<i>Cotesia</i> sp.*	<Polyommadini	<i>Scolitantides orion</i> ; <i>Polyommatus coridon</i> ; <i>P. caelestissima</i>
<i>Cotesia</i> sp. nov.* ¹⁴	<i>Boloria eunomia</i>	<i>Boloria eunomia</i>
<i>Cotesia</i> sp. nov.* ¹⁴	<Heliconiinae	<i>Argynnis aglaja</i> ; <i>A. adippe</i>
<i>Cotesia</i> sp. nov.* ¹⁴	<Heliconiinae	<i>Boloria selene</i>
<i>Cotesia</i> sp.*	<Pyrginae	<i>Carcharodus boeticus</i>
<i>Diolcogaster abdominalis</i> (Nees)	<i>Coenonympha</i>	<i>Coenonympha tullia</i> ; <i>C. oedippus</i>
<i>Distatrix sancus</i> (Nixon)*	Theclini, Eumaeini and possibly Lycaenini	? <i>Lycena</i> sp.; <i>Thecla betulae</i> ; <i>Neozephyrus quercus</i> ; <i>Callophrys rubi</i> ¹⁵
<i>Dolichogenidea sicarius</i> (Marshall)	Broad (seldom butterflies)	<i>Carcharodus alceae</i> ; <i>Vanessa cardui</i>
<i>Glyptapanteles vitripennis</i> (Curtis)	Broad (?seldom butterflies)	<i>Leptidea sinapis</i> ^{16,17} ; <i>Limenitis populi</i>
<i>Microgaster australis</i> Thomson	<Pyrginae	<i>Carcharodus alceae</i> ; <i>Muschampia proto</i> ; <i>M. tessellum</i> ; <i>Pyrgus serratulae</i> ; <i>P. onopordi</i> ; <i>P. armoricanus</i> ; <i>Pyrgus</i> sp.
<i>Microgaster nixalebion</i> Shaw	<i>Anthophila</i> , <i>Prochoreutis</i> , <i>Pleuroptya</i> and <i>Vanessa atalanta</i>	<i>Vanessa atalanta</i> ; <i>Aglais urticae</i> ¹⁶
<i>Microgaster nobilis</i> Reinhard	<Pyrginae	<i>Carcharodus alceae</i> ; <i>C. baeticus</i> ; <i>Muschampia proto</i>
<i>Microgaster subcompletus</i> Nees*	<Pyralidae, including <i>Pleuroptya ruralis</i> , and <i>Vanessa atalanta</i>	<i>Vanessa atalanta</i> ; <i>V. cardui</i> ¹⁶ ; <i>Polygona c-album</i> ¹⁶
<i>Microplitis retenta</i> Papp	Anthocharini	<i>Anthocharis euphenoides</i> ; <i>Euchloe</i> sp.
<i>Protapanteles anchisiades</i> (Nixon)	Broad (?seldom butterflies)	<i>Leptidea sinapis</i> ^{17,+18}
<i>Protapanteles incertus</i> (Ruthe) (= <i>caberae</i> (Marshall))	Broad (?seldom butterflies)	<i>Pararge aegeria</i>
<i>Protapanteles</i> sp.	?	<i>Limenitis populi</i>

Notes: *Gregarious species. Generic classification follows Mason (1981). Single rearings of unidentified species have been excluded from the table. 1. Kankare & Shaw (2004); Kankare *et al.* (2005a). 2. Reared specimens are from Spain and differ a little from the non-reared type series from Switzerland. 3. The parasitoid specimens differ a little and may belong to another species. 4. Nixon (1974). 5. There is evidence for the existence of two species, both using only *E. aurinia*. 6. Various authors give species of Polyommadini as hosts but we have not been able to verify any. 7. As 1; also Kankare *et al.* (2005b). 8. There must also be a late-summer host, as yet unknown. 9. Baumgarten & Fiedler (1998). 10. Including ssp. *arragonensis*. 11. Some populations in South Europe are thelytokous. 12. Lloyd (see Wilkinson, 1939) demonstrated, through rearing experiments, that the parasitoid of *A. urticae* and *P. xylostella* are the same species. 13. Also ssp. *ichnusa* from Corsica. 14. To be described by M. R. Shaw (in press). 15. Fiedler *et al.* (1995). 16. Infrequent host. 17. From England, where the only *Leptidea* is *L. sinapis*. 18. BMNH.

Subfamily Rogadinae

As currently restricted, Rogadinae are all koinobiont endoparasitoids of Lepidoptera larvae and make characteristic shrunken and hardened ‘mummies’ from their hosts, inside which they pupate. Most species are solitary and the large genus *Aleiodes* dominates the subfamily, usually attacking the host as a small larva and killing it in its penultimate instar. Two species parasitise butterflies in Europe: *A. coxalis* (Spinola) (= *tristis* Wesmæl) which has been reared from a range of Satyrinae (*Coenonympha tullia*, *C. pamphilus*, *Maniola jurtina*, *Erebia* sp., *Melanargia lachesis*, and several unidentified species) and is also a frequent parasitoid of the hesperiid *Thymelicus lineola*; and *A. bicolor* (Spinola) which parasitises polyommata Lycaenidae (*Cupido alcetas*, *Plebejus idas*, *Aricia agestis*, *A. artaxerxes*, *Polyommatus icarus*, *P. eros* (in BMNH), *P. coridon*, *P. albicans*, *P. damon* and ?*Cupido minimus*). (A closely related species, *A. assimilis* (Nees), parasitises *Zygaena* species (Zygaenidae) and has often been misidentified in the literature as *A. bicolor*.)

CHALCIDOIDEA

All but the most esoteric of the approximately 20 families in this large and biologically diverse superfamily occur in Europe, but only a few species in the families Chalcididae, Pteromalidae, Eulophidae, and several groups of egg parasitoids (Trichogrammatidae, and small elements of Eupelmidae, Encyrtidae and perhaps others) are likely to be reared as primary parasitoids of butterflies. More families might arise as hyperparasitoids, with certain Eulophidae (particularly gregarious *Baryscapus* species) and Perilampidae acting as true hyperparasitoids, and a number of families (mostly not dealt with further) furnishing potential pseudohyperparasitoids.¹

Pteromalidae

This is a very big and biologically diverse family. A few gregarious species in the large genus *Pteromalus* attack butterfly pupae, preferentially ovipositing through the fresh cuticle while it is still soft. To be on hand for this, the female

