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Vol. 7, Part 11

CLASSIFICATION AND BIOLOGY OF BRACONID WASPS

(HYMENOPTERA: BRACONIDAE)

M. R. Shaw and T. Huddleston

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CLASSIFICATION AND BIOLOGY OF BRACONID WASPS

(HYMENOPTERA: BRACONIDAE)

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Introduction

Hymenoptera constitute one of the largest and most successful orders of insects. The order is divided into two sub-orders, Symphyta (sawflies) and Apocrita. The larger of these is Apocrita, which is best known to the layman for the remarkable levels of social organisation attained by some species of bees, wasps and ants, the so-called aculeate Hymenoptera. However, apocritans are of at least equally great significance and interest on account of the parasitoid lineages that have evolved as the so-called parasitic Hymenoptera. In fact, these two groups are rather arbitrary divisions of the sub-order Apocrita, and have much in common with one another biologically, as is stressed by Gauld & Bolton (1988) in their comprehensive introductory account of the biology and systematics of the order Hymenoptera.

Typically the parasitoids, the 'parasitic Hymenoptera', develop as larvae by feeding on the immature stages of other insects: the fact that the latter are killed in the process is one of several features that set parasitoids (known also as protelean parasites) apart from conventional parasites (Askew, 1971). In parasitoids the adult stage is free-living, though it has the job of locating the 'host' for the next generation. The larvae of parasitoids differ from typical predators in that they do not pursue successive prey items, but are generally rather helpless creatures dependent on their mother to place them, as eggs, on or in the body of a single 'host', which must then provide sufficient food for all their growth to take place. There are several rather minor variations on this life-style (e.g. attacking adult instead of immature insects; consuming spiders instead of insects; feeding on successive host eggs in a concealed batch, thereby inflicting more than the usual single host mortality; or having first-instar larvae or even eggs that make first contact with the host), and the biological distinction between the 'parasitic' and the 'aculeate' Hymenoptera can run very thin. This is chiefly because all apocritans share and still exhibit the ancestry of a free-living adult form that provides for a larva feeding on a high-protein diet that it cannot locate for itself (Gauld & Bolton, 1988). Indeed, some species in 'aculeate' groups behave as typical parasitoids in developing on a single 'prey' item which, in extreme cases, may have been scarcely or not at all moved by the female parent and might even recover its activity for a while.

In Britain there are about 6500 species of Hymenoptera – more than in any other insect order – and just one of the parasitoid superfamilies, Ichneumonoidea, contains nearly half of them. Most workers now recognise only two families in Ichneumonoidea. These are Ichneumonidae, with over two thousand British species, and Braconidae, with nearly 1200 representatives in Britain. They are, respectively, the largest and the second largest families of British insects, with only Staphylinidae (Coleoptera) otherwise near the thousand mark. Ichneumonoids also include the biggest parasitoids.

Although in size British Ichneumonidae (mostly 6–17 mm long) tend to overshadow Braconidae (mostly 2–6 mm in Britain), both groups contain some large and attractive species and Braconidae exhibit the greater range of morphological diversity. All braconids are parasitoids of other insects, developing as larvae on the tissues of the host, which is killed as a result of the association. They are mostly very host-specialised, being adapted to attack and feed as larvae on a narrow range of hosts that is delimited according to a complex and fascinating mix of extrinsic and intrinsic factors. In attaining this intimate association with their hosts, they have evolved specialised and often remarkable behavioural and other biological adaptations, manifest to a greater or lesser extent in the adult's morphology. They are important in the population dynamics of their hosts, many of which are plant-feeding insects, and braconids have been particularly heavily involved in the so-called classical biological control of insect pests (and more recently in integrated pest management programmes), often with considerable success (Clausen, 1978). Being so specialised also gives braconids, along with all parasitoids, a high potential as indicators of environmental richness and stability.

In view of their numbers, interesting biology and economic significance it is surprising that Braconidae (and indeed Ichneumonidae) are studied by so few entomologists. Even in Britain, where knowledge of our insect fauna in general is unrivalled, very little is known about the biology or distribution of the great majority of the species belonging to the two largest families. Why has the enthusiasm of amateur entomologists, on whose painstaking fieldwork so much of our knowledge of British insects has depended, so rarely been channelled into studying the larger parasitic Hymenoptera? It is certainly not because they are uncommon or unimportant; but it may be because of a lack of introductory texts. Without an introduction, they have perhaps seemed hopelessly difficult and obscure even to the point of dullness.

Several recent publications, particularly Gauld & Bolton (1988), have made Hymenoptera more accessible to non-specialists. From that base, the purpose of this Handbook is to bring Braconidae into focus: to provide access to the information needed to study them in Britain confidently and to best effect. Rather than take up space on topics that have been fully discussed elsewhere, such as ways of collecting, rearing, mounting and storing specimens (e.g. Gauld & Bolton, 1988; Fitton *et al.*, 1988; Shaw, 1990) and the general biology of parasitoids (Askew, 1971) or Hymenoptera (Gauld & Bolton, 1988), we have concentrated on two main aims. First, we have tried to provide a simple and workable illustrated key to the 24 subfamilies of Braconidae known to occur in Britain, and a guide to the literature that is available for species-level identification for each of these. We hope that this will make trying to identify braconids much easier. Second, we have attempted to summarise the host-associations and biology of each subfamily at the level of current knowledge, as far as possible pointing out what important aspects are not known as well as summarising those that are. We hope that this account, which occupies the greater part of this work, will encourage interest in the biology of Braconidae. In drawing together a lot of otherwise scattered literature we also hope to provide an easy means for the user to relate new information, when it arises, to existing knowledge. We have attempted to consider all relevant literature to the end of 1989, but include only a few titles thereafter.

In Britain relatively little has been published on the developmental biology of parasitoids, partly because the conditions in which biological pest control becomes attractive are not strongly promoted by our Atlantic climate and relatively varied agriculture. In parts of continental Europe, on the other hand, and especially in North America, many more studies on the ecology of pest species and their actual or potential parasitoids have been undertaken, and some of the statements made here are necessarily derived from these non-British studies. However, many such studies have involved parasitoid species that do also occur in Britain, and others have concerned species that would not be expected to differ materially from their British congeners in the characteristics mentioned: any exceptions have been clearly indicated.

Although this Handbook is orientated towards the British fauna it also serves as a practically complete summary of the known general biology of Braconidae, as the subfamilies that are excluded are mostly very small and poorly known biologically. Van Achterberg (1984b) recognised 35 subfamilies, to which should be added Apozyginae as it is no longer generally regarded as a separate family (e.g. Rasnitsyn, 1988). Two further subfamilies have been described since van Achterberg's (1984b) classification (van Achterberg, 1985b; Quicke, 1987c) and with our recognition of Meteorinae, following S. R. Shaw (1985, 1988), the number rises to 39. (We discount Sharma's (1984) subfamily Excultinae as the species on which this was based, though described as a braconid, appears to be a chrysidid.) Twenty four of these subfamilies occur in the British Isles and are treated in detail here. Cardiochilinae and Meteorideinae are the best known biologically of the non-British subfamilies, and some reference to both is included: Cardiochilinae is accorded a brief entry in the account of subfamilies in the context of deleting it from the British list, and the aberrant biology of *Meteoridea* is discussed and referenced in the section on general biology. This leaves thirteen very small subfamilies, all of restricted distribution. Nothing is known of the biology of eight of them (Apozyginae, Telengaiinae, Cercobarconinae, Trachypetinae, Betylobraconinae, Khoikhoiinae, Ecnomiinae and Vaepellinae) and for the remaining five the biology is known only in faint outline: Ypsistocerinae live in termite nests, but it is not clear what they are parasitising (Cushman, 1923; Brues, 1923); Mesostoinae have been reared from unidentified galls (Quicke & Huddleston, 1989); Dirrhopinae have been reared from nepticulid Lepidoptera (Muesebeck, 1936b), pupating in the host cocoon (Čapek, 1970); Xiphozelinae are recorded as larval endoparasitoids of noctuid Lepidoptera (van Achterberg, 1979b); and Amicrocentrinae are known as solitary parasitoids of large stem-boring lepidopteran larvae such as Cossidae and Noctuidae (van Achterberg, 1979a).

Additional literature

In addition to the literature cited in the text, there are some more general literature sources that are important for the study of Braconidae. These can be split into three categories:

(1) **Catalogues**. Because they are arranged systematically these provide an especially valuable route to the biological and taxonomic literature concerning particular taxa. Workers on Braconidae have been magnificently served in comparison with students of most other groups of hymenopteran parasitoids. Thanks largely to R. D. Shenefelt, all the subfamilies of Braconidae except Opiinae (in prep.) have been catalogued on a world basis in the new series of Hymenopterorum Catalogus (Mackauer, 1968; Shenefelt, 1969–1980; Shenefelt & Marsh, 1976), though sometimes under different subfamily groupings from those now recognised. In a different series, Opiinae have been catalogued by Fischer (1971b). In addition, Aphidiinae have been treated in alternative ways by Mackauer & Starý (1967) and Starý (1987). The North American braconid fauna has been catalogued (though with poor inclusion of biological literature) by Marsh (1979). There is no catalogue exclusively of the British fauna but checklists, which are more limited in scope, have been produced from time to time. The most recent British checklist (Huddleston, 1978) was compiled by abstraction from the existing world catalogues mentioned above and, unfortunately, includes errors from these sources. Both checklists and catalogues are vitally important for evaluating and reconciling the nomenclature used in other publications.

(2) **Identification literature**. Unfortunately much work needs to be done even on the relatively well-known western European braconid fauna, and there are no modern revisions available for many of the groups of Braconidae that occur in Britain. If no key is cited under the 'identification' heading at the end of a given subfamily section in the present account, the best general works for the species-level identification of British Braconidae remain those of Marshall (1885–1899) and Marshall (in André, 1888–1900). Although now badly out of date, in terms of both nomenclature and faunistics, Marshall's keys were compiled by a gifted taxonomist working from first-hand experience, making them very much more reliable than the more skimpy and derived accounts that were produced by various authors seeking greater completeness in the middle part of the present century. While Marshall's work may not enable a species to be determined with complete confidence, it is unlikely to give results that are wholly misleading and, with subsequent checking in catalogues to trace the fate of names and to assess what species unknown to Marshall may be present, it is surprising how useful his considerable contribution remains. A recent key direct to the genera of Braconidae occurring in North America (Marsh *et al.*, 1987) works quite well for the British fauna owing to the very high overlap at the generic level. Tobias's (1971; English translation 1975) a generic-level treatment of the braconid fauna of the USSR is also useful for the British members of some groups. Van Achterberg (1990b) provided a key to subfamilies for the Holarctic fauna, including a number of non-British genera that would not run correctly in the key we give here.

(3) **Reviews and other compilations**. Shenefelt (1965) gave a fairly comprehensive listing of the literature concerning Braconidae to that date, arranged alphabetically by author; Matthews (1974) reviewed some aspects of the biology of Braconidae; and Gauld & Bolton (1988) set Braconidae in the context of other Hymenoptera. Most of the reviews that include information on Braconidae in the context of particular aspects of parasitoid biology are cited in the present section on general biology, but some additional topics are covered in Waage & Greathead (1986).

General biology

This section explains the biological terminology used in the sections on subfamilies. In addition, some general trends in the biology of Braconidae are outlined: further detail can be found in the sections devoted to the subfamilies indicated.

Braconidae share with other groups of parasitoids many biological features that can be described using standard terminology. Thus the parasitoid larva can feed from a position external to the host, in which case it is termed ectoparasitic, or from inside the host's body endoparasitically. The majority of Braconidae are endoparasitoids, though in a substantial number of subfamilies the final-instar larva erupts from the host to complete its feeding externally. Ectoparasitism throughout larval life occurs in just one group of closely related subfamilies, the so-called cyclostome group, represented in Britain by Doryctinae, Braconinae, Histeromerinae and Rogadinae.

The relationship a parasitoid has to its host can be described in another way, reflecting the extent to which the host's active life continues after being parasitised (Haeselbarth, 1979; Askew & Shaw, 1986). Parasitoids that do not permit the host significant activity or development after attack are termed idiobionts, while those whose host continues to feed, develop, move around or otherwise look after itself for a time following oviposition are called koinobionts. These terms reflect a difference in physiological adaptation by parasitoids: idiobionts feed on corpses or paralysed hosts that have been rendered physiologically and behaviourally helpless, while koinobionts have to be able to fit in with the continuing life of their hosts and, in particular, evade their physiological defences. These biological differences have some bearing on host-specialisation: idiobionts have at least the potential for relatively broader host ranges than koinobionts, and the difference between them has been useful in analysing the structure of parasitoid communities of various kinds (Askew & Shaw, 1986; Hawkins *et al.*, 1990). Evolutionary pathways are also fruitfully examined and expressed in these terms (Gauld & Bolton, 1988; Gauld, 1988). There is in general a high degree of overlap between idiobiosis and ectoparasitism on the one hand, and between koinobiosis and endoparasitism on the other, and in Braconidae these correlations are probably more nearly complete than in any other family of Hymenoptera in which the whole span is found. That is to say, there are remarkably few ectoparasitic koinobionts or endoparasitic idiobionts in the Braconidae, these habits being known (or suspected) only in the subfamilies Rogadinae, Doryctinae and Braconinae. In fact an estimated 92 per cent of British braconids but only 50 per cent of ichneumonids are endoparasitic koinobionts (Gauld, 1988).

A parasitoid can be primary – that is, developing at the expense of a non-parasitoid host – or it can be a secondary parasitoid (also called a hyperparasitoid) with respect to such a host if it is parasitising a parasitoid of that host. Primary and secondary parasitoids have opposite effects in the population dynamics of the host. Secondary parasitoids can be further divided (Shaw & Askew, 1976b) according to whether the primary parasitoid is attacked while it is still feeding on the original host (true hyperparasitism), or only after its direct association with the host is over (pseudohyperparasitism). Some groups of Hymenoptera behave as obligatory true hyperparasitoids, sometimes exhibiting extremely specialised and unusual life-histories. In others, niche-dependent secondary parasitism has arisen in a more or less facultative way, a common example being the pseudohyperparasitism resulting when parasitoids that attack small cocoons discover those made by the larvae of ichneumonid or braconid parasitoids.