Parasitoid	Suggested host range	Supporting host records
<i>(Coelopisthia caledonica</i> Askew)	Usually <Noctuidae	<i>Melitaea cinxia</i> ¹
<i>Coelopisthia pachycera</i> Masi	?	<i>Maniola jurtina</i> ⁺²
<i>(Dibrachys</i> spp.)	Broad, mostly pseudohyperparasitoids	No direct records of primary parasitism, but see ³
<i>(Psychophagus omnivorus</i> (Walker))	Large Lepidoptera, especially those pupating below ground	<i>Satyrium w-album</i> ; <i>Polygona c-album</i>
<i>Pteromalus apum</i> (Retzius)	Megachilinae bees and <butterflies, especially Melitaeini	<i>Gonepteryx rhamni</i> ; <i>Aglais urticae</i> ⁴ ; <i>Euphydryas maturna</i> ; <i>E. desfontainii</i> ; <i>E. aurinia</i> ; <i>Melitaea cinxia</i> ; <i>M. didyma</i> ; <i>M. athalia</i>
<i>Pteromalus puparum</i> (Linnaeus)	<Butterflies, especially Papilionidae, Pieridae and <Nymphalidae	<i>Papilio machaon</i> ; <i>Aporia crataegi</i> ; <i>Pieris brassicae</i> ; <i>P. rapae</i> ; <i>Pontia daplidice</i> ; <i>Libythea celtis</i> ; <i>Argynnis pandora</i> ; <i>A. adippe</i> ; <i>Vanessa atalanta</i> ; <i>V. cardui</i> ; <i>Aglais urticae</i> ; <i>Polygona c-album</i> ; <i>Araschnia levana</i> ; <i>Nymphalis antiopa</i> ; <i>N. polychloros</i> ; <i>Euphydryas desfontainii</i> ; <i>E. aurinia</i> ; <i>Melitaea cinxia</i> ⁵ ; <i>Limnitis camilla</i>

Unreferenced records include those from R. R. Askew's collection as well as NMS.

Notes: 1. Probably abnormal host. 2. Honey (1998). 3. Askew & Shaw (1997). 4. Pyörnilä (1977) as *P. venustus*; see also Shaw (2002b). 5. Lei *et al.* (1997).

¹ A database containing information on world Chalcidoidea is maintained at <http://www.nhm.ac.uk/research-curation/projects/chalcidoids> by J. S. Noyes.

parasitoid often adopts a caterpillar before it chooses its pupation site, then sits inconspicuously on it until pupation occurs. While *Pteromalus puparum* seems only to attack Lepidoptera (and essentially butterfly) pupae and has a wide host range (Plates 12a and 12b), *P. apum* has a remarkable host range as it attacks both the cells of megachiline bees (Hymenoptera: Apidae) and the pupae of butterflies, especially Melitaeini (Askew & Shaw, 1997; Shaw, 2002b). Related genera contain similarly gregarious and endoparasitic pupal parasitoids of Lepidoptera, but although several have been reared from butterfly pupae mostly the relationship is more incidental (Askew & Shaw, 1997). The entire brood usually egress as adults through one or very few emergence holes chewed through the host pupa (Plate 12a). Different *Pteromalus* species, and also those of various other genera, are common pseudohyperparasitoids ex Ichneumonoidea cocoons or Tachinidae puparia.

Chalcididae

This is a rather small family in Europe, albeit of mainly relatively large species. A few species of *Brachymeria* are solitary primary parasitoids of Lepidoptera pupae, and two attack butterflies in grassland habitats regularly though not exclusively: *B. femorata* (Panzer) which we have seen from *Pieris brassicae*, *Melitaea didyma*, *M. deione* and *Maniola jurtina*; and *B. tibialis* (Walker) from *Euphydryas aurinia* and *E. desfontainii*. The latter (= *B. intermedia*) was recorded by Carl (1968) from *Thymelicus lineola*, and our records from Melitaeini probably reflect considerable sampling effort rather than any particular affinity. The pupa seems to be attacked soon after its formation. A few other Chalcididae (including further species of *Brachymeria*) arise as pseudohyperparasitoids ex Ichneumonoidea cocoons.

Eulophidae

Few records of Eulophidae attacking European butterflies as primary parasitoids exist, but we have seen one brood of the gregarious koinobiont ectoparasitoid *Euplectrus* ?*flavipes* (Fonscolombe) reared from *Charaxes jasius* (Plate 13a), and species of *Eulophus* with broadly similar biology might also occasionally use exposed butterfly caterpillars. Butterflies having endophytic feeding stages, or those resting in deep concealment, might be prone to parasitism from various genera (e.g. *Elasmus*, *Elachertus* and *Sympiesis*). Some gregarious *Baryscapus* species are true hyperparasitoids, and some regularly attack Microgastrinae (Braconidae) parasitising butterflies (Askew & Shaw, 2005). Pseudohyperparasitism could arise from a number of genera (in a few of which there seem to be specialist parasitoids of Ichneumonoidea cocoons).

Egg parasitoids (Chalcidoidea and Platygastroidea)

Parasitism of insect eggs, and full development to the adult stage therein, is practised by the entire family Scelionidae (Platygastroidea), two entire families of Chalcidoidea (Trichogrammatidae and Mymaridae), and one or more genera in several additional families of Chalcidoidea and also a few Platygastriidae (Platygastroidea). Representatives of at least nine families altogether have been recorded (whether correctly or not) as egg parasitoids of Lepidoptera in Europe (B. Pintureau, pers. comm.), though most are much more strongly associated with the eggs of other insects. The most important parasitoids of butterfly eggs are in the genera *Trichogramma* (Trichogrammatidae) (Plates 13b and 14), *Anastatus* (Eupelmidae) and *Ooencyrtus* (Encyrtidae) in the Chalcidoidea, and also *Telenomus* (Scelionidae) and possibly related genera in the Platygastroidea.

With notable exceptions, Lepidoptera eggs are neither easy to find nor to identify. This, and the difficult taxonomy of major genera such as *Trichogramma* and *Telenomus*, has so hampered knowledge of host range in egg parasitoids that we do not attempt to give specific host data here. It does seem, however, that for many butterfly species egg parasitism is an extremely important cause of mortality, that in some cases it can outweigh all other parasitism (e.g. Stefanescu *et al.*, 2003b), and that parasitism by *Trichogramma* species is particularly prevalent.

Considerable biological and behavioural differences between groups of egg parasitoids exist, even though the host's egg stage is in general poorly defended. Most *Telenomus* species need to attack rather young eggs and, like *Anastatus* which also fails to develop in older eggs, usually develop solitarily with respect to each egg attacked, though a high proportion of batched eggs might be parasitised at a single visit. *Trichogramma* species are especially small, often developing in surprisingly large broods per egg, are capable of using eggs of almost any age (though young eggs may be the most suitable: Ruberson & Kring, 1993), and can even behave as hyperparasitoids (Strand & Vinson, 1984). These attributes suggest that *Trichogramma* species will have broader host ranges, perhaps determined more by searching environment than by the hosts themselves, than scelionid species, which does indeed seem to be the case (see Babendreier *et al.*, 2003a, b; Roemis *et al.*, 2005), although a *Telenomus* species has also been recorded as a hyperparasitoid (Viktorov, 1966). While *Ooencyrtus* species are often gregarious and quite small, *Anastatus* are relatively large and for them host size might also be a constraint.