Hyperparasitism of any kind is extremely rarely practised by Braconidae, perhaps for two main reasons, which may be interconnected. First, braconids on the whole eschew the pupal or cocoon stages of endopterygote hosts: not only are these structures not attacked (except facultatively, and probably also by Aspidobraconina, a small exotic group of braconine endoparasitoids of Lepidoptera), but also the pupal stage is extremely rarely the stage killed by koinobionts (except for Opiinae and Alysiinae, all of which pupate within dipteran puparia, and the non-British subfamily Meteorideinae). Second, very little use of Hymenoptera as a host group is found among Braconidae (only the small subfamily Ichneutinae and a few ectoparasitoids in the subfamilies Doryctinae, Rogadinae and Braconinae attack Symphyta, and only single species of Doryctinae (Marsh, 1982) and Meteorideinae (see below) have been recorded attacking immature Apocrita, though adult apocritans are attacked by a few Euphorinae and by Neoneurinae). In both of these respects Braconidae differ markedly from their nearest relatives, Ichneumonidae, in which oviposition through silk occurs very widely and using Hymenoptera as hosts has been central to the evolution of various lineages (Gauld, 1988). Not surprisingly, various forms of hyperparasitism are commonly found in Ichneumonidae. There are no known instances of Braconidae attacking Hymenoptera as true hyperparasitoids, but there are at least two groups which can behave as pseudohyperparasitoids. First, some species of *Syntretus* (Euphorinae) parasitise adult Ichneumonidae and, as all ichneumonids are parasitoids, these braconids always fall into the definition of pseudohyperparasitoids, though clearly only as a peripheral consequence of the subfamily's association with a range of adult insects. Second, the genus *Meteoridea* (Meteorideinae) has been found to be capable of facultative pseudohyperparasitism, ovipositing into larvae of endoparasitic microgastrine braconids that have left their hosts but have not yet had time to spin their cocoons: the *Meteoridea* larva is said then to develop as an endoparasitoid of the microgastrine pupa in its cocoon (Ghosh & Abdurahiman, 1986). Meteorideinae is a small subfamily, remarkable even in its more usual development as a primary parasitoid: biologically known species are solitary or gregarious parasitoids of pyralid and noctuid Lepidoptera, ovipositing into the host larva but delaying their full development until the host reaches the pupal stage, in which the parasitoid's cocoons are spun (Čapek, 1970; Ghosh & Abdurahiman, 1984).

In contrast to the weak relationship between Braconidae and hymenopteran hosts, there has been a major radiation of braconids (Opiinae plus Alysiinae) in association with cyclorrhaphous Diptera. While all opiines and many alysiines attack phytophagous hosts, some of the latter group parasitise saprophagous Diptera, a habit of the host group from which the progression to truly parasitoid behaviour (e.g. Hodson, 1939) has rather frequently arisen. Not surprisingly, several alysiines attacking for example larvae of Phoridae and Sarcophagidae qualify as hyperparasitoids under some circumstances (e.g. Witter & Kulman, 1979). However, it is questionable whether these should be regarded as true hyperparasitoids or pseudohyperparasitoids, because even though the dipteran is attacked while still larval and feeding, the attack probably happens very late and only after the original host is dead and becoming putrid. Indeed, orientation to putrefaction or fermentation is evidently the dominant behavioural cue, as is demonstrated by the almost (but cf. Godfray, 1987) universal failure of Alysiinae to engage the fully parasitoid and koinobiont Tachinidae as a host group. For this reason the categorisation of these alysiines as true hyperparasitoids carries little conceptual value, as they seem to exhibit no specialisations leading them into contact with the original host or its substrate in life. The behaviour of alysiines as hyperparasitoids is really only incidental, in much the same way as that of *Syntretus*.

Parasitoids can be solitary, in which case only one parasitoid larva develops on or in each host individual, or they can be gregarious if several individuals, called a brood on the tacit assumption that they are the progeny of a single female, develop at the expense of a single host. Gregariousness has arisen widely in the Braconidae, being found (if uncommonly, in some cases) in at least ten of the 24 British subfamilies, particularly commonly in Microgastrinae and Macrocentrinae. Gregariousness in endoparasitoids may help to overcome the host's haemocytic defences (Kitano, 1986). Although in some quite large and relatively well-studied braconid groups (e.g. Aphidiinae, Opiinae, Cheloninae, Helconinae, Agathidinae) gregariousness is completely unknown, the contrast between Ichneumonidae and Braconidae is again strong: gregariousness in ichneumonids is extremely rare outside ectoparasitoid subfamilies and even in these it is usually of only sporadic occurrence. A peculiar form of gregarious development is polyembryony, in which a single egg laid in a host gives rise to many larvae (cf. Hagen, 1964). Polyembryony has arisen independently in several mostly small groups of endoparasitic Hymenoptera, including the braconid subfamily Macrocentrinae.

The term superparasitism refers to the deposition of an egg (or eggs) on or in a host individual that has already been parasitised by the same species. While this definition is deliberately neutral about the outcome (H. C. J. Godfray, personal communication), the term has traditionally been applied in the sense that 'supernumaries' result – that is, that more immature conspecific parasitoids come to be present than can develop. Many immature parasitoids (especially endoparasitoids) are strictly solitary in their development and are known to compete lethally for sole possession of the host's body, the first parasitoid larva to establish itself usually being the victor in competitions between conspecifics (e.g. Eller *et al.*, 1990). Thus it is not surprising that many species as adults adopt behaviours or have sensory abilities that tend to lead them to avoid superparasitism under a range of circumstances (van Lenteren, 1981). It is nevertheless left open to interpret superparasitism as adaptive (van Alphen & Visser, 1990) under circumstances in which it does tend to occur, such as when there is a shortage of hosts, or among gregarious species under wider conditions, whether or not some individuals are eliminated as a result. When superparasitism leads to supernumaries, the usual outcome is for them to be eliminated very quicly by competition of one kind or another. Although first-instar braconid larvae – especially those of solitary koinobiont endoparasitoids – are often conspicuously adapted for physical struggles (e.g. having powerful mandibles for fighting, or puncturing eggs), physiological means of suppressing rivals are also widely employed (Vinson & Iwantsch, 1980a). Multiparasitism is the term applied to the presence of two (or more) parasitoid species both developing on or in the same host individual, whether both succeed in developing fully, or one is eventually eliminated, or both die.

The general sex-determination mechanism in Hymenoptera is known as haplodiploidy, in which males are haploid and develop from unfertilised eggs (arrhenotokous parthenogenesis) while females are diploid and result only from fertilised eggs after a mating has taken place (Kerr, 1962; Crozier, 1975). However, in some species unfertilised eggs produce diploid females (thelytokous parthenogenesis), making males not only extremely rare but also redundant, at least in the short term. Such species are sometimes called uniparental, and their occurrence is common in Hymenoptera, especially among sawflies and most groups of parasitoids including Braconidae. As might be expected from the range of mechanisms that seem to be involved (White, 1973), sex ratios of progeny produced uniparentally are sometimes influenced by environmental conditions.

Most primary parasitoids attack and develop on or in their hosts at fairly precise life-history stages, and they can be referred to by categories reflecting differences in the host stages used. Egg parasitoids attack, and complete all development in, the host egg; larval parasitoids attack the host larva, also killing this stage; and pupal parasitoids attack and kill (and usually emerge as adults from) the host pupa. Those developing entirely in the nymphs of exopterygote insects could reasonably be called nymphal parasitoids, but (to avoid confusion) shortened terminology is not usually extended to parasitoids that attack the adult stage of their hosts. Some koinobiont endoparasitoids complete their feeding in, and kill, a later host stage than the one attacked, and they are then referred to as egg-larval parasitoids, larva-pupal parasitoids or nymph-adult parasitoids.

Egg parasitism is not practised by Braconidae, though egg-larval parasitism (Clausen, 1954) is known in six British subfamilies and suspected in several others. Although in some (Opiinae, Alysiinae, Microgastrinae) it is of only sporadic occurrence, it is general in Cheloninae and a major feature of at least some tribes of Helconinae and probably Ichneutinae. In fact, egg-larval parasitism may predominate in most of the various braconids that have, to a greater or lesser extent, developed an abdominal carapace (Dudarenko, 1974), as this adaptation probably helps the ovipositor to be held rigidly and precisely in position for penetrating a small hard structure such as an insect egg. Several factors may have contributed to the evolution of egg-larval parasitism, which is quite commonly found in various groups of hymenopterous parasitoids. One is that insect eggs are poorly defended immunologically in comparison with the larvae that will hatch from them. Another is that many host groups lay eggs in positions that are much more accessible to parasitoids than those in which the larva subsequently feeds. Furthermore, some hosts lay aggregated eggs but feed solitarily as dispersed larvae, and the former may be easier to find. Finally, in competitions between endoparasitoids for possession of the host's body the first parasitoid larva present is generally successful, and this situation may have encouraged adult females of koinobiont larval parasitoids to attack earlier and earlier stages of the host. This evolutionary process might culminate in oviposition into the first-instar host larva just before it leaves the egg, or progress to the more extreme ability to attack eggs early in their embryonic development, as is seen in Cheloninae.

At the other extreme, the small braconid subfamily Neoneurinae and some Euphorinae oviposit into adult holometabolous insects, and Aphidiinae and the rest of Euphorinae attack nymphal or adult exopterygotes. Attack on adult insects has evolved at least three times in Braconidae, resulting in substantial radiations in two cases (Euphorinae and Aphidiinae). The majority of braconids, however, attack the larval stage of their endopterygote host, killing it as a larva (or very often as a prepupa). This habit is also seen in many Ichneumonidae, although they also commonly practise larva-pupal parasitism of host groups having more or less obtect pupae (e.g. most Lepidoptera, some Diptera). In contrast, larva-pupal parasitism is extremely unusual in Braconidae, being known for certain only in the very small exotic subfamily Meteorideinae which parasitises Lepidoptera (Ghosh & Abdurahiman, 1984) – although it may occur also in one small exotic group of Braconinae, and the large subfamilies Opiinae and Alysiinae approximate to it as koinobiont parasitoids (of cyclorrhaphan Diptera) that pupate within the host puparium. (Certain genera of Rogadinae have had the reputation of being larva-pupal in error: cf. Whitfield, 1988).

Further important differences in the overall host ranges of Ichneumonidae and Braconidae include the restriction of Braconidae to insect hosts in contrast to the use of spiders made by several groups of cocoon-orientated Ichneumonidae (cf. Fitton *et al.*, 1987); and the complete absence of both exopterygote insects and adult insects from the host spectrum of Ichneumonidae. The evolutionary patterns of host utilisation in the two families have been discussed by Gauld (1988), who stressed especially the much greater importance of Hymenoptera as a host group for Ichneumonidae than for Braconidae. In habitat preferences, too, Ichneumonidae and Braconidae have a somewhat different overall slant, most groups of braconids (with the particular exceptions of Alysiinae, Blacinae and Ichneutinae) being characteristic of relatively warm and dry habitats while ichneumonids are generally more prevalent under cooler and moister conditions (Townes, 1958; Juillet, 1964). Thus Braconidae have proved much more useful than Ichneumonidae for the biological control of pest insects in field crops, though in temperate forests the reverse is often true (Greathead, 1976, 1986; Clausen, 1978).

The known host-associations of the subfamilies of Braconidae as they are represented in Britain are given in Table 1. Adding non-British species and subfamilies would extend the overall host spectrum only a little, by the inclusion of Neuroptera and Orthoptera (for Euphorinae), Embioptera (Doryctinae) and, probably, Isoptera (Ypsistocerinae).

Subfamily	**Hosts**
Doryctinae (I)	Coleoptera.
Rogadinae (I, K)	Lepidoptera, Diptera, Hymenoptera (Tenthredinidae), Coleoptera.
Braconinae (I)	Coleoptera, Lepidoptera, Diptera, Hymenoptera (Symphyta).
Histeromerinae (?I)	Coleoptera.
Opiinae (K)	Diptera (Cyclorrhapha).
Alysiinae (K)	Diptera (Cyclorrhapha).
Gnamptodontinae (K)	Lepidoptera (Nepticulidae).
Ichneutinae (K)	Hymenoptera (Symphyta).
Miracinae (K)	Lepidoptera (Nepticulidae).
Adeliinae (K)	Lepidoptera (Nepticulidae).
Aphidiinae (K)	Hemiptera (Aphididae, *sensu lato*).
Helconinae (K)	Coleoptera.
Blacinae (K)	? Coleoptera, Mecoptera.
Meteorinae (K)	Lepidoptera, Coleoptera.
Euphorinae (K)	Coleoptera, Hemiptera (Heteroptera), Psocoptera, Hymenoptera (Apocrita).
Homolobinae (K)	Lepidoptera.
Sigalphinae (K)	Lepidoptera.
Cenocoeliinae (K)	Coleoptera.
Agathidinae (K)	Lepidoptera.
Macrocentrinae (K)	Lepidoptera.
Orgilinae (K)	Lepidoptera.
Cheloninae (K)	Lepidoptera.
Neoneurinae (?K)	Hymenoptera (Formicidae).
Microgastrinae (K)	Lepidoptera.

Table 1. The known host associations of subfamilies of Braconidae in Britain (I = Idiobiotic, K = Koinobiotic).

The process by which female parasitoids successfully parasitise their hosts has been split by Doutt (1959) into four successive steps, or conditions to be met: host-habitat finding; host finding; host acceptance; and host suitability. The first three of these aspects of parasitoid biology have been well reviewed, with varying degrees of overlap, by several authors (e.g. Vinson, 1976, 1981, 1984a,b, 1988; Weseloh, 1981; Arthur, 1981; van Alphen & Vet, 1986) and a fairly high proportion of the examples given concern species of Braconidae, albeit mostly belonging to only a small number of subfamilies under close investigation in biological control projects (see also Matthews, 1974). Both physical and chemical cues, derived from the host's substrate as well as from the host itself, are important in the location and acceptance process.

Idiobiont ectoparasitoids usually paralyse the host at the time of attack, permanently disabling it and sometimes enhancing its preservation through the use of biochemically complex paralysing venoms (Beard, 1978; Piek, 1986). The parasitoid larva then has relatively few problems in utilising the host's body and larval development is usually swift. For koinobionts, especially if they are endoparasitic (as most koinobiont braconids are), host suitability (Vinson & Iwantsch, 1980a) is a much more complex subject, involving not only nutrition (Slansky, 1986; Vinson & Barbosa, 1987) but also overcoming the host's various defences (Salt, 1968, 1970) and a range of endocrine and other interactions (Beckage, 1985; D. Jones, 1985, 1987; Lawrence, 1986; Vinson & Barbosa, 1987; Tanaka, 1987a) between host and parasitoid that together ensure that the parasitoid's sometimes prolonged development is successful.

Understanding this tuning, and especially 'regulation' of the host by the parasitoid (Vinson, 1975b; Vinson & Iwantsch, 1980b; Vinson & Barbosa, 1987), has been the aim of considerable research effort by biochemists, physiologists and, more recently, virologists. The latter became involved when it was realised that the venoms injected along with eggs by the females of some endoparasitic braconids and ichneumonids contain virus-like particles that originate and replicate in the calyx epithelium of the female's oviduct (Stolz & Vinson, 1979). Such particles had long been known (Rotheram, 1967) but it was some time before they were characterised as the new virus family Polydnaviridae, a group of baculoviruses (Stolz *et al.*, 1984). There is some evidence that polydnaviruses (as found in ichneumonids, at least) may be inherited from mother to offspring by incorporation in the genome (Flemming & Summers, 1986; Stoltz *et al.*, 1986). They penetrate host cells but do not appear to replicate there: co-occurring viruses of a different kind that do replicate in host cells have, however, been noted in some Microgastrinae (Stoltz & Faulkner, 1978; Styler *et al.*, 1987; Stoltz, Krell *et al.*, 1988), but these may not belong to the Polydnaviridae. Once in the host cells polydnaviruses appear to play a major role in allowing the parasitoid to become established, apparently through some sort of immunosuppressive action. However, as the viruses are introduced with a range of other biochemically complex factors in the venom, some of which (in the investigated braconid systems) appear to be essential for the virus to function in this way (Kitano, 1982, 1986; Tanaka, 1987b; Stoltz, Guzo *et al.*, 1988), it has not been easy to ascribe effects to viruses or other venom components unequivocally. Indeed, the literature to date on the effects of endoparasitoid venoms and viruses – and also supposed secretions from the eggs, larvae or associated teratocytes – is somewhat confusing (cf. Stoltz, 1986) and there is also a clear need for extensive comparative studies if their origins and evolutionary significance are to be fully understood. The associated viruses similarly need comparative review and assessment: several morphologically different sorts of polydnaviruses have been described, and viruses of possibly completely different kinds have also been found. At least two distinct kinds occur in the Braconidae: the more usual differ markedly from those noted so far in Ichneumonidae (Stoltz & Vinson, 1979), but the less frequent exhibit several similarities. Viruses have been found in the Microgastrinae, Cardiochilinae and Cheloninae, but a thorough search has not been made for them in other groups. Stoltz & Vinson (1979) state that they may be absent in Rogadinae, Opiinae and Alysiinae (but see Edson *et al.*, 1982, who suggested that particles seen in the venom apparatus of Meteorinae and Opiinae might be viral).

Idiobiont ectoparasitic braconids (and also the endoparasitic Rogadinae, even though koinobionts) are synovigenic (cf. Flanders, 1942); that is, they lay relatively large and fully-yolked eggs that are matured successively by the adult female. In contrast, most koinobiont endoparasitic braconids are proovigenic; that is, they start their adult lives with all their eggs more or less mature and lay small and poorly-yolked eggs. Iwata (1959) has surveyed the form and structure of the ovary and ovarian egg in Braconidae. Most synovigenic female parasitoids feed as adults on the body fluids of a proportion of the hosts they encounter, either killing and mutilating the host specifically for the purpose (destructive host-feeding) or else using the host individual also for oviposition (concurrent host-feeding). Host-feeding is well-known in various Braconinae and Rogadinae, but has been reported only rarely in proovigenic koinobiont subfamilies (Clausen, 1940; Bartlett, 1964; Jervis & Kidd, 1986). However, some synovigenic idiobionts (e.g. Doryctinae and certain Braconinae) attacking deeply concealed hosts have not been observed to host-feed, and may depend on some other source of food. Flowers are known to be important to the adults of many braconids (especially in arid habitats), and morphological adaptations for feeding on them are found in several groups (in Britain chiefly in Agathidinae).

Larval development in idiobiont braconids is normally unremarkable except for the speed with which transition to the better-protected cocoon stage is usually achieved, facilitated by the rapid moulting that apocritan Hymenoptera (possibly in part because they lack a mid-gut/hind-gut connection) can accomplish. Often the entire feeding period is over within a very few days if the conditions are favourable. The first-instar larva of most ectoparasitoids is somewhat adapted for mobility as the egg may be deposited near rather than on the paralysed host, but succeeding instars are generally closely similar to one another. In contrast, koinobiotic endoparasitoids usually take much longer to reach the cocoon stage, in part because the host is often attacked while it is still small, and they pass through a succession of more or less distinctive developmental phases in the process.

Although some braconids (most notably Agathidinae and also some Aphidiinae) oviposit into special organs such as nerve ganglia, most species of most endoparasitic subfamilies place their eggs directly into the haemocoel. The eggs of all studied endoparasitic braconid subfamilies, except for Rogadinae, are alecithal (=hydropic sensu Flanders, 1942): that is, they absorb nutrients from the host's haemolymph, swelling considerably, during the embryonic development of the larva within (Hagen, 1964). Production of small eggs rather than large ones may have several advantages, including allowing females to carry larger numbers of them, to attack younger hosts, and to invest more time in searching for hosts as opposed to feeding, without loss of size in the first instar larva when it first faces the host's haemocytic defences. The greatest increases in size have been recorded in Euphorinae, but the extent to which endoparasitic braconid eggs absorb nutrients varies greatly, not only between subfamilies but also within them.

The cells comprising the trophamnion grow, just as the embryo does, before the eggs hatch, and a mass of these swollen serosal cells in some cases still partially surrounds the first-instar larva for a time after it has hatched (e.g. in some Agathidinae, Microgastrinae, Orgilinae, Opiinae and Alysiinae) and may be fed upon during early larval development, at least in Agathidinae. In other cases the cells may completely dissociate and continue growing to become teratocytes (Hinton, 1954) – cells from the trophamnion that float free in the haemolymph absorbing nutrients and become conspicuously large, without dividing further. Teratocytes are known in several subfamilies of Braconidae (Euphorinae, Aphidiinae, Microgastrinae, Cardiochilinae, Cheloninae and Meteorinae, with somewhat similar phenomena arising in Macrocentrinae) and occur also in Scelionidae, Platygastridae and perhaps Trichogrammatidae.

In the braconid subfamilies in which teratocytes have been most intensively studied (Euphorinae and Aphidiinae) they seem to have a clear trophic role, and are extensively fed upon by middle-instar parasitoid larvae, whose mandibles are reduced or absent. In Microgastrinae and some other subfamilies feeding on teratocytes has also been detected, though with difficulty, despite claims that it does not occur. A wide range of other functions, including the dissipation of the host's haemocytic defences, and the secretion of factors suppressing other parasitoids or microorganisms or in some way controlling the host itself, have been claimed for teratocytes originating from braconids (reviewed by Führer & Elsufty, 1979; Vinson & Iwantsch, 1980b; Gauld & Bolton, 1988). Although Stoltz (1986) considered that the evidence behind most of these suggestions was rather insubstantial, the involvement, if not the exact role, of teratocytes seems clear from some later studies (e.g. Zhang & Dalman, 1989). Whatever else may be involved, the trophic use of teratocytes by certain braconids enables the middle-instar larvae to minimise direct damage to the host's vital organs, and the diversion of nutrients in this way correlates with the success that various endoparasitic braconid subfamilies have had as essentially haemolymph feeders dispensing with a final ectophagous phase. Perhaps it underlies the successful exploitation of exopterygote and adult insects as well.

The first-instar larva in many groups (especially in solitary species) is specialised not for feeding but for retaining possession of the host by fighting or otherwise suppressing competitors (reviews by Salt, 1961; Vinson & Iwantsch, 1980a), and development beyond this specialised stage may therefore be delayed until the host has grown past the stages most susceptible to attack from conspecific or other endoparasitoids. In several groups the moult to the second instar takes place only when the host ceases feeding and seeks a pupation site: the egg-larval groups such as Cheloninae furnish the most extreme examples of this kind of delayed development.

While the first-instar larva is typically armed with large, sickle-shaped mandibles and may have various locomotory adaptations, including a tail-like caudal process, the middle instars tend to be rather featureless, with entirely smooth integuments and mandibles that are either very reduced in form or even in some groups (e.g. Aphidiinae) entirely absent. In several subfamilies (e.g. Microgastrinae, Cheloninae, Orgilinae, Helconinae and in a less pronounced form in Macrocentrinae) an anal vesicle develops in the first and persists in the second and sometimes subsequent instars: this is an evagination of the proctodeum, and it seems to assist in excretion and the absorption of certain nutrients (Edson & Vinson, 1976, 1977). Fleshy processes on various segments are borne by larvae in a few subfamilies: these structures are of uncertain function (but perhaps largely locomotory) and are not necessarily all homologous. They are found especially in the first-instar larvae of Agathidinae, Macrocentrinae, Opiinae and (rarely) Aphidiinae and Alysiinae. They also occur, in clearly different form, in the final-instar larvae of a very few Euphorinae.

The first and final instars of most braconid larvae are very distinctive, but there is much confusion in the literature over the number of intermediate instars passed through in most subfamilies, one, two and three often being reported by different workers. It seems that some expansion of the head capsule takes place in each instar, and mandibles of the next instar are sometimes confusingly visible: the general impression given by particularly careful studies (e.g. O'Donnell, 1987a,b for Aphidiinae) is that the number of intermediate instars has been overestimated more often than underestimated. In most subfamilies a closed tracheal system is visible in some or all instars before the final one, but again it is difficult to compare subfamilies with much confidence from the inconsistent and incomplete accounts given in the literature. Closed spiracles have also sometimes been noted in early instars, but open spiracles first appear in the final instar, and the form of the mandibles and integument also then differ markedly from the middle instars. The mandibles in the final instar are relatively well developed and, especially in the groups that then practise ectophagy, have serrations more or less like those of the idiobiont ectoparasitoids. Clausen (1940), Hagen (1964), Čapek (1973) and Finlayson & Hagen (1979) have given comparative accounts of larval forms.

Beirne (1941) and Short (1952) pioneered morphological study of final-instar larvae as an important aid to the study of, respectively, Ichneumonidae and

Braconidae at the tribal and subfamilial levels, and Čapek (1965, 1969, 1970) augmented various kinds of biological information with extensive study of final-instar larvae to launch what was essentially a new approach to the classification of Braconidae. These studies concentrated on the final-instar larva chiefly for convenience: exuviae of this instar are easily recovered from cocoons that accompany reared adult braconids in collections. Unfortunately, the existing literature on earlier instars is too uneven in quality to serve as a basis for seriously considering these perhaps even more revealing stages and, although we have attempted to summarise what appears in the literature in our treatment of subfamilies in this work, we strongly caution others not to use this information uncritically. Indeed, its greatest value is perhaps to point to uncertainties or unanswered questions. The work of O'Donnell (1987a,b, 1989) on the larvae of Aphidiinae provides a good demonstration of the benefit of a single worker investigating in detail and at first hand the larval morphology and behaviour of a group on a comparative basis. It is this kind of approach, rather than a further digesting of the piecemeal literature, that is most likely to unlock the considerable wealth of phylogenetic and other interesting information that is undoubtedly available from the accurate study of early stages, especially as living entities.

Führer (1968) pointed out that, in general, parasitised and unparasitised hosts might be expected to respond differently to the environment and, indeed, this does seem to be true of a wide range of hosts parasitised by koinobiont braconids. Quite often it has been found that hosts parasitised by braconids have been under- or over-represented by particular sampling methods (e.g. Powell, 1980; Ryan, 1985; Nealis & Régnière, 1987), and it seems to be decidedly unusual for overwintering parasitised and unparasitised hosts to be found to break diapause at the same time when such subtleties have been investigated. A very large number of macrolepidopteran larvae parasitised by Microgastrinae (especially), koinobiont Rogadinae and others have been found to climb vegetation, or sometimes to descend, just before succumbing, in ways that are completely uncharacteristic of healthy individuals of the host species. The coleopteran larvae harbouring some Helconinae make abnormal pupation chambers, and hosts parasitised by Aphidiinae and Euphorinae have also often been found to behave abnormally. The rather different cases of precocious formation of the host cocoon induced by some Cheloninae and Rogadinae are known to be caused by venom. Despite some evidence that, under certain conditions, parasitised hosts can be subjected to higher mortality than unparasitised ones as a result of differential behaviour (e.g. R. E. Jones, 1987; McAllister & Roitberg, 1987, 1988), the evidence that changes in the host's behaviour are controlled by, in the sense of being adaptive for, the parasitoids is on the whole compelling over a wide range of situations (Haeselbarth, 1962; Stamp, 1981; Fritz, 1982; Brodeur & McNeil, 1989).

Silk from the labial glands of the final-instar larva is used to spin a cocoon in all investigated subfamilies of Braconidae with the exception of Opiinae, in which cocoon formation has not been reported and may be universally absent. In the other British groups that similarly pupate inside their host's cuticle (all Alysiinae; most Aphidiinae; endoparasitoid Rogadinae) the cocoon is reduced to varying extents or occasionally altogether lost. Some parasitoids of deeply endophytic hosts also make relatively weak cocoons. In some subfamilies adults eclose from the cocoon by cutting a circular, detachable cap from its apex: the neat emergence holes produced are so distinctive that empty cocoons found in the field can easily be sorted into those from which braconids have emerged successfully and those that have produced hyperparasitoids (which chew irregular emergence holes). In other braconid subfamilies, however, the emerging adults chew more ragged holes resembling those made by hyperparasitoids. Many gregarious braconids produce communal cocoon masses (in which discrete individual cocoons are nevertheless present): although the most familiar examples are in the Microgastrinae, complex and highly ordered structures have been noted in most subfamilies in which gregarious development occurs. The cocoon is important in protecting the soft, exarate pupa from mechanical damage and predation, but it also prevents invasion by pathogenic microorganisms. Not surprisingly, cocoons in which braconids dispause are usually much tougher than those from which adults are destined to emerge within a week or two. The contrast between the winter and summer cocoons of some plurivoltine Microgastrinae, Aphidiinae and Braconinae illustrates this difference well. Defaecation by the final-instar larva takes place after cocoon construction but before pupation in almost all groups, but in Opiinae and Alysiinae the meconium is retained until adult eclosion.

In temperate areas such as Britain a means of overwintering is an important requirement and often has a bearing on a parasitoid's realised host range. Braconids can get through the winter in various ways, though the way in which a given species does so is usually absolutely consistent (a few exceptions, in which the winter can be passed either as a prepupa or as a larva in a diapausing host, are known in Microgastrinae, Ichneutinae and exotic Cenocoeliinae). The idiobiont ectoparasitoids practically all overwinter as cocooned prepupae, though some species of Braconinae possibly do so as adults. Some koinobiont endoparasitoids also overwinter as cocooned prepupae, but if the host overwinters as a partly-fed form the braconids attacking it will almost invariably go through within it as a first-instar larva and, indeed, may be unable to use closely related hosts that overwinter in different ways. Some of the braconids that overwinter as first-instar larvae are plurivoltine and have an alternation of univoltine hosts throughout the year, often with a much greater spread of summer hosts than winter ones.

In many cases it seems to be adaptive for essentially monophagous species to slow down the host's development, perhaps to achieve synchrony for the next generation, and parasitised hosts have often been noticed to break winter diapause later than unparasitised individuals (e.g. Askew & Shaw, 1986; Nealis & Régnière, 1987). On the other hand, overwintering hosts parasitised by some braconids break diapause earlier than unparasitised ones. Early termination of the host's diapause is clearly advantageous in groups such as Euphorinae and Microgastrinae, in which certain species follow their overwintering generation with one or more subsequent generations on the same host generation. There are some circumstances in which the exploitation of hosts very early in the season is facilitated by different overwintering strategies. Thus some Euphorinae overwinter as cocooned pharate adults, and some Rogadinae go through as adult females. Although overwintering as female adults is known to occur also in a few Blacinae, it is a very rare habit among British braconids.