Eggs parasitised by Chalcidoidea often darken abnormally, but early signs of parasitism due to Scelionidae are

typically less evident. All emerging adults of gregarious species of *Trichogramma* usually leave the host egg through a single hole, in contrast with *Ooencyrtus* (Stefanescu *et al.*, 2003b). In both Trichogrammatidae and Scelionidae females of some species are known to locate and attach themselves to the parent host before she oviposits (Plate 14), through this phoresy being able to parasitise eggs that might otherwise be difficult to locate – also gaining access while eggs are young and before competitors. Male *Pieris brassicae* are almost as attractive to *Trichogramma brassicae* Bezdenko hitching a ride as are mated females, while virgin females are shunned, because the mounting allomone used is a male-derived host pheromone (Fatouros *et al.*, 2005). Some Trichogrammatidae and Scelionidae mark eggs into which they have oviposited, either physically or with pheromones that deter conspecifics.

Diptera

Tachinidae

This is one of the largest of approximately 125 families of Diptera in Europe. All Tachinidae are koinobiont endoparasitoids, and a wide range of medium to large terrestrial insects (and a few other arthropods) comprise the host spectrum overall, though Lepidoptera predominate. Some tachinids parasitise long-lived adult insects but all of those reared from Lepidoptera attack only the larval stage (though either obligatorily or facultatively the host is sometimes not killed until it has pupated). Out of four subfamilies in Europe, three (Dexiinae, Exoristinae and Tachininae) contain parasitoids of Lepidoptera – though none of them exclusively – but only the last two (especially Exoristinae) include species that regularly attack butterflies (Plate 15). Most species associated with Lepidoptera use only that order, but a few of the most polyphagous sometimes also develop in sawfly larvae.²

In general, Tachinidae parasitising Lepidoptera are substantially less narrowly host-specialised than koinobiont parasitic wasps, and the physiological interaction with the host is less sophisticated (Askew & Shaw, 1986; Eggleton & Gaston, 1992; Belshaw, 1994). Two attributes underlie their capacity for diffuse host ranges. Firstly, rather than placing

an inactive egg into the host's haemocoel, incurring a major risk of encapsulation by the host's haemocytes, either (i) in the tribe Goniini (Exoristinae), specialised minute 'micro-type' eggs (Salkeld, 1980) are laid on vegetation to be ingested by the host and hatch in its gut, or (ii) the active first-instar larva first penetrates the host, boring into it either straight from eggs laid externally on the host (Plate 16) or following the laying of well-incubated eggs (or even larviposition) onto vegetation nearby. Exceptionally (e.g. in *Blondelia* and *Compsilura*) the female tachinid gouges a wound on the host with a specialised abdominal piercing structure and places first-instar larvae or eggs close to hatching directly into the host's body. Secondly, the larva, once in the haemocoel, avoids suffocation by diverting the host's encapsulation response so that only a sheath is formed, which the tachinid larva keeps open in the region of its mouth by its feeding activity, and at the other end by connecting its large posterior spiracles directly to an air supply, either piercing through the host's integument or via its tracheal system. In contrast, koinobiont endoparasitic Hymenoptera typically not only place an immobile egg in the host, but also live as larvae free in the haemocoel and depend for respiration on diffused oxygen – in both cases making them highly vulnerable to suffocation in any host for which they do not have a specific way of disrupting the encapsulation response.

Because of the plasticity in many tachinid host ranges, it is pointless to list any but the rather few species that use

Tachinidae more or less specialised to butterfly species	Main hosts
Subfamily Exoristinae	
<i>Apomyia confinis</i> (Fallén)	Lycaenidae
<i>Buquetia musca</i> Robineau-Desvoidy	<i>Papilio</i>
<i>Cadurciella tritaeniata</i> (Rondani)	<i>Callophrys</i>
<i>Epicampocera succincta</i> (Meigen)	<i>Pieris</i>
<i>Erycia fasciata</i> Villeneuve	Melitaeini (<i>Melitaea</i>)
<i>Erycia fatua</i> (Meigen)	Melitaeini (<i>Euphydryas</i> ; <i>Melitaea</i>)
<i>Erycia festinans</i> (Meigen)	Melitaeini (<i>Melitaea</i>)
<i>Erycia furibunda</i> (Zetterstedt)	Melitaeini (<i>Euphydryas</i>)
<i>Sturmia bella</i> (Meigen)	Nymphalini
<i>Thecocarcelia acutangulata</i> (Macquart)	Hesperiinae
Subfamily Tachininae	
<i>Pelatachina tibialis</i> (Fallén)	Nymphalini

² Herting (1960), Belshaw (1993) and Stireman *et al.* (2006) provide biological overviews and rearing records, and there is a website covering especially British species (<http://tachinidae.org.uk>). Reared Tachinidae can be sent to H.-P. Tschorsnig (Naturkundemuseum, Rosenstein 1, 70191 Stuttgart, Germany; tschorsnig.smns@naturkundemuseum-bw.de) for identification.

butterflies significantly more than other hosts. As the records largely come from an unpublished private database (H.-P. Tschorsch, pers. comm.), we tabulate just an indication of the hosts. Additionally, several polyphagous species are regularly reared from various butterflies, but as part of much broader host ranges. These include (all in the sub-family Exoristinae): *Compsilura concinnata* (Meigen), *Phryxe vulgaris* (Fallén), *P. nemea* (Meigen) and to a lesser extent *Blondelia nigripes* (Fallén), *Phryxe magnicornis* (Zetterstedt), *Exorista larvarum* (Linnaeus), *E. segregata* (Rondani), *Bactromyia aurulenta* (Meigen), *Pales pavidata* (Meigen) and *Masicera sphingivora* (Robineau-Desvoidy). Many of these are extremely abundant and more often reared from butterflies than the more specialised species. More than 20 further species have been recorded (perhaps correctly) from one or more butterfly species on at least one occasion.