Information on courtship behaviour in Braconidae can be sought through Matthews (1975) and Sivinski & Webb (1989). Although females of most braconids apparently refuse to mate once they have started to oviposit, receptivity and the ability to mate successfully can persist in some Aphidiinae (Liu & Carver, 1985) and Rogadinae (M. R. Shaw, unpublished). Whether or not a female has mated may have a bearing on clutch size in some gregarious Microgastrinae (Tagawa, 1987).

Phylogeny and classification

The superfamily Ichneumonoidea, now generally considered to contain only the two extant families Braconidae and Ichneumonidae, seems to have been one of the first major parasitoid lineages to evolve in the order Hymenoptera (Rasnitsyn, 1980, 1988; see also Gauld & Bolton, 1988). The Braconidae and Ichneumonidae diverged relatively early and the nature of their common ancestor is no longer easy to surmise. Both families have radiated extensively, and today they are of roughly comparable size. There are about 13000 described species of Braconidae, from an estimated total world fauna of at least 40000 (e.g. van Achterberg, 1984b): estimates of 15000 and 60000 respectively have been made for Ichneumonidae (Townes, 1969). Approaching 1200 species of Braconidae in nearly 150 genera are known in Britain. These represent 24 of the currently recognised 39 subfamilies (counting Meteorinae and Apozyginae as subfamilies).

Van Achterberg (1976d) gives an historical summary of various views on the internal classification of Braconidae, which has always been problematical owing to the high incidence of convergent trends in the family, mostly in the form of character reductions (van Achterberg, 1988c). These have often been interpreted only superficially, with little phylogenetic pretension. The most recent phylogenetic classification of Braconidae is that proposed by van Achterberg (1984b). While it is open to criticism on various grounds, we have adopted his classification and (in the checklist) arrangement of subfamilies here, except that we have taken account of subsequent views on tribal composition (e.g. in Rogadinae and Euphorinae) and, more significantly, we have followed S.R. Shaw (1985, 1988) in recognising Meteorinae as a subfamily distinct from Euphorinae. It should nevertheless be stressed that the classification is tentative; in other words, relationships within and between subfamilies of Braconidae are still only poorly understood.

Van Achterberg's (1984b) classification is rooted especially in the work of Čapek (1965, 1969, 1970) and Tobias (1967), whose approaches taken together include consideration of host associations, larval morphology and behaviour, and a critical assessment of the apomorphy (=derived nature) or plesiomorphy (=relict nature) of adult character states. As more data of phylogenetic value became available and awareness of parallelism grew, more powerful techniques for phylogenetic analysis were developed and van Achterberg's (1984b) hypothesis represents a considerable refinement of the views advanced previously. Since then, of course, more information has accrued, and in some cases additional sources of useful data have been found (e.g. Barlin & Vinson, 1981; Edson *et al.*, 1982; Maetô, 1987; Buckingham & Sharkey, 1988), so that major improvements to the classification hypothesis are shortly to be expected (e.g. Quicke & van Achterberg, 1990, published while our work was in press). This process will no doubt continue for some time, as the data available for analysis improve.

The grounds for viewing ectoparasitism as ancestral in Braconidae have never seriously been disputed, and there are good reasons for regarding beetle larvae living in wood or bark as the earliest hosts. Tobias (1967), in particular, expressed the clear view that there are two principal lineages of Braconidae, each originating as parasitoids of this host group. One lineage includes all the relatively plesiomorphic ectoparasitic groups (which, indeed, can be difficult to separate from one another in terms both of classification decisions and recognition) plus the endoparasitic Rogadinae – often called the 'cyclostome' groups on account of the presence in all of them of a strongly emarginate clypeus and an exposed, concave labrum, forming a characteristic opening (properly the hypoclypeal depression) above the mandibles. The other lineage in Tobias's (1967) view comprises the rest of the endoparasitoids (including several rather diverse subfamilies now often called the 'helconine' group).

In advancing his views, Tobias was explicit in rejecting Čapek's (1965) suggestion that the closely related subfamilies Opiinae and Alysiinae had evolved from ectoparasitic ancestors within the cyclostome group. This idea is, however, now gaining acceptance (e.g. Wharton, 1988b) and, indeed, it is in the placement of these relatively specialised endoparasitic parasitoids of cyclorrhaphous Diptera as offshoots of the cyclostome branch of the Braconidae that van Achterberg's (1984b) classification departs most significantly from Tobias's scheme. Nevertheless, Tobias's view of the evolution of endoparasitism in the cyclostome group has been largely supported, at least to the extent that in Rogadinae it has involved a shift to only temporary paralysis at the time of oviposition in conjunction with exploiting progressively more exposed hosts (M. R. Shaw, 1983b). The current view that Opiinae and Alysiinae, and possibly some other independent endoparasitic groups, also arose more or less directly from these ectoparasitic origins does, of course, imply that the transition to endoparasitism has occurred more than once within the cyclostome lineage.

Regarding the other major group, the helconine lineage, Tobias (1967) suggested that large, non-cyclostome ectoparasitic ancestors (a group that is now apparently completely extinct) switched to endoparasitism by injecting the egg, without prior paralysis, into host beetle larvae deeply concealed in plant tissue. This view is also better supported now than when he advanced it. In the first place, while endoparasitoids that inject venom into the host as a separate action before again inserting the ovipositor to lay the egg are known in the cyclostome lineage (M. R. Shaw, 1983b), this habit of dual insertion still remains unknown in the helconine lineage as currently perceived. In the second place, Tobias stressed that the problem of anoxia deep in plant tissue faced by the large ancestors would have meant that endoparasitism, favoured for other reasons, could be endured only while the surface-to-volume ratio of the parasitoid larva remained high, and he suggested this constraint as the origin of the final external feeding phase of some endoparasitic braconid larvae. Tobias cited only four subfamilies (in current senses) in which a final ectophagous phase was known (and in fact he was in error about Meteorinae, leaving only three), but such activity is now known to occur, though sometimes not universally, in ten subfamilies: Helconinae, Homolobinae, Sigalphinae, Cenocoeliinae, Agathidinae, Macrocentrinae, Orgilinae, Cheloninae, Cardiochilinae and Microgastrinae.

In van Achterberg's (1984b) phylogenetic classification it can be seen that all of these endoparasitic subfamilies in which a final ectophagous phase is known are placed in his groups III and IV (although van Achterberg was aware of the habit in only five subfamilies), which comprise one of his major lineages. It might be expected that the remaining subfamilies in van Achterberg's groups III and IV (only Euphorinae, Meteorinae, Blacinae and Neoneurinae in the British fauna) either will be found also to feed externally in the final instar or will be seen to have largely or entirely lost this habit – as indeed has clearly happened in Euphorinae, Meteorinae and in most Microgastrinae, in all of which a non-feeding final-instar larva is commonly found. It might lend further support to Tobias's anoxia hypothesis that the insects that have abandoned their final ectophagy are among the smallest in the lineage and certainly of a very much smaller size than the postulated ancestors in which the habit arose.

Van Achterberg's (1984b) classification places the subfamily Aphidiinae closer to the other major lineage that he calls group II. The isolated position of Aphidiinae suggests an independent evolution of endoparasitism in association with aphids as hosts, but gives little idea of how this may have arisen. Group II includes all the ectoparasitoids and the endoparasitic Rogadinae that evolved from them (M. R. Shaw, 1983b) as group IIa (i.e. the cyclostomes sensu stricto), with an offshoot consisting of the specialised parasitoids of cyclorrhaphous Diptera – Opiinae and Alysiinae – placed close to it. The remainder of group II (Gnamptodontinae, Ichneutinae, Miracinae and Adeliinae in the British fauna, and Dirrhopinae) is termed the 'ichneutine' group.

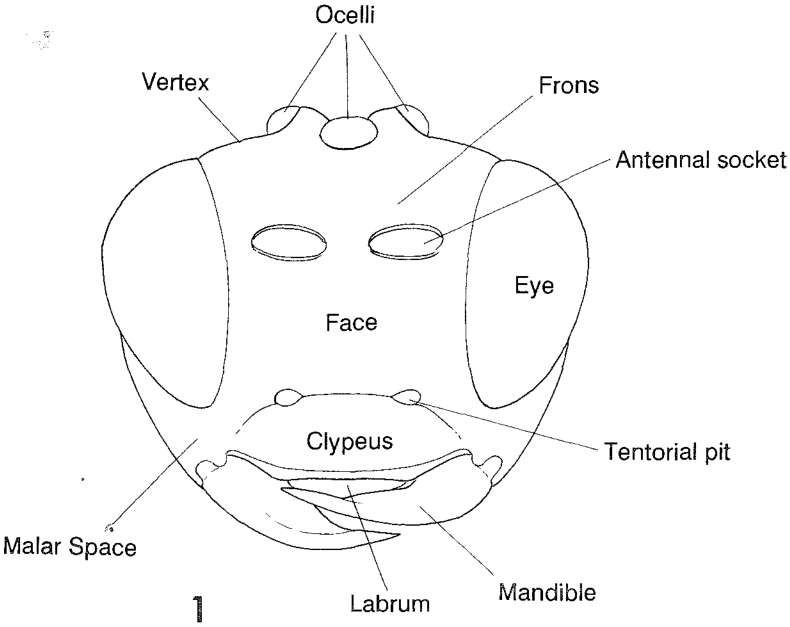
All subfamilies in the ichneutine group include specialist, and apparently internal, parasitoids of nepticulid Lepidoptera, presumably reflecting an important switch between leaf-mining hosts as nepticulids are otherwise parasitised only facultatively by braconids (e.g. Shaw & Askew, 1976a). This subgroup is placed closer to the cyclostome subfamilies (group IIa) plus Opiinae and Alysiinae, and also to the Aphidiinae – in all of which parasitism is either wholly external or wholly internal – than to the group III and IV subfamilies, which correspond to Tobias's (1967) concept of the other major lineage, in which the larval habit of feeding at first internally but later externally is basal. Although their hosts are well known, the developmental biology of Gnamptodontinae, Adeliinae and Miracinae is almost completely unstudied, and only marginally more detail is available for Ichneutinae. In each case they are known to form a cocoon outside the host's prepupal remains but within the host cocoon; otherwise, the crucially important behaviour of the final-instar larva remains unknown.

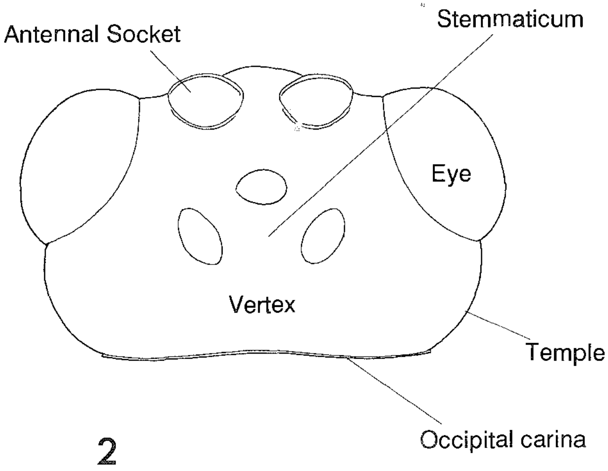
In view of the somewhat intermediate position of the ichneutine group, between the rest of group II on the one hand and groups III & IV on the other, the prediction implied by van Achterberg's (1984b) proposed phylogeny is not especially strong, but it does appear to suggest that they should be wholly endoparasitic until fully fed, with no non-feeding final-instar larva. Eclosion of the post-feeding final-instar larva from the host remains would then be a synapomorphy of this group, in contrast with the normal habit of pupating inside the host remains (lost in a few Aphidiinae) seen in all other endoparasitoids outside groups III and IV. According to Tobias's hypothesis this behaviour was not a characteristic of the common ancestor of groups III and IV either, posing the question as to how this form of endoparasitism arose in the Braconidae if not as a further instance of an evolution of endoparasitism from ectoparasitic ancestors attacking leaf-mining hosts within the cyclostome group.

If the cyclostome condition in Braconidae is considered to be derived (Tobias, 1967; van Achterberg, 1984b), the conclusion that the ectoparasitic common ancestral group that gave rise to the two major lineages has become extinct seems inescapable, as all of the extant wholly ectoparasitic Braconidae, so far as is known, exhibit the cyclostome condition.

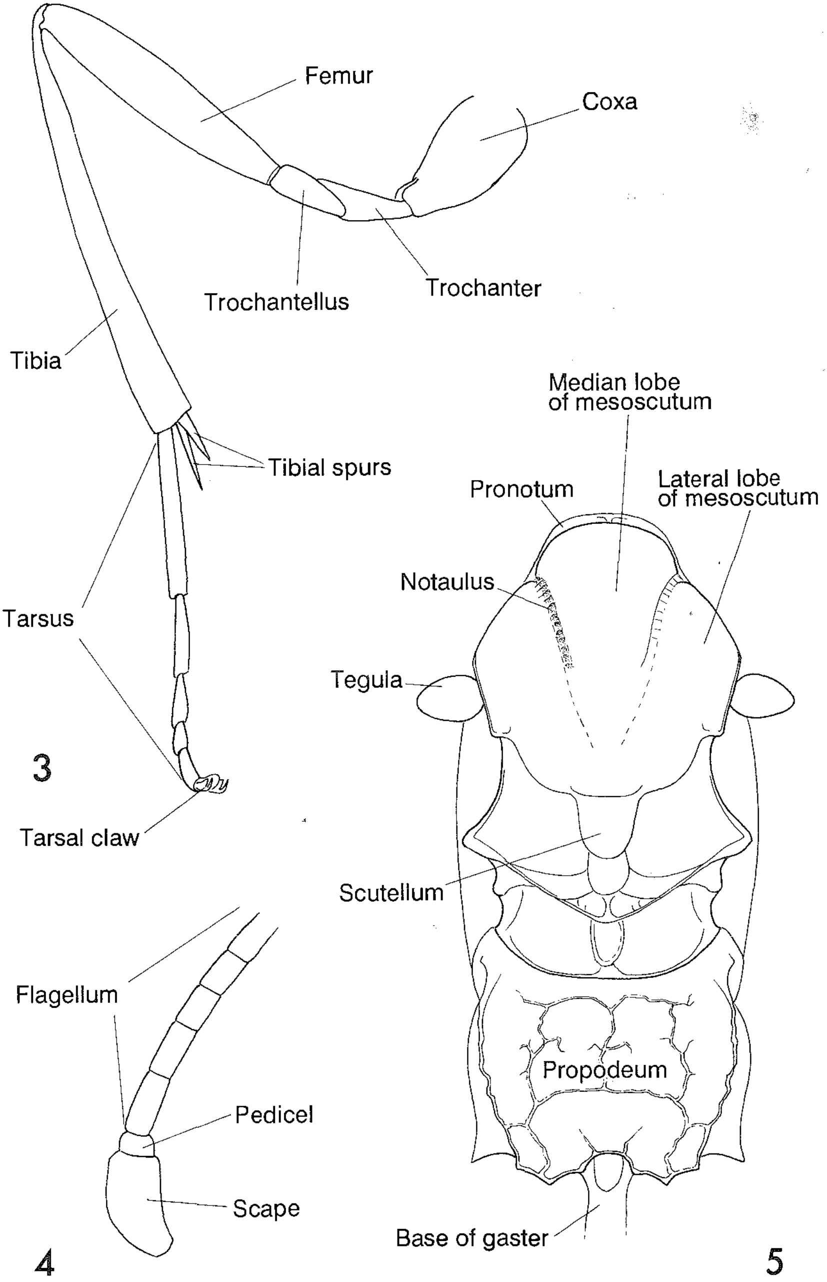
Morphological terminology

Richards (1977) surveyed the comparative morphology and associated terminology of Hymenoptera in considerable detail; it is, however, rather difficult to abstract from his account the information pertaining to a particular family. Gauld & Bolton (1988) included a less comprehensive review of the subject but incorporated recent advances in understanding, particularly of the terminology of wing veins. The morphological terms most used in taxonomic work on Braconidae are summarised here by means of labelled figures (figs 1–8). All terms used in the present work are included, but of course additional or alternative terms may be encountered in some of the keys for species-level identification to which we refer. Most will be traceable through Richards (1977), van Achterberg (1976c, 1979c) or Gauld & Bolton (1988). However, the older literature is sometimes difficult to interpret. In particular, different systems of venational terminology have been widely used for Braconidae, and authors have often used somewhat different interpretations within each framework. Eady (1974) reviewed the main systems and their variants with particular reference to the Braconidae and he proposed nomenclature that, slightly modified, has been used by Sigwalt (1977) and by van Achterberg (1979c), and is illustrated here (fig. 8). Mason (1986) proposed a system for standardising illustrations of wings in taxonomic work. The terminology of other parts of the body has been much more stable and, except that the propodeum used often to be called the metathorax (in error) in the older literature, confusion is unlikely to arise (but see van Achterberg, 1976c, 1979c). Eady (1968) and Harris (1979) have given illustrated accounts of surface sculpture.