Bombyliidae

This fairly large family of flies is widespread in Europe but most numerous in the Mediterranean area. They are all essentially parasitoids, though the overall host relations of the family are extremely broad and only partly understood (Yeates & Greathead, 1997). Relatively few species parasitise Lepidoptera. Eggs are laid, often individually though always in very large numbers, in sites likely to support hosts, which are actively sought by the first-instar larva. This is a specialised form (shared by several groups of parasitoids) called a planidium, being minute, highly mobile and adapted to withstand desiccation during a long period of host-seeking. The few species that have been (infrequently) recorded as parasitoids of Lepidoptera in Europe oviposit onto the soil, and consequently butterfly species with larvae that spend time at the soil surface, e.g. Satyrinae, are the most likely to be attacked, especially by polyphagous species of the genus *Villa*. While most Bombyliidae are ectoparasitoids, *Villa* is endoparasitic, and the biology of one species has been described by Du Merle (1964, 1979a, b, c). The planidial larva attaches itself externally to the caterpillar and is carried to the host's pupation site, where it will penetrate the fresh pupal cuticle to develop internally. Although pupation is inside the host, the tough and heavily spiny bombyliid pupa is highly mobile, and it breaks out of the host's pupal shell and makes its way to the soil surface where the adult fly emerges. Rearing records from European butterflies are scarce, but García-Barros (1989a) reported an unidentified species of *Villa* from both *Hipparchia statilinus* and *H. semele*. Bombyliidae can also behave as hyperparasitoids.

CASE STUDIES

Here we present case studies on parasitism of the six butterfly taxa which have been most quantitatively studied in Europe. Our aim is to illustrate the range of parasitoid assemblages and the extent to which parasitoids account for butterfly mortality.

Papilionidae: *Iphichides podalirius*

With the exception of *Iphichides podalirius*, information on parasitoids attacking the few species of European Papilionidae is mainly based on casual records. Surprisingly, in a 4-year study carried out in Norfolk, England, to determine pre-adult mortality of *Papilio machaon*, not a single parasitoid was recorded from monitoring over 300 eggs, 293 larvae and 40 pupae (Dempster *et al.*, 1976). However, the specialist larva-pupal parasitoid *Trogus lapidator* (Ichneumonidae: Ichneumoninae) (Plate 9a) was later found to be established in the general area (Shaw, 1978) and further sampling would presumably have revealed the generalist and regular pupal parasitoids *Pteromalus puparum* (Plates 12a and 12b) and *Pimpla rufipes* (Plate 10a).

The parasitoid complex of *I. podalirius* was studied at a site in Catalonia, Spain, from 1996 to 1999. From over 1000 eggs, 124 larvae and 32 pupae, eight species of parasitoids were reared, some of them regularly attacking the host and having an important impact on population size (Stefanescu *et al.*, 2003b). Egg parasitoids were by far the most abundant and diverse, perhaps a common pattern for Papilionidae (e.g. Watanabe *et al.*, 1984; Garraway & Bailey, 1992). Larval parasitoids were scarce and no parasitoids were recorded from the rather small sample of pupae.

The egg parasitoids comprised *Trichogramma cordubense* Vargas & Cabello and *T. gicai* Pintureau & Stefanescu (Trichogrammatidae), *Ooencyrtus telenomicida* (Vassiliev) and *O. vinulae* (Masi) (Encyrtidae) and *Anastatus bifasciatus* (Geoffroy) (Eupelmidae). With the possible exceptions of *O. vinulae* (recorded only once) and the poorly known *T. gicai*, all these are plurivoltine and broad generalists, and parasitise eggs of several insect orders.

In the study area *I. podalirius* has two, and a partial third, annual generations. Parasitism had a strong seasonal pattern. In summer, egg parasitoids killed 25–45% of the eggs, and vertebrate predation of the overwintering pupae caused most of the remaining mortality (Stefanescu, 2004). In the spring parasitism was negligible, and most mortality was due to invertebrate predation of young larvae and bird predation of old larvae and pupae (Stefanescu, 2000b; and unpublished data). This seasonal pattern of parasitism, whereby

increasing levels occur as summer progresses, has been noted by Dempster (1984) and Askew & Shaw (1986), and may be a common feature in plurivoltine temperate Lepidoptera regularly attacked by generalist parasitoids.

The extremely polyphagous tachinid *Compsilura concinnata* was the only regular larval parasitoid, but it was restricted to summer generations when it caused widely varying mortality up to 20%. Two other polyphagous larval parasitoids, *Blepharipa pratensis* (Meigen) (Tachinidae) and *Meteorus pulchricornis* (Braconidae: Euphorinae), were recorded twice and once, respectively. *Blepharipa pratensis* is particularly a parasitoid of *Lymantria dispar* (but also other moths), and *M. pulchricornis* parasitises various macrolepidoptera.

Pieridae: *Pieris* spp.

Some *Pieris* butterflies are synanthropic as well as being conspicuous in the European landscape, so it is not surprising that some of the earliest documentation of parasitoid life history involves *Cotesia glomerata* parasitising *Pieris brassicae* (for example, Goedart, 1662; Ray, 1710; as reported in Feltwell, 1982). Much attention has been paid to the world-wide agricultural pests *Pieris rapae* and *P. brassicae*, and their commonest parasitoids are well known (also through laboratory experiments). However, there are relatively few parasitoid species regularly associated with European *Pieris* (summarised for *P. brassicae* by Shaw, 1982), and many of them are known to use a wide range of hosts.

Three large-scale studies on mortality of *P. rapae* and *P. brassicae* in Europe have been published. One by Moss (1933) details his collections of *Cotesia glomerata* and *Pteromalus puparum* (Plates 12a and 12b) for importation to Australia to control *P. rapae*. Incidentally, both proved to be bad choices: *C. glomerata* is better adapted to *P. brassicae*; and *P. puparum* has a wide host range. The second is a 4-year study in the UK by Richards (1940) which is outlined below. The third is a 3-year study of the effects of the insecticide DDT on *P. rapae* and its parasitoids (Dempster, 1967, 1968). Several smaller studies include pupal parasitism of *P. rapae* and *P. brassicae* (Bisset, 1938; Littlewood, 1983), and egg and larval mortality of *P. brassicae* and *P. rapae* in the UK (Baker, 1970) and *P. brassicae* in Denmark (Kristensen, 1994). In Europe there has been very little work on parasitism of *P. napi*, which is not a pest (but see Lee & Archer, 1974). However, it has been investigated in Japan, where *P. napi* co-occurs with *P. rapae* and *P. melete* Ménétriès (Ohsaki & Sato, 1999), as has parasitism of the closely related *P. virginensis* Edwards in North America, which has

declined owing to non-target effects of the biological control of *P. rapae* (Benson *et al.*, 2003).

Richards' (1940) study was conducted near Slough in England between 1932 and 1936. *Pieris brassicae*, *P. rapae* and *P. napi* were present, but only the first two were abundant and sampled. Richards reared 3581 *P. rapae* and 949 *P. brassicae* larvae, collected in each instar and during all of the three annual generations, primarily from cabbage. He followed many fewer pupae and eggs. His text and tabulation illustrate clearly the complexities of reporting rates of parasitism as a continuing process.

The most important parasitoids were the braconids *Cotesia rubecula* and *C. glomerata*. *Cotesia rubecula* is solitary and parasitises *P. rapae*, while *C. glomerata* is gregarious and uses primarily *P. brassicae*. A total of 24% of the *P. rapae* reared were parasitised by *C. rubecula*. This differed between years (ranging from 3% to 61%) and, as is generally the case for plurivoltine parasitoids in temperate climates, it increased in successive generations within a year. About 17% of the *C. rubecula* were themselves parasitised by the gregarious secondary parasitoid *Baryscapus galactopus* (Ratzeburg) (misidentified as *Tetrastichus rapo*) (Eulophidae) and 4% by the solitary *Mesochorus olerum* Curtis (misidentified as *tachypus*) (Ichneumonidae: Mesochorinae). *Cotesia glomerata* parasitised *P. rapae* only sparingly (none most generations, up to 15% occasionally), but consistently parasitised a large fraction (on average 53%) of early-instar gregarious *P. brassicae* larvae. The same two true hyperparasitoids were found as from *C. rubecula*, but at a lower rate.

Of several tachinid species reared, only the polyphagous *Phryxe vulgaris* and to a lesser extent the specialist *Epicampocera succincta* were in any numbers, and they were at a competitive disadvantage to the *Cotesia* species. The polyphagous pupal parasitoid *Pteromalus puparum* (Pteromalidae) emerged from six out of the 155 *P. rapae* pupae collected, but another generalist, *Pimpla rufipes* (Plate 10a), which is a very regular pupal parasitoid of *Pieris* species, was not found. Polyphagous *Trichogramma* (Trichogrammatidae) egg parasitoids regularly use *Pieris* hosts in Europe (see Feltwell, 1982, for a review) but were apparently absent at Slough. Similarly, Kristensen (1994) found no parasitism of 48 *P. brassicae* egg batches observed in Denmark.

In Richards' study parasitism caused significant mortality of *P. rapae* and *P. brassicae*, on par with the effects of disease, climate and predators. On average, about 25% of the total mortality of *P. rapae* was due to parasitism, primarily (80%) by *C. rubecula*. For *P. brassicae* it was somewhat higher

because the rate of parasitism of *P. brassicae* by *C. glomerata* was on average twice that of *C. rubecula* on *P. rapae*.

Moss (1933) and Dempster (1967) found broadly similar patterns to Richards', though recording respectively somewhat higher and lower rates of parasitism. Dempster (1968) showed that application of DDT increased the *P. rapae* population by reducing the impact of ground-dwelling predators and eliminating *C. rubecula*. In a small study, Kristensen (1994) found a high rate of larval predation on *P. brassicae*. Only 30 of 960 larvae escaped arthropod and avian predation, suggesting that at least under some conditions (see also Dempster, 1967, 1968; Baker, 1970) predation outweighs parasitism.

Differences in the learning and memory characteristics of the two *Cotesia* species have been elucidated by Smid *et al.* (2007), and other work on their behavioural ecology can be traced through this reference.

Lycaenidae: *Maculinea rebeli*

Although only the *Maculinea rebeli* parasitoid associations have been studied in detail, egg, larval and pupal parasitoids are known from several other European Lycaenidae (e.g. Bink, 1970; Fiedler *et al.*, 1995; Shaw, 1996; Horstmann *et al.*, 1997; Gil-T, 2001, 2004) and the few available data suggest that parasitism can be heavy. Bink (1970) gives quantitative data showing high parasitism in several populations of *Lycaena* species. Shaw (1996) found that 67% of 214 larvae of *Aricia artexerxes* from 13 sites in south Cumbria and southeastern Scotland were parasitised, mostly by *Hyposoter notatus* (Ichneumonidae: Campopleginae), and Gil-T (2001) recorded 55% parasitism in 58 larvae of *Iolana iolas* collected at a locality in southern Spain, mostly due to *Anisobas cephalotes* (Ichneumonidae: Ichneumoninae). In an unquantified report Martín Cano (1981) stated that between 70% and 100% of an unspecified number of larvae of *Glaucopsyche melanops* and more than 50% of those of *G. alexis* collected in several Spanish sites were parasitised by Ichneumonidae, Braconidae and Tachinidae. Such figures might seem surprising, as the larvae of these butterflies establish associations with ants (Fiedler, 1991; see also Gil-T, 2004), which have been presumed to provide protection against parasitoids (see Pierce & Easteal, 1986; Pierce *et al.*, 1987). These casual findings, along with those of Seufert & Fiedler (1999), call into question the generality of such conclusions, as specialised parasitoids can clearly flourish. Fiedler and collaborators (Fiedler *et al.*, 1995; Baumgarten & Fiedler, 1998)

have explored multi-species interactions between myrmecophilous lycaenid caterpillars, their tending ants and specialised parasitoids.

Even more surprisingly, carnivorous *Maculinea* butterflies, which spend most of their larval stage and then pupate inside ant nests, are regularly attacked by host-specific ichneumonid parasitoids of the subfamily Ichneumoninae (Thomas & Elmes, 1993; Munguira & Martín, 1999; Tartally, 2005). A compilation recording in detail recent findings on parasitism of *Maculinea* species (Anton *et al.*, in prep) underlies some of the information given below (and also in the Ichneumoninae rearing table). Unfortunately the taxonomy of some of the parasitoids concerned has been confused, and in one genus (*Ichneumon*) some uncertainty remains. Thus apparently three *Neotypus* species have been reported from the three European species of the predatory clade, *Maculinea arion*, *M. nausithous* and *M. teleius*, though partly as a result of confusion over the validity of the name *N. melanocephalus* and the occasional use of its junior synonym *N. pusillus* (see Horstmann, 1999). There is no doubt that *Neotypus coreensis*, parasitising *M. arion*, is distinct (though it is less certain that its name is correct), but the perception that there are two further species, differing in leg colour, has not been upheld following a recent review of all available material from a range of sources (K. Horstmann, pers. comm.). Specimens associated with *M. nausithous* could not be separated from those much less often reared from *M. teleius*, with colour differences in the plentiful *M. nausithous*-associated material not even proving to be consistent geographically (K. Horstmann, pers. comm.), and we here regard them as belonging to the same species, *N. melanocephalus* (= *pusillus*). In the genus *Ichneumon* uncertainty remains unresolved. One well-defined species, *I. fulvicornis*, parasitises certainly *M. teleius* and possibly *M. nausithous* (usually the host pupae from which it has been reared could not be separated, and the two butterflies very often co-occur). However, another, *I. eumerus* (Plate 9b), is reported to have populations parasitising *M. rebeli* in southwest Europe that overwinter in the host (Thomas & Elmes, 1993), unlike the central European populations (reared at several sites, from *M.alcon*, *M. teleius* and probably also *M. rebeli*) which overwinter as adults and thus conform to the general biology of the genus *Ichneumon*. The two supposed races are indistinguishable morphologically (Hinz & Horstmann, 2007; K. Horstmann, pers. comm.), but if the biological differences are consistent then they should be regarded as distinct species. If so, it is not clear which would take the name *I. eumerus*, but it is used in the sense of Thomas & Elmes (1993) in the following summary.