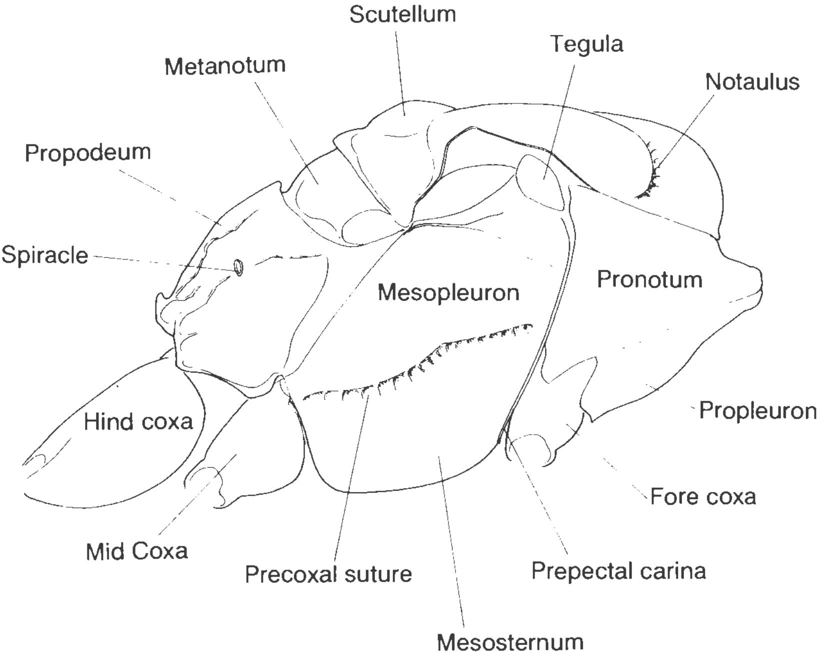




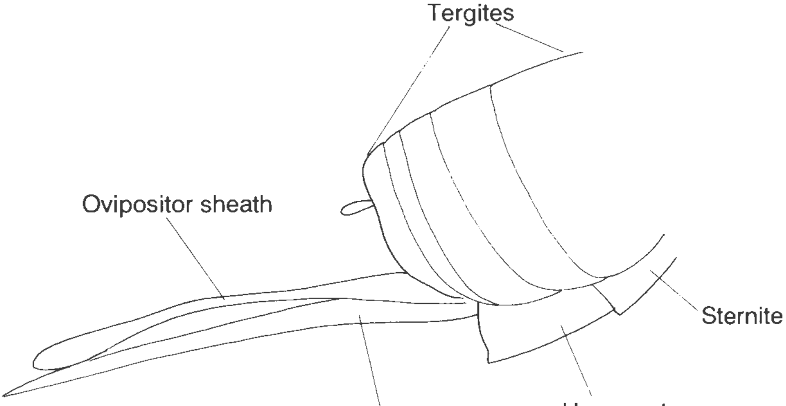
Figs 1–2. *Zele albiditarsus* Curtis. 1, head, anterior, 2, head, dorsal.



Figs 3–5. *Zele albiditarsus*. 3, hind leg, 4, base of antenna, 5, thorax and propodeum, dorsal.

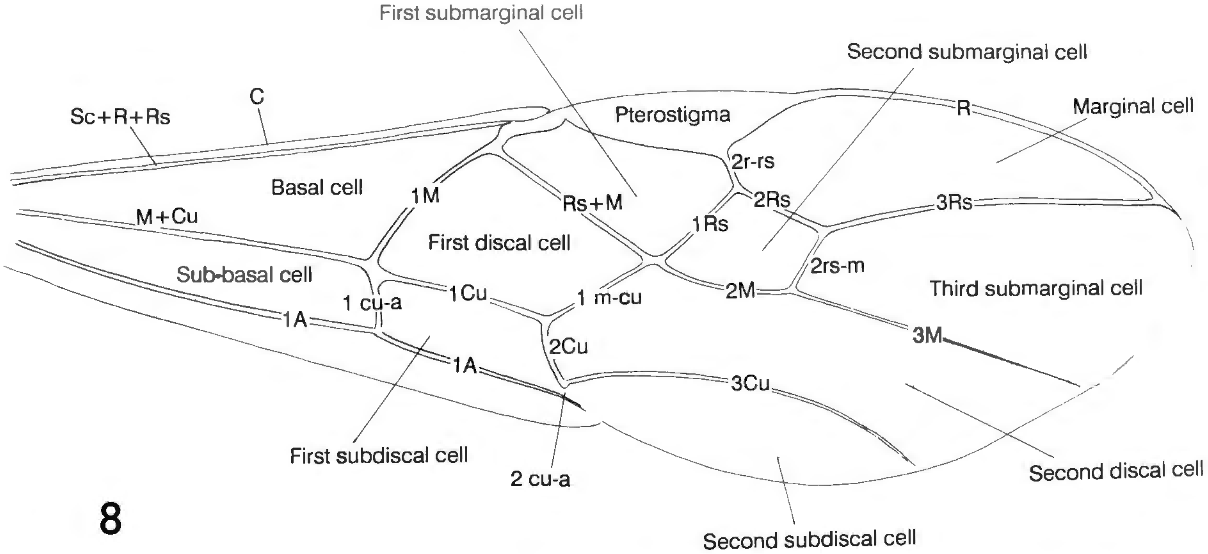


6

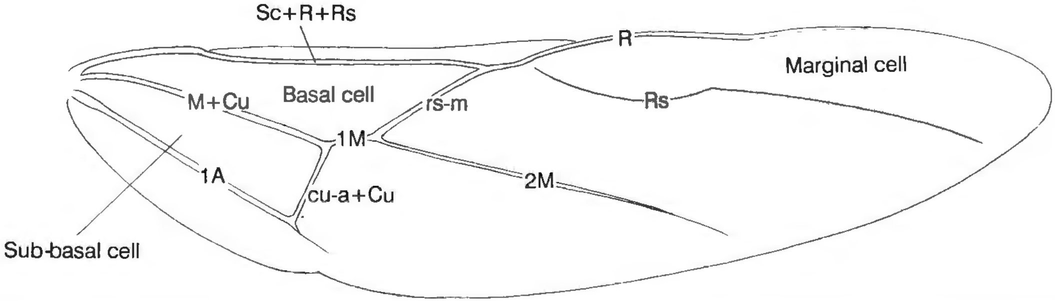


7

Figs 6–7. *Zele albiditarsus*. 6, thorax and propodeum, lateral, 7, apex of gaster, lateral.


First submarginal cell
Second submarginal cell
C
Sc+R+Rs
Pterostigma
R
Marginal cell
2r-rs
Basal cell
1M
Rs+M
2Rs
3Rs
M+Cu
1Rs
First discal cell
2rs-m
Sub-basal cell
1Cu
2M
Third submarginal cell
1 cu-a
1 m-cu
1A
3M
2Cu
1A
3Cu
First subdiscal cell
2 cu-a
Second discal cell
Second subdiscal cell

8


Sc+R+Rs
R
Marginal cell
Basal cell
M+Cu
rs-m
Rs
1M
1A
2M
cu-a+Cu
Sub-basal cell

Recognition of Braconidae

Ichneumonoidea can be separated from other groups of Hymenoptera by the following combination of characteristics: hind leg with a clearly differentiated trochantellus; forewing with a pterostigma and at least one enclosed cell; veins C and Sc+R+Rs in the proximal part of the forewing fused, resulting in the virtual obliteration of the costal cell; antenna with sixteen, or often many more, segments – only infrequently with fewer. Wingless ichneumonoids can be distinguished from other wingless Hymenoptera by their somewhat membranous gastral sternites that dry in longitudinal folds, almost always sixteen or more antennal segments and, often, exserted ovipositor.

Braconids and ichneumonids can be differentiated by using the following key. It should be borne in mind that the wing venation in Ichneumonidae is relatively stable (see figs 10, 13–15 for range of variation) whereas in Braconidae it is much more variable and, in particular, it is more or less reduced in several groups (see, for instance, figs 26, 47–52, 63–66). It is commonly thought that braconids are smaller than ichneumonids but, although this is indeed the general tendency, there is much too much overlap in the size ranges of the two groups for size to be a reliable way of distinguishing them.

Key to ichneumonoid families

(This key also gives subfamily placements of all apterous or brachypterous Braconidae known in Britain)

1 Fully winged 2

— Wingless or brachypterous 4

2 Forewing with vein 2m-cu present (fig. 10), rarely only weakly indicated (figs 13, 14); hindwing with vein rs-m meeting Rs after that vein diverges from Sc+R+Rs (fig. 12); first discoidal and submarginal cells of forewing always confluent . . . **Ichneumonidae** (part)

— Forewing with vein 2m-cu absent (figs 9, 15); hindwing with vein rs-m meeting Sc+R+Rs before Rs diverges (fig. 11), if at or slightly after junction then first discoidal and submarginal cells of forewing separated by Rs+M except in Paxylommatinae which has forewing venation as in fig. 15 3

3 Gaster attached distinctly above hind coxa (fig. 16); venation as in fig. 15; hind coxa at least four times as long as broad (fig. 16); . . . . **Ichneumonidae (Paxylommatinae)**

— If rarely gaster attached distinctly above hind coxae (fig. 58) then venation not as in fig. 15 but with three submarginal cells (cf. fig. 9); hind coxa never so elongate . . . . **Braconidae** (part)

4 Mandibles exodont (not meeting when closed) with three teeth that turn outwards (fig. 17) . . . . **Braconidae (Alysiinae)**

— Mandibles meeting or crossing at tips when closed, with two teeth 5

5 Clypeus strongly emarginate, forming a cyclostome mouth opening (figs 18, 19) . . . . **(Braconidae)** 6

— Clypeus not emarginate, so that there is no cyclostome mouth opening 7

6 First tergite of gaster subsessile, distinctly broader apically than long (fig. 20); ovipositor about as long as hind tarsus . . . . **Braconidae (Rogadinae:** ***Pambolus*****)**

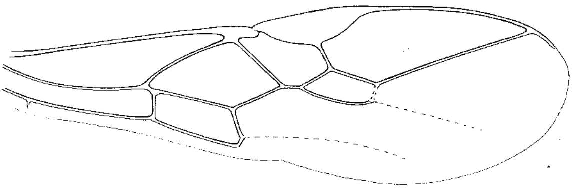
— First tergite of gaster petiolate, about twice as long as apically broad (fig. 21); ovipositor about twice as long as hind tarsus . . . . **Braconidae (Doryctinae:** ***Spathius*****)**

7 Ovipositor clearly longer than the gaster (brachypterous; wings with some obvious venation) . . . . **Braconidae (Orgilinae:** ***Orgilus*****)**

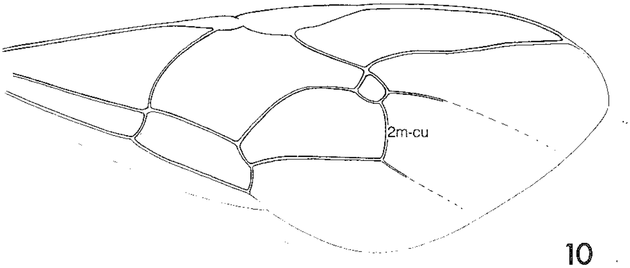
— Ovipositor always distinctly shorter than the gaster 8

8 Gastral tergites strongly sclerotised, firmly rounded (if with a tendency to crumple in dead specimens then wing remnants at least equal in length to the propodeum); ovipositor often distinctly exserted . . . . **Ichneumonidae** (part)

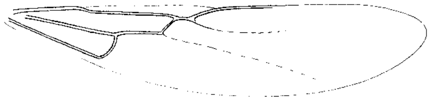
— Gastral tergites weakly sclerotised (often more or less crumpled in dead specimens); wing remnants minute, clearly much shorter than propodeum; ovipositor short, barely exserted . . . . **Braconidae (Aphidiinae:** ***Diaeretellus*****)**