The complex relationships among the parasitoid, the host and the ants were studied in detail by Thomas & Elmes (1993) for the 'cuckoo' species *M. rebeli*, which is regularly parasitised by *Ichneumon eumerus* in France and Spain. Failure to detect parasitism of *M. rebeli* caterpillars during their free-living phase and when being adopted by *Myrmica schencki* or *M. sabuleti* workers, and the observation of several females of *I. eumerus* trying (unsuccessfully) to enter *M. sabuleti* nests known to contain *Maculinea* caterpillars, suggested that parasitism takes place inside the ant nests. This was confirmed in the laboratory. In contrast, the *Neotypus* species parasitising predatory *Maculinea* species attack the young caterpillars while they are still feeding on flower heads. Thomas & Elmes (1993) suggest that the specialised behaviour of *I. eumerus* precludes the use of other hosts. Females identify nests of the right ant species by odour, and can ascertain at the nest entrance whether a *Maculinea* caterpillar is inside. On entering the selected host-supporting nest (in which hosts tend to be clumped), the female is fiercely attacked, but is well armoured and soon spreads an allomone which induces the worker ants to fight each other (Thomas *et al.*, 2002). This sophisticated behaviour goes with an exceptionally low fecundity, most females entering just one or two suitable ant nests, and laying only five to ten eggs. The impact of the parasitoid on host populations seems to be slight (Hochberg *et al.*, 1998), with parasitism rates ranging from 6% to 23%. Considerable theoretical work on this extraordinary system (Hochberg *et al.*, 1992, 1994), aimed at the conservation of both *I. eumerus* and *M. rebeli* (Hochberg *et al.*, 1996, 1998), suggests that *I. eumerus* is slightly more vulnerable to extinction than *M. rebeli*, which is a species considered globally endangered (Munguira & Martín, 1999). Therefore, providing it is distinct from the race that has a broader host range, *I. eumerus* provides an excellent example of the need to consider parasitoid conservation specifically when dealing with biodiversity conservation (Shaw & Hochberg, 2001; Thomas *et al.*, 2002). This discussion of *Maculinea* parasitoids also shows the need to gain a clear understanding of the taxonomy of parasitoids in relation to their ecology, and the difficulty in doing so.³

Nymphalidae: *Aglais urticae*

Because caterpillars in the attractive tribe Nymphalini are conspicuous and easily reared, frequent small-scale rearings of parasitoids have led to many literature records. However,

³ Continuing research on this system can be traced via www.macman-project.de.

although most of the Nymphalini are very common throughout Europe, only one detailed study of a parasitoid complex has been made.

Between 1971 and 1973, Pyörnilä (1976a, b, 1977) collected 387 egg clusters, 3908 larvae and 132 pupae from an *A. urticae* population in eastern Finland. Eight parasitoid species were reared. The most numerous larval parasitoids were *Pelatachina tibialis* and *Phryxe vulgaris* (both Tachinidae) and *Phobocampe confusa* (misidentified as *Hyposoter horticola*) (Ichneumonidae: Campopleginae). *Pteromalus puparum* (Pteromalidae) (Plates 12a and 12b) was a very important pupal parasitoid in the area, unlike single specimens of *Pteromalus apum* and three species of Ichneumonidae (*Ichneumon gracilicornis*, *Pimpla flavicoxis* Thomson (misidentified as *aquilonia*) and *Apechthis rufata* (Gmelin)). No egg parasitoids were detected.

The commonest larval parasitoid in three consecutive summers was *P. tibialis*, a near specialist of Nymphalini butterflies (sometimes also recorded from Noctuidae). It attacks larvae throughout their development, parasitisation rates increasing steadily until the last larval instar. *Phryxe vulgaris*, an extremely polyphagous species, also attacks larvae throughout their development, especially those occurring in late summer. Both kill the host in its last larval instar or, occasionally, soon after pupation. From 23.5% to 65.0% of larvae collected in their fourth instar were parasitised by these tachinids.

The ichneumonid *P. confusa* was reared each year from about 10% of the collected larvae. Its cocoons were subject to unquantified pseudohyperparasitism by *Gelis agilis* (Fabricius) (= *instabilis*) (Ichneumonidae: Cryptinae), which is highly polyphagous (Schwarz & Shaw, 1999). Finally, 35–58% of the collected pupae were killed by *P. puparum*, comparable to Julliard's (1948) findings in Switzerland.

Although there are many reports of the same and other species parasitising *A. urticae*, Pyörnilä's study is the only one that provides a fairly comprehensive picture of the parasitoid complex at a given locality. Interestingly, this common butterfly is believed to be decreasing in some parts of its range (e.g. Kulfan *et al.*, 1997), and it has been suggested that parasitoids such as *Sturmia bella* (Plate 15) increasing their geographical range could be partly responsible (Greatorex-Davies & Roy, 2005).

Nymphalidae: Genera *Melitaea* and *Euphydryas*

Melitaeini butterflies share many life-history characteristics that are relevant to their parasitoids: eggs are laid in clusters,

larvae live gregariously under a web for at least the first couple of instars, and there is larval diapause in the summer (where it is dry) or winter (where it is cold) (Kuussaari *et al.*, 2004). Most Melitaeini feed on herbaceous plants chemically defended by iridoid glycosides or secoiridoids (Wahlberg, 2001), and several species commonly co-occur in meadows or forest clearings, sometimes even sharing foodplants (Kankare *et al.*, 2005a). Thus we might expect the butterflies to have the same or closely related parasitoids, or ones with life-history characteristics in common.

Parasitoids of the European Melitaeini are among the best known of any butterflies (Porter, 1981; Komonen, 1997, 1998; Wahlberg *et al.*, 2001; Eliasson & Shaw, 2003; Kankare & Shaw, 2004; van Nouhuys & Hanski, 2004; Kankare *et al.*, 2005a; Stefanescu *et al.*, 2009). These parasitoid complexes are rather atypical in that they are so strongly dominated by specialists, notably gregarious *Cotesia* species (Plate 10b). In the Åland Islands in southwest Finland the parasitoid complex of *Melitaea cinxia* has been studied for more than a decade. There are two specialist primary larval endoparasitoids, each with their own secondary parasitoids, and several generalist pupal parasitoids (Lei *et al.*, 1997; van Nouhuys & Hanski, 2004).