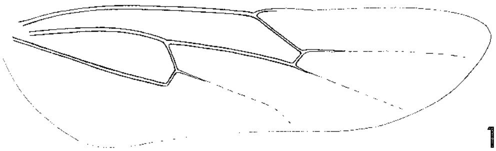
9



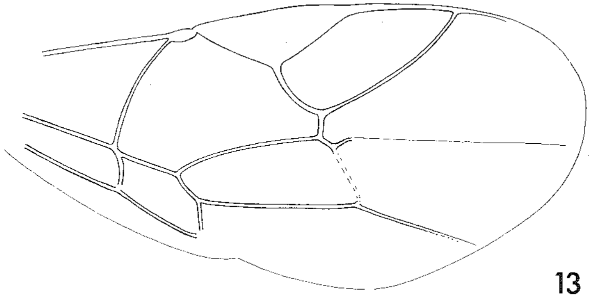
10



11

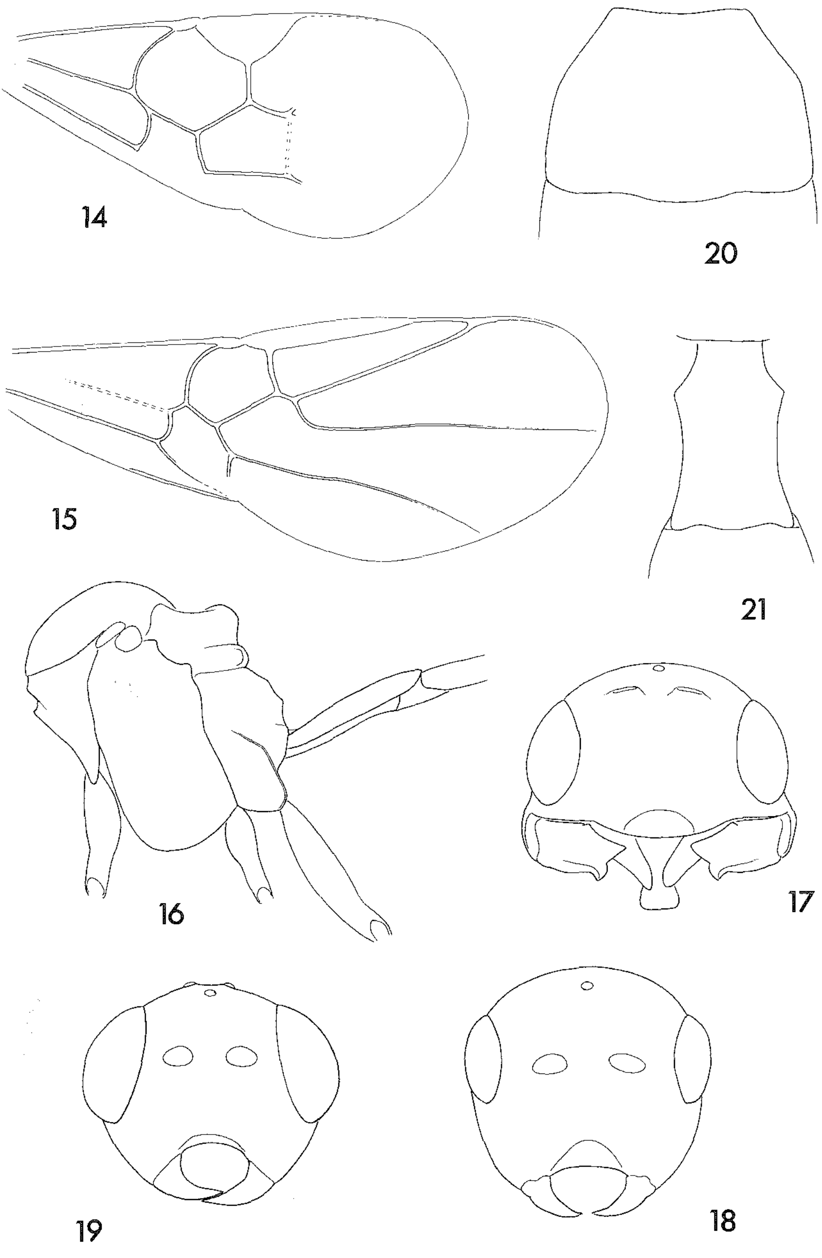


12



13

Figs 9–13. 9, *Macrocentrus linearis* (Nees von Esenbeck), forewing, 10, *Cidaphus alarius* (Gravenhorst) (Ichneumonidae), forewing, 11, *M. linearis*, hindwing, 12, *C. alarius*, hindwing, 13, *Aclastus* sp. (Ichneumonidae), forewing.



Figs 14–21. 14, *Neorhacodes enslini* (Ruschka) (Ichneumonidae), forewing, 15, *Hybrizon buccatum* (de Brébisson) (Ichneumonidae), forewing, 16, *H. buccatum*, thorax and propodeum, lateral, 17, *Chasmodon apterus* (Nees von Esenbeck), head, anterior, 18, *Pambolus mirus* (Ruthe), head, anterior, 19, *Spathius pedestris* Wesmael, head, anterior, 20, *P. mirus*, first tergite, dorsal, 21, *S. pedestris*, first tergite, dorsal.

Checklist of the British genera

The 148 genera of Braconidae believed to occur in Britain are listed here in the subfamily arrangement proposed by van Achterberg (1984b), except that Meteorinae is recognised as a subfamily separate from Euphorinae following S.R. Shaw (1985, 1988).

Synonyms are included only where confusion might otherwise arise in reconciling this list with the most recent Kloet & Hincks checklist (Huddleston, 1978), or because the literature cited in the sections on subfamilies uses obsolete generic names that might otherwise prove difficult to trace. In the latter cases the names listed in synonymy do not necessarily have a history of usage in the British literature.

Valid generic names that did not appear as such, or that were applied to different taxa, in the last Kloet & Hincks checklist are asterisked. A few represent genuine additions to the British fauna but most are just the result of taxonomists splitting genera or raising subgenera. However, some have more complicated nomenclatural origins, mainly to do with correcting previous mistakes in the application of generic names. These cases, in which names that appeared in the last Kloet & Hincks checklist are now applied in a different way, are the most likely to cause confusion and the most important are explained in the accounts of the subfamilies concerned.

DORYCTINAE
DORYCTINI
- DORYCTES Haliday, 1836
- WACHSMANNIA Szépligeti, 1900
- ONTSIRA Cameron, 1900
- DENDROSOTER Wesmael, 1838
  - CAENOPACHYS Foerster, 1862

SPATHIINI
- SPATHIUS Nees von Esenbeck, 1819

ECPHYLINI
- ECPHYLUS Foerster, 1862

HECABOLINI
- HECABOLUS Curtis, 1834
- MONOLEXIS Foerster, 1862

ROGADINAE
HORMIINI
- HORMIUS Nees von Esenbeck, 1818

PAMBOLINI
- CHREMYLUS Haliday, 1833
- PAMBOLUS Haliday, 1836

ACRISIDINI
- ACRISIS Foerster, 1862

EXOTHECINI
- COLASTES Haliday, 1833
  - EXOTHECUS Wesmael, 1838
- *SHAWIANA van Achterberg, 1983
  - PHANOMERIS of authors
- XENARCHA Foerster, 1862
  - PHANOMERIS Foerster, 1862

RHYSSALINI
- RHYSSALUS Haliday, 1833
- *DOLOPSIDEA Hincks, 1944
  - DOLOPS Marshall, 1889 preoccupied
- *PSEUDOBATHYSTOMUS Belokobylskij, 1986
  - BATHYSTOMUS of authors
- ONCOPHANES Foerster, 1862
- RHYSIPOLIS Foerster, 1862

ROGADINI
- CLINOCENTRUS Haliday, 1833
- *ROGAS Nees von Esenbeck, 1818
  - PELECYSTOMA Wesmael, 1838
- ALEIODES Wesmael, 1838
  - HETEROGAMUS Wesmael, 1838
  - ROGAS of authors
  - RHOGAS of authors
  - PETALODES Wesmael, 1838

BRACONINAE
BRACONINI
- ATANYCOLUS Foerster, 1862
- BARYPROCTUS Ashmead, 1900
- *PIGERIA van Achterberg, 1985
- BRACON Fabricius, 1804
- *HABROBRACON Johnson, 1895

COELOIDINI
- COELOIDES Wesmael, 1838

GLYPTOMORPHINI
- GLYPTOMORPHA Holmgren, 1868
- *ISOMECUS Kriechbaumer, 1895
  - VIPIO of authors

HISTEROMERINAE
- HISTEROMERUS Wesmael, 1838

OPIINAE
ADEMONINI
- ADEMON Haliday, 1833

OPIINI
- OPIUS Wesmael, 1835
  - DESMIOSTOMA Foerster, 1862
  - DIACHASMA Foerster, 1862

- BIOSTERES Foerster, 1862
- EURYTENES Foerster, 1862

ALYSIINAE
ALYSIINI

- ALYSIA Latreille, 1804
- PENTAPLEURA Foerster, 1862
- TANYCARPA Foerster, 1862
- DAPSILARTHRA Foerster, 1862
  - MESOCRINA Foerster, 1862
  - PSEUDOMESOCRINA Königsmann, 1959
- *ADELUROLA Strand, 1928
- ORTHOSTIGMA Ratzeburg, 1844
- *DINOTREMA Foerster, 1862
  - PROSAPHA Foerster, 1862
  - SYNALDIS Foerster, 1862
- ASPILOTA Foerster, 1862
  - SYNALDIS of authors, in part
- *LEPTOTREMA van Achterberg, 1988
- *EUDINOSTIGMA Tobias, 1986
- *PANEREMA Foerster, 1862
- *PTERUSA Fischer, 1958
- APHAERETA Foerster, 1862
- PHAENOCARPA Foerster, 1862
- ASOBARA Foerster, 1862
- IDIOLEXIS Foerster, 1862
- CRATOSPILA Foerster, 1862
- SYNCRASIS Foerster, 1862
- IDIASTA Foerster, 1862
- ALLOEA Haliday, 1833
- ANISOCYRTA Foerster, 1862
- TRACHYUSA Ruthe, 1854
- ATOPANDRIUM Graham, 1952
- CHASMODON Haliday, 1838

DACNUSINI

- COELINIUS Nees von Esenbeck, 1818
- COELINIDEA Viereck, 1913
- POLEMOCHARTUS Schulz, 1911
- SYMPHYA Foerster, 1862
- EPIMICTA Foerster, 1862
- ARISTELIX Nixon, 1943
- LAOTRIS Nixon, 1943
- SYNELIX Foerster, 1862
- CHAENUSA Haliday, 1839
- CHOREBUS Haliday, 1833
- EXOTELA Foerster, 1862
- PROTODACNUSA Griffiths, 1964
- AMYRAS Nixon, 1943
- TATES Nixon, 1943
- COLONEURA Foerster, 1862
- DACNUSA Haliday, 1833

GNAMPTODONTINAE

- GNAMPTODON Haliday, 1836
  - GNAPTODON of authors

ICHNEUTINAE
ICHNEUTINI

- ICHNEUTES Nees von Esenbeck, 1818

PROTEROPINI

- PROTEROPS Wesmael, 1835

MIRACINAE

- MIRAX Haliday, 1833

ADELIINAE

- ADELIUS Haliday, 1833
  - ACAELIUS Haliday, 1834
  - ACOELIUS of authors

APHIDIINAE
EPHEDRINI

- EPHEDRUS Haliday, 1833
  - LYSEPHEDRUS Starý, 1958
- TOXARES Haliday, 1840

PRAINI

- AREOPRAON Mackauer, 1959
- PRAON Haliday, 1833
- DYSCRITULUS Hincks, 1943

APHIDIINI

- PARALIPSIS Foerster, 1862
- LYSIPHLEBUS Foerster, 1862
- PAUESIA Quilis, 1931
- DIAERETUS Foerster, 1862
- DIAERETIELLA Starý, 1960
- DIAERETELLUS Starý, 1960
- APHIDIUS Nees von Esenbeck, 1818
- MONOCTONUS Haliday, 1833
- *HARKERIA Cameron, 1900
- TRIOXYS Haliday, 1833
- BINODOXYS Mackauer, 1960

HELCONINAE
HELCONINI

- HELCON Nees von Esenbeck, 1814
- HELCONIDEA Viereck, 1914
- *WROUGHTONIA Cameron 1899

DIOSPILINI

- DIOSPILUS Haliday, 1833
- ASPIGONUS Wesmael, 1835
- BAEACIS Foerster, 1878
- TAPHAEUS Wesmael, 1835

BRACHISTINI

- EUBAZUS Nees von Esenbeck, 1814
  - EUBADIZUS Nees von Esenbeck, 1834
  - EUBADIZON Nees von Esenbeck, 1834
  - BRACHISTES Wesmael, 1835
  - CALYPTUS Haliday, 1835
  - ALIOLUS Say, 1836
  - ALLODORUS Foerster, 1862
- *FOERSTERIA Szépligeti, 1896
- SCHIZOPRYMNUS Foerster, 1862
- TRIASPIS Haliday, 1835

BLACINAE
DYSCOLETINI

- DYSCOLETES Haliday, 1840

BLACINI

- BLACUS Nees von Esenbeck, 1818
- *BLACOMETEORUS Tobias, 1976

METEORINAE
METEORUS Haliday, 1835
*ZELE Curtis, 1832
  ZEMIOTES Foerster, 1862

EUPHORINAE
PERILITINI
PERILITUS Nees von Esenbeck, 1818
DINOCAMPINI
*DINOCAMPUS Foerster, 1862
  PERILITUS of authors, in part
ROPALOPHORUS Curtis, 1837
EUPHORINI
WESMAELIA Foerster, 1862
PERISTENUS Foerster, 1862
LEIOPHRON Nees von Esenbeck, 1818
*EUPHORIELLA Ashmead, 1900
TOWNESILITINI
*TOWNESILITUS Haeselbarth & Loan, 1983
MICROCTONINI
MICROCTONUS Wesmael, 1835
STREBLOCERA Westwood, 1833
CENTISTINI
PYGOSTOLUS Haliday, 1833
ALLURUS Foerster, 1862
CENTISTES Haliday, 1835
  ANCYLOCENTRUS Foerster, 1862
  SYRRHIZUS Foerster, 1862
LOXOCEPHALINI
*LOXOCEPHALUS Foerster, 1862
  MYIOCEPHALUS Marshall, 1898
  SPILOMMA Morley, 1909
COSMOPHORINI
*COSMOPHORUS Ratzeburg, 1848
SYNTRETINI
SYNTRETUS Foerster, 1862

HOMOLOBINAE
HOMOLOBINI
*HOMOLOBUS Foerster, 1862
  ZELE of authors
CHARMONTINI
CHARMON Haliday, 1833
  EUBADIZON of authors, in part

SIGALPHINAE
ACAMPSINI
ACAMPSIS Wesmael, 1835

CENOCOELIINAE
CENOCOELIUS Haliday, 1840

AGATHIDINAE
AGATHIS Latreille, 1804
EARINUS Wesmael, 1837
*BASSUS Fabricius, 1804
  MICRODUS Nees von Esenbeck, 1812

MACROCENTRINAE
MACROCENTRUS Curtis, 1833
  AMICROPLUS Foerster, 1862
*AUSTROZELE Roman, 1910

ORGILINAE
ORGILINI
ORGILUS Haliday, 1833

CHELONINAE
CHELONINI
CHELONUS Jurine, 1801
  MICROCHELONUS Szépligeti, 1908
ASCOGASTER Wesmael, 1835
PHANEROTOMINI
PHANEROTOMA Wesmael, 1838
  BRACOTRITOMA Csiki, 1909

NEONEURINAE
NEONEURUS Haliday, 1838

MICROGASTRINAE
MICROGASTRINI
APANTELES Foerster, 1862
MICROPLITIS Foerster, 1862
MICROGASTER Latreille, 1804
  LISSOGASTER Bengtsson, 1926
HYPOMICROGASTER Ashmead, 1897
PROTOMICROPLITIS Ashmead, 1897

The generic classification of British Microgastrinae according to Mason (1981) is included here as an alternative:

**MICROGASTRINAE**
**APANTELINI**
*_DOLICHOGENIDEA Viereck, 1911_
*_PHOLETESOR Mason, 1981_
APANTELES Foerster, 1862
*_ILLIDOPS Mason, 1981_
**MICROGASTRINI**
*_PAROPLITIS Mason, 1981_
*_HYGROPLITIS Thomson, 1895_
*_ICONELLA Mason, 1981_
*_CHOERAS Mason, 1981_
*_SATHON Mason, 1981_
MICROGASTER Latreille, 1804
**COTESIINI**
*_RASIVALVA Mason, 1981_
*_DISTATRIX Mason, 1981_
*_GLYPTAPANTELES Ashmead, 1905_
*_DIOLCOGASTER Ashmead, 1900_
*_PROTAPANTELES Ashmead, 1898_
*_COTESIA Cameron, 1891_
*_DEUTERIXYS Mason, 1981_
PROTOMICROPLITIS Ashmead, 1898
**MICROPLITINI**
MICROPLITIS Foerster, 1862

Key to subfamilies of British Braconidae

The key given below is to fully winged forms, and is designed for use only with the British fauna. Apterous or brachypterous specimens should be run in the key given in the section entitled 'Recognition of Braconidae', which will give subfamily placements for braconids that are not fully winged (p. 24).

1 Mouth opening present between the usually distinctly excised clypeus and the mandibles, subcircular (figs 27, 32) or wide elliptical; labrum usually concave, shining and clypeus narrow, short 2

— Mouth opening not present between clypeus and mandibles; if somewhat developed (Opiinae, Gnamptodontinae, Neoneurinae: fig. 28) then labrum not concave and clypeus not distinctly narrow 6

2 Head large, produced forwards (figs 22–25); rim of antennal sockets and distal border of scape produced into dentate projections; mandibles massive; forewing with two submarginal cells (fig. 26) .... **Euphorinae** (*Cosmophorus*)

— Head not large and produced forwards or, if so (fig. 40), antennal sockets and scape not produced into dentate projections, mandibles less massive and forewing with three submarginal cells (cf. fig. 37) 3

3 Occipital carina absent (fig. 31) or at most represented by an angulation of the head capsule; 1cu-a of forewing more or less opposite 1M (fig. 37); prepectal carina absent laterally; sub-basal cell of hindwing small, at most one-third as long as basal cell (fig. 34) .... **Braconinae**

— Occipital carina present (figs 29, 30), sometimes medially effaced (fig. 33); if indistinct then 1cu-a of forewing clearly distal to 1M (fig. 36) and/or prepectal carina present laterally; sub-basal cell of hindwing larger, distinctly more than one-third as long as basal cell (fig. 35) 4

4 Head large, distinctly larger than mesonotum in dorsal view (fig. 40) and produced forwards so that face is very short (figs 38, 39); basal segment of hind tarsus conspicuously longer than remainder of tarsus (fig. 42); outer surface of fore tibia with a dense cluster of stout spines (fig. 41) .... **Histeromerinae**

— Head often large but never larger than mesonotum in dorsal view and face never so short; basal segment of hind tarsus at most as long as rest of tarsus, usually shorter; stout spines on fore tibia, if present, not in a dense cluster on outer surface 5

5 Fore tibia with a number of stout spines on its anterior surface, arranged more or less as a row (fig. 43) and with a transverse row of small, stout spines apically (fig. 43); in small species, in which tibial spines are difficult to see, forewing often with only two submarginal cells .... **Doryctinae**

— Fore tibia with no spines conspicuously thicker than normal tibial pilosity either on the anterior surface or apically; forewing always with three submarginal cells (except male *Pambolus*) .... **Rogadinae**

6 Mandibles not meeting even when closed (figs 44, 45), always with three or more teeth .... **Alysiinae**

— Mandibles meeting when closed and generally overlapping at the tips, always bidentate although sometimes appearing unidentate and occasionally with a ventral keel ending in a dentate projection (fig. 46) 7

7 Second submarginal cell small (figs 47, 48), sometimes open (figs 49, 50) or 1Rs meeting or almost meeting the pterostigma (figs 51, 52); 3Rs absent distally, or at most visible as a weakly pigmented line and Rs+M always distinct (figs 47–52); notauli generally absent or weak 8

— Second submarginal cell larger (e.g. figs 54, 62) or fused with third (figs 63–65, 72, 102, 111, 112); if small, then 3Rs strongly developed, reaching to wing margin (fig. 66) or marginal cell narrow and divided (fig. 59); if 1Rs meeting or almost meeting the pterostigma then 2Rs+3Rs strongly curved so that marginal cell short (fig. 72); if 3Rs present only as a trace then Rs+M absent or weak (figs 63–65); notauli usually well developed 10

8 Vein 2r-rs absent or minute, 1Rs and 2Rs thus both meeting or almost meeting pterostigma (figs 51, 52); antenna with 14 or 20 segments 9

— Vein 2r-rs distinct (figs 47–50); antenna with 18 segments .... **Microgastrinae**

9 Antenna with 14 segments; occipital carina absent; wing venation as in fig. 51 .. **Miracinae**

— Antenna with 20 segments; occipital carina present; wing venation as in fig. 52 .. **Adeliinae**

10 Posterior transverse carina of mesosternum complete (fig. 53); forewing always with three submarginal cells (fig. 54); gaster either in the form of an unarticulated carapace (figs 55–57) or inserted high on propodeum (fig. 58) 11

— Posterior transverse carina of mesosternum usually absent or, if present, clearly incomplete; if gaster in form of carapace, forewing with only two submarginal cells (fig. 105) or carapace articulated between first and second tergites (figs 77, 78) 12

11 Gaster close to coxal insertions and forming a carapace (figs 55–57) which is not articulated though it may have two transverse, crenulate grooves (figs 55, 56) .... **Cheloninae**

— Gaster inserted high on propodeum, distinctly separated from coxal insertions (fig. 58), never forming a carapace .... **Cenocoeliinae**

12 Marginal cell of forewing divided (fig. 59); vein 1M angled centrally (fig. 59) .... **Neoneurinae**

— Marginal cell of forewing not divided; vein 1M not angled centrally 13

13 Hindwing with cu-a + Cu absent (fig. 60); forewing usually with second submarginal cell fused with third and 3Rs incomplete, present only as a trace (figs 63–65); if 3Rs complete (fig. 62) then large second submarginal cell present, first subdiscal cell narrow, and antenna with 11 segments (except in *Toxares*) .... **Aphidiinae**

— Hindwing with cu-a + Cu present (fig. 61); forewing with 3Rs complete, distinct to wing margin (e.g. figs 91, 97) except in *Ademon* (fig. 90) and a few Euphorinae (cf. fig. 72); if second submarginal cell large then first subdiscal cell broad and antenna with substantially more than 11 segments 14

14 Marginal cell very narrow (fig. 66); second submarginal cell small, sometimes fused with third; occipital carina absent .... **Agathidinae**

— Marginal cell broad (figs 79, 97, 98); if somewhat narrow then occipital carina present laterally; second submarginal cell, if present, much larger (e.g. figs 79, 81, 91, 98) 15

15 Forewing with three submarginal cells (e.g. figs 79, 80, 89, 90) 16

— Forewing with two submarginal cells (figs 72, 102, 105, 111, 112) 24

16 First tergite of gaster petiolate (figs 68, 69, 71), its spiracles at about mid-segment or behind; second submarginal cell higher than wide, often narrowed anteriorly .... **Meteorinae**

— First tergite of gaster not petiolate (figs 95, 96, 108, 109), its spiracles usually considerably in front of mid-segment; second submarginal cell rarely higher than wide or narrowed anteriorly (but see fig. 81) 17

17 Trochantellus of hind leg with several teeth apically (fig. 73); median lobe of mesoscutum strongly protruding (figs 75, 76); head conspicuously transverse (fig. 74); occipital carina absent .... **Macrocentrinae**

— Trochantellus of hind leg with no apical teeth; median lobe of mesoscutum not strongly protruding; head not conspicuously transverse (figs 82, 103); occipital carina usually present, at least laterally 18

18 Gaster in form of carapace, articulated only between first and second tergites (figs 77, 78) .... **Sigalphinae**

— Gaster not in form of carapace, all tergites normally articulated 19

19 Marginal cell of forewing very short (figs 80, 81) and either second submarginal cell strongly narrowed distally (fig. 80) or anterior ocellus situated between bases of antennae (fig. 82) .... **Ichneutinae**

— Marginal cell of forewing longer (figs 89–91, 97, 99); second submarginal cell generally not narrowed; anterior ocellus not between bases of antennae 20

20 Prepectal carina absent (fig. 83) (except in *Ademon*); gaster short, rounded (figs 85, 86); ovipositor usually projecting beyond apex of gaster by much less than length of gaster, if about equal then second submarginal cell distinctly elongate (fig. 91) 21

— Prepectal carina present, though sometimes obscured by coarse sculpture (fig. 84); gaster often longer, more slender (figs 87, 88), or if short and rounded then ovipositor longer than gaster and second submarginal cell as high as wide (fig. 97) 22

21 Second tergite at base without a transverse raised area, at most with some striate sculpture or, in *Ademon*, second tergite conspicuously granulate; 2Rs usually conspicuously longer than 1Rs (fig. 91), occasionally about equal (fig. 90) .... **Opiinae**

— Second tergite with a transverse, slightly raised area at base (fig. 86); 2Rs always distinctly shorter than 1Rs (fig. 89) .... **Gnamptodontinae**

22 Tibial spurs long, spur of hind tibia about half as long as first segment of hind tarsus or longer (fig. 92); ovipositor short, not more than half as long as gaster (fig. 94); body colour often yellowish-brown .... **Homolobinae** (*Homolobus*)

— Tibial spurs short, spur of hind tibia clearly much less than half as long as first segment of hind tarsus (fig. 93); ovipositor long, at least equal in length to gaster; body colour usually predominantly dark 23

23 First tergite with two rather deep dorsal pits at base (fig. 95); 1m-cu joining second submarginal cell (fig. 99) .... **Blacinae** (*Dyscoletes*)

— First tergite with no dorsal pits (fig. 96); 1m-cu joining first submarginal cell (figs 97, 98) .... **Helconinae** (Helconini, Diospilini)

24 First tergite of gaster petiolate, its spiracles at about mid-segment or behind (figs 67, 70), or, if subpetiolate or spiracles in front of mid-segment, then 2Rs + 3Rs strongly curved (fig. 72) .... **Euphorinae** (except Centistini)

— First tergite of gaster sessile, its spiracles usually considerably in front of mid-segment (figs 95, 96, 108, 109); 2Rs + 3Rs never strongly curved 25

25 First three tergites strongly carinate laterally and immovably joined, forming a carapace which covers remainder of gaster (figs 100, 101). . **Helconinae** (*Triaspis*, *Schizoprymnus*)

— Second and third tergites not strongly carinate laterally, not forming a carapace or if, occasionally, carinate and forming a carapace then first and second tergites with a movable articulation 26

26 1Rs aligned with the straight 2Rs + 3Rs (fig. 102); marginal cell rather narrow and short; head narrow, face and clypeus strongly protuberant (figs 103, 104); first subdiscal cell closed postero-apically (fig. 102) .... **Orgilinae**

— 1Rs conspicuously angled with 2Rs + 3Rs (fig. 105); if marginal cell rather short, 2Rs + 3Rs distinctly curved (fig. 72); if head narrow and face protuberant then first subdiscal cell open postero-apically (fig. 111) 27

27 Ovipositor broad and blade-like (figs 106, 107), either very short and reflexed under gaster (fig. 106) or longer, though never distinctly longer than gaster, and at most downcurved (fig. 107); first tergite broad at base (fig. 108); second tergite with no trace of a lateral fold (fig. 106) .... **Euphorinae** (Centistini)

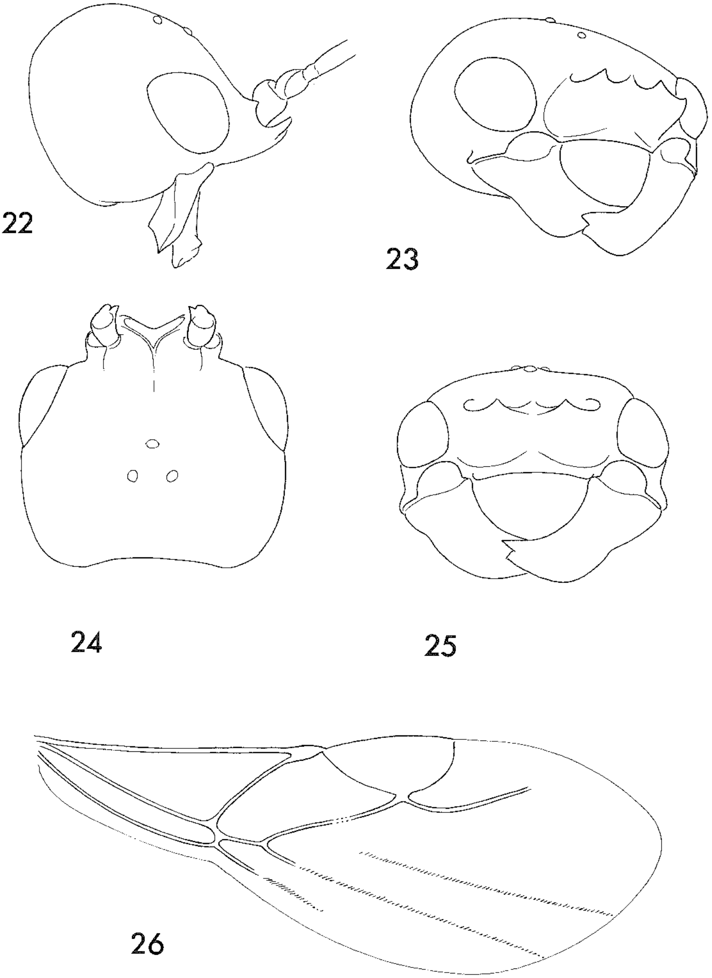
— Ovipositor slender and straight, sometimes conspicuously longer than gaster, never strongly reflexed but if somewhat downcurved then first tergite narrow at base (fig. 109); second tergite usually with a lateral fold, at least basally (fig. 110) 28

28 First subdiscal cell open postero-apically (fig. 111); first tergite with conspicuous dorsal pits (fig. 109); ovipositor usually distinctly shorter than gaster, rarely longer .... **Blacinae** (*Blacus*)