The gregarious primary parasitoid *Cotesia melitaeorum* (agg.; see table of Braconidae: Microgastrinae) has two or three generations per host generation and is locally monophagous. Despite its high reproductive potential and close relationship with *M. cinxia*, *C. melitaeorum* (agg.) generally forms small populations in Åland, for three reasons. Firstly, the wasp has weak dispersal ability relative to the scale of the fragmented landscape. Secondly, the host has relatively fast dynamics for unrelated reasons (Lei & Hanski, 1997; van Nouhuys & Hanski, 2002). Finally, the parasitoid is constrained on a local scale by density-dependent secondary parasitism (van Nouhuys & Hanski, 2000; van Nouhuys & Tay, 2001). Nevertheless, where host density is high, *C. melitaeorum* (agg.) can impact host population size, perhaps causing local host extinctions (Lei & Hanski, 1997). Similarly strong influence in *Euphydryas aurinia* population dynamics by *Cotesia bignellii* was observed by Porter (1981) in England. Though studied in less detail, in eastern North America the related *Euphydryas phaeton* (Drury) also sustains variable, sometimes high rates of parasitism by *Cotesia euphyridis* (Muesebeck) (Stamp, 1981a), as does western North American *Euphydryas editha* (Boisduval) by *Cotesia koebelei* (Riley) (Moore, 1987).

The second parasitoid of *M. cinxia* in Finland, *Hyposoter horticola* (Ichneumonidae: Campopleginae) (Plate 8a), is also

restricted to Melitaeini hosts and uses only *M. cinxia* locally. It consistently parasitises about a third of host larvae at all spatial scales and natural densities. As a consequence, its impact is simply to reduce overall population size, leaving local populations prone to extinction by other means. This unexpected relationship results from the behaviour of the adult parasitoid (van Nouhuys & Ehrnsten, 2004; see caption to Plate 8a).

Each of the two primary parasitoids has abundant secondary parasitoids. The wingless and thelytokous *Gelis agilis* (Ichneumonidae: Cryptinae) is a generalist pseudohyperparasitoid of *C. melitaeorum* (agg.). It aggregates in response to high *Cotesia* density, and apparently can drive local populations of *C. melitaeorum* (agg.) to extinction (Lei & Hanski, 1998; van Nouhuys & Hanski, 2000). Two other species, *G. acarorum* (Linnaeus) and *G. spurius* (Foerster) (misidentified as *ruficornis*), have occasionally been reared from *C. melitaeorum* (agg.) in this system, and *G. agilis* has been reared from *H. horticola*, but their importance is unknown. The true hyperparasitoid *Mesochorus* sp. (Ichneumonidae: Mesochorinae) predominantly uses *H. horticola* as a host, with only infrequent development through *Cotesia*. It parasitises about a quarter of the *H. horticola* in all but the most isolated local populations in the Åland Islands (van Nouhuys & Hanski, 2005). Because, like its host, it has a relatively uniform rate of parasitism at most spatial scales, it does not directly affect the dynamics of the primary parasitoid or the butterfly.

Melitaea cinxia in Finland also hosts pupal parasitoids. Lei *et al.* (1997) reared the solitary *Ichneumon gracilicornis* (Ichneumonidae: Ichneumoninae), and the gregarious pteromalids *Coelopisthia caledonica*, *Pteromalus apum* and *P. puparum* (Plates 12a and 12b). Experimental field exposure of fresh pupae has also revealed *Ichneumon cinxiae*. While the *Ichneumon* species are probably uncommon as well as being rather specialised, the pteromalids have broader host ranges and can be abundant, but the impact of pupal parasitoids on host dynamics is unknown. No egg parasitoids have yet been associated with *M. cinxia* in Finland, nor are there tachinid flies.

Other Melitaeini host some of the same or closely related parasitoids, especially gregarious species of *Cotesia* (Eliasson & Shaw, 2003; Kankare & Shaw, 2004) (Plate 10b). Recent studies using molecular, morphological and behavioural data have found surprising host specificity among these parasitoids, with several supposed *Cotesia* 'species' actually being groups of cryptic species (see table of Braconidae: Microgastrinae). However, a variety of patterns of host specificity are seen, suggesting ecologically and phylogenetically dynamic host-parasitoid relationships (Kankare & Shaw, 2004; Kankare *et al.*, 2005a, b).

In addition to *Hyposoter horticola* and *Cotesia* species, specialist parasitoids of European Melitaeini include large solitary ichneumonids in the genera *Benjamini* and *Ichneumon*, and tachinid flies in the genus *Erycia* (for example studies see Wahlberg *et al.*, 2001; Eliasson & Shaw, 2003; Kankare *et al.*, 2005a; Stefanescu *et al.*, 2009). Being generally much less abundant than the *Cotesia* species, however, their host ranges remain poorly understood. Generalist parasitoids attacking pupae are sometimes quite abundant, and one, *Pteromalus apum*, has a strong (though not exclusive) relationship with the group. Because they typically rely on other hosts as well, generalists may strongly affect local population sizes, but are not themselves greatly affected by the densities of specific hosts.

Hesperiidae: *Thymelicus lineola*

Although a few firm parasitoid–host associations are known for butterflies belonging to the Hesperiidae (e.g. *Cotesia glabrata* attacking *Carcharodus alceae*), a moderately good knowledge of a whole parasitoid complex has been gathered only for *Thymelicus lineola*. This butterfly was accidentally introduced to Canada in the early twentieth century, and has since spread to the USA. In contrast to European populations, in North America *T. lineola* is a pest, causing extensive damage to hay-fields and pastures (Pengelly, 1961). This prompted a comparative study of its parasitoid complexes in both regions, in search of possible biological control of American populations (Arthur, 1962, 1966; Carl, 1968).

The parasitoid complex at sites in Switzerland, France and Austria was assessed by Carl (1968), in a 4-year study based on a sample of over 3400 larvae and an unspecified (but much lower) number of pupae. Egg parasitism was not included in the study.

Six primary and two secondary parasitoids were found. The most important were two larval parasitoids, the generalist *Phryxe vulgaris* (Tachinidae) and *Aleiodes coxalis* (= *tristis*) (Braconidae: Rogadinae), which is an oligophagous species attacking also Satyrinae (M. R. Shaw, unpublished data) but not the wider hosts ascribed to it by Carl (1968), and the specialised pupal parasitoid *Syspasis scutellator* (Ichneumonidae: Ichneumoninae), all of which had a high incidence in all sampled populations. More rarely, the larval parasitoid *Thecocarcelia acutangulata* (= *incidens*) (Tachinidae), the larval–pupal parasitoid *Agrypon delarvatum* (Ichneumonidae: Anomaloninae) and the pupal parasitoid *Brachymeria tibialis* (= *intermedia*) (Chalcididae) were

reared. In a few samples, an unidentified Mermithidae (Phylum Nematoda) was also detected.

Phryxe vulgaris was present in 3–44% of larvae collected, and was especially prevalent at high host densities. Being plurivoltine as well as polyphagous, *P. vulgaris* was inevitably also depending on other hosts. *Aleiodes coxalis* is also a plurivoltine koinobiont species, and parasitised 3–57% of the collected larvae. In 1–10% of cases it was hyperparasitised by *Mesochorus tetricus* Holmgren (= *macrurus*) (Ichneumonidae: Mesochorinae). *Syspasis scutellator* is univoltine and probably has a very narrow host range. It caused apparently high pupal mortality ranging from 30% to 50% (but sample sizes were low). The generalist pseudohyperparasitoid *Gelis cursitans* (Fabricius) (Ichneumonidae: Cryptinae) developed from 9% to 17% of host pupae harbouring *S. scutellator*.

In Canada up to 22 generalist species were recorded (Pengelly, 1961; Arthur, 1962), but parasitism was light and appeared to be largely incidental, with many sparse records despite heavy sampling. Carl (1968) suggested that the ineffective parasitoid complex in Canada might progress to become less species-rich but more specialised, and it would be interesting to resurvey Canadian *T. lineola* populations to see if there are signs of this 40 years on.

Overview of case studies

In spite of the work that has gone into each case study, our knowledge of these parasitoid assemblages is incomplete for several reasons. As well as low sampling of the pupal or egg stages and inadequate taxonomic and autecological knowledge of the parasitoids, the sampling has generally been conducted in only one or a few areas, where not all of the parasitoids that will regularly attack that host necessarily occurred. For example, although both *Cotesia vestalis* and *C. vanessae* are frequently abundant as parasitoids of *Aglais urticae* over most of Europe, they were not found in Finland by Pyörnilä (1976a, b, 1977), and the regular parasitoid of *Pieris* species, *Hyposoter ebeninus*, is absent from all British populations.

Finally, while it is relatively straightforward to tabulate the mortality factors for a host, it is more difficult to assess the effects of a parasitoid on the dynamics of host populations; that is, the extent to which the abundance of a butterfly over time is influenced by its parasitoids. It is important to appreciate that, however severe parasitoid-induced mortality may become, local host population dynamics will only be directly regulated by parasitoids if

the mortality they cause depends, at some spatial scale, on the density of the host (see Hassell, 2000). Few studies have run for long enough to examine this, though it was attempted on a small scale by measuring the density dependence of parasitism of *Pieris* (Richards, 1940). At a regional (or landscape) scale the role of parasitoids in determining host population dynamics will depend to a large extent on the relative rates of movement of the host and the parasitoids in the landscape, and local density dependence may not necessarily be pivotal for explaining population dynamics at larger spatial scales (Holt, 1997). The interaction of butterflies and parasitoids at both local and landscape scales has only been addressed for *Melitaea cinxia* and its parasitoids (see above, but see also Menéndez *et al.*, 2008).

Nevertheless, the case studies illustrate that parasitoid assemblage sizes differ, and contain species using different host stages and exhibiting differing degrees of host specificity. Clearly, some patterns of parasitoid assemblages result from the biology of the butterfly. For example the lycaenids *Maculinea* spp. host few parasitoid species, each with narrow host ranges, undoubtedly connected with the specialised life history of the hosts. In contrast *Iphiclides podalirius* (Papilionidae) has a generalised life history and is attacked by a set of parasitoids with wide host ranges. In each case study a few key parasitoids explain an important fraction of host mortality. However, their prominence can vary seasonally, as illustrated by plurivoltine *Pieris* species and *Iphiclides podalirius*; among years, for instance *Cotesia* parasitoids of *Melitaea cinxia* and *Pieris*; and among locations, as for *Thymelicus lineola*.

CONCLUDING REMARKS

In this chapter we have tried to do two things. The first is simply to open the way for a more informed interest to be taken by butterfly ecologists and enthusiasts in the parasitoids they encounter. We have exposed the paucity of reliable information partly in the hope that this will engage others to help build better knowledge about parasitoids. We encourage researchers and collectors to seek and preserve parasitoids reared from butterflies, and to pass them on to taxonomists and/or to deposit them in active research collections.

The second aim of this chapter is to assert that parasitoids can be expected to have many important effects in the ecology of butterfly species. In ways that differ substantially between host species, they can influence population size and can be a cause of strong fluctuations at different spatial

scales. But the effects of parasitoids can be subtler. Host sex ratios can sometimes be distorted through disproportionate parasitism of one sex for a variety of reasons (see Shaw, 1975; Porter, 1984). Apparent competition (see Holt & Lawton, 1993) mediated by shared parasitoids might altogether exclude a butterfly from a particular region, and secondary parasitoids can have profound effects on primary parasitoid population sizes (e.g. van Nouhuys & Hanski, 2000; Stefanescu *et al.*, 2009) and thus on butterfly population dynamics. On an evolutionary timescale, defence against parasitoids has shaped aspects of the physiology of immature stages, and the behaviour of both larvae and adult butterflies. For example, Ohsaki & Sato (1999) suggest that *Pieris napi*, *P. rapae* and *P. melete* in Japan have each evolved to use habitats and host plant species that minimise parasitism by the braconid wasp *Cotesia glomerata* and the tachinid fly *Epicampocera succincta*.

For us to understand the place of parasitoids in the lives of butterflies there is still much to be gained from close attention to natural history, careful experimentation and thorough taxonomic investigation. The importance of parasitoids can also be dramatically revealed by changes caused by humans; for instance, the introduction of *Cotesia rubecula* to North America from Europe that was followed by the precipitate decline of native *Pieris virginiensis* Edwards (Benson *et al.*, 2003), and the increase in crop damage after the application of insecticide as shown experimentally with DDT in the *Pieris* and *Cotesia* system by Dempster (1967).

The decline of many butterflies and their shifting distributions with changing land-use practices and climate has surely led to corresponding changes among their parasitoids. It seems safe to say that parasitoids are likely to be more vulnerable to habitat degradation than their hosts (Komonen *et al.*, 2000; Shaw & Hochberg, 2001; van Nouhuys & Hanski, 2005). However, although there are indications of serious declines (Thirion, 1976, 1981), for the most part too little is known about parasitoids for us to see this clearly enough to address it.

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