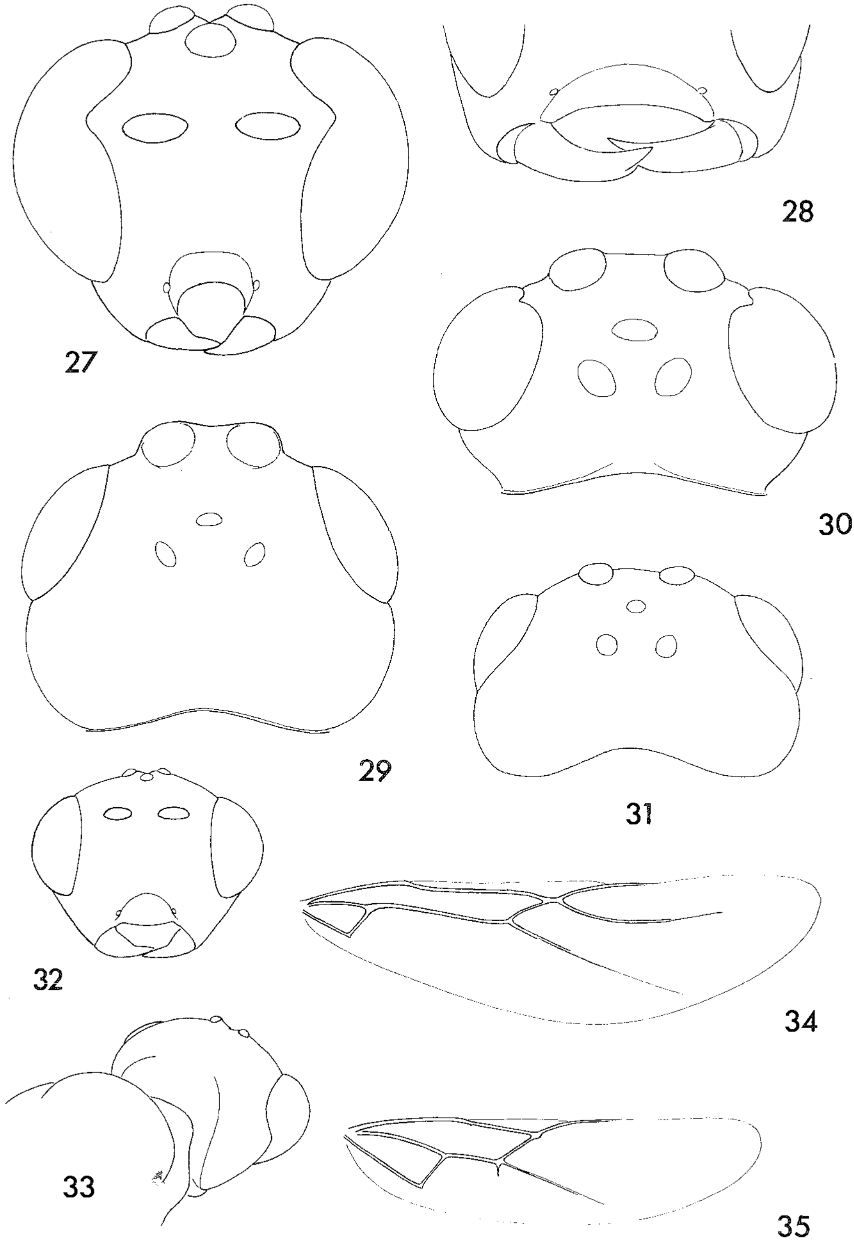
— First subdiscal cell closed postero-apically (fig. 112) (except some *Eubazus*); first tergite with no dorsal pits; if either character unclear then ovipositor conspicuously longer than gaster 29

29 Propodeum dorsally with no distinct carinae, at most with a longitudinal band of weak rugosity, otherwise smooth and punctate; 2A present in hindwing (fig. 113) .... **Homolobinae** (*Charmon*)

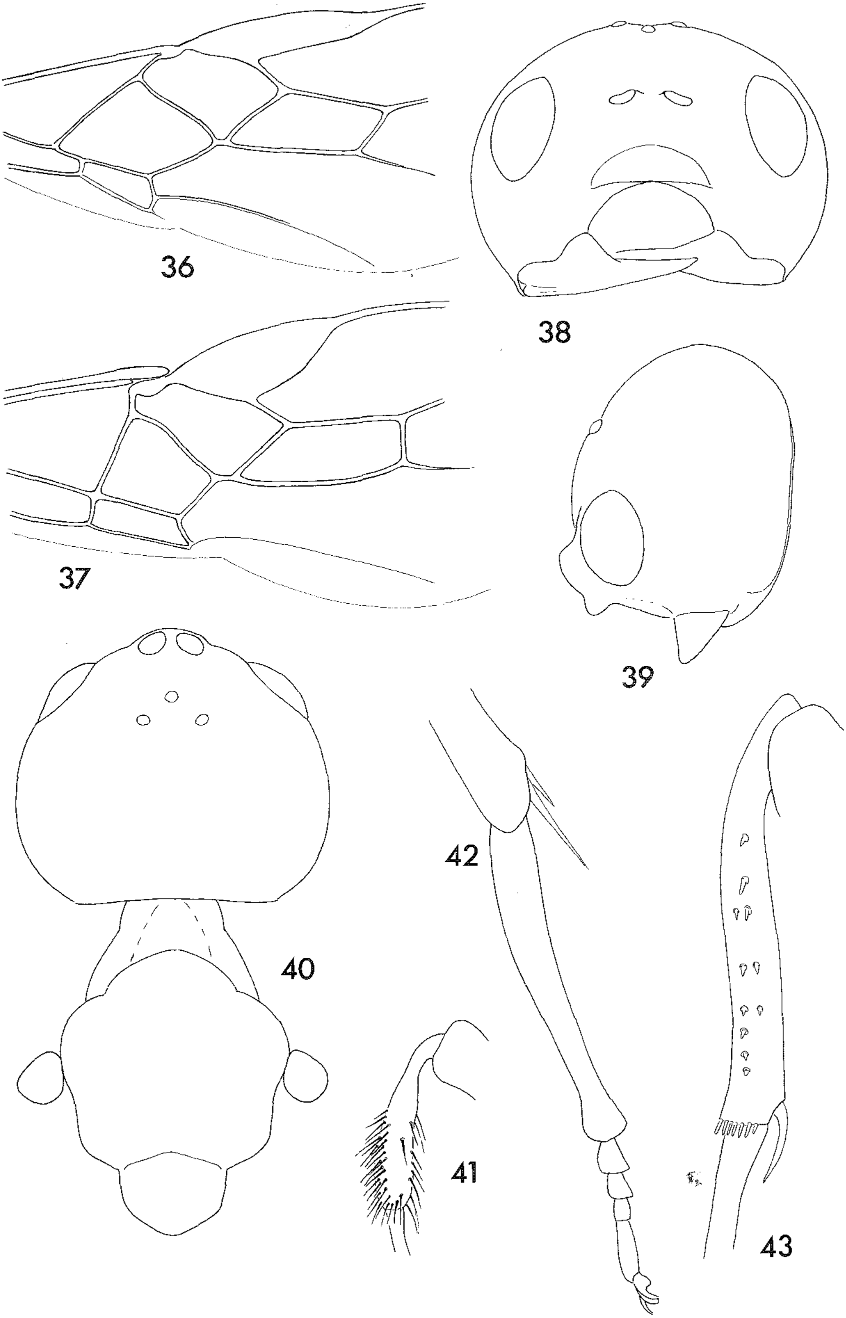
— Propodeum dorsally carinate, and rugose all over; 2A not present in hindwing (fig. 114). . ... **Helconinae** (Brachistini except *Triaspis*, *Schizoprymnus*)



Figs 22–26. *Cosmophorus cembrae* Ruschka. 22, head, lateral, 23, head, antero-lateral, 24, head, dorsal, 25, head, anterior, 26, forewing.



Figs 27–35. 27, *Aleiodes praetor* (Reinhard), head, anterior, 28, *Opius nitidulator* (Nees von Esenbeck), lower part of head, anterior, 29, *Doryctes heydeni* Reinhard, head, dorsal, 30, *Aleiodes nigricornis* Wesmael, head, dorsal, 31, *Bracon* sp., head, dorsal, 32, *Rhyssalus clavator* Haliday, head, anterior, 33, *Colastes braconius* Haliday, head and part of thorax, posterolateral, 34, *Bracon* sp., hindwing, 35, *Aleiodes alternator* (Nees von Esenbeck), hindwing.



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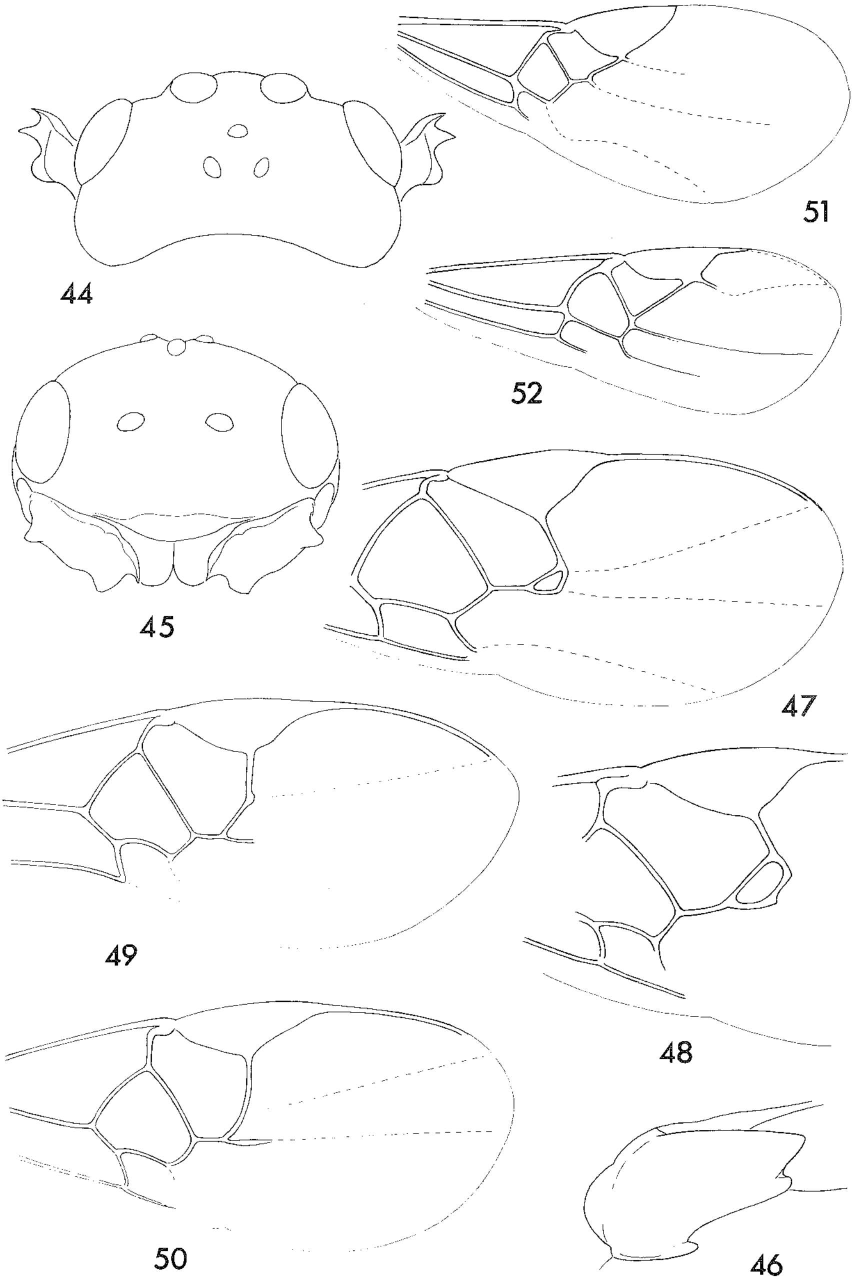

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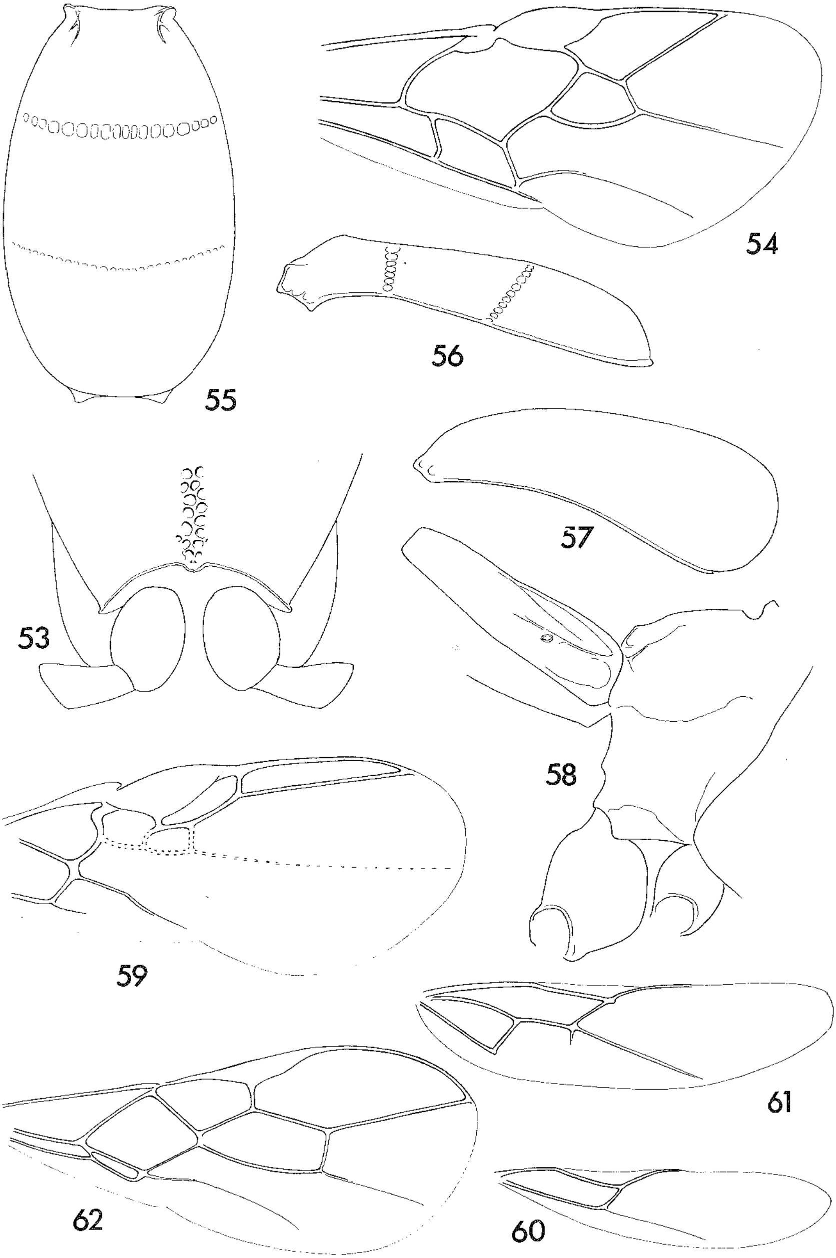

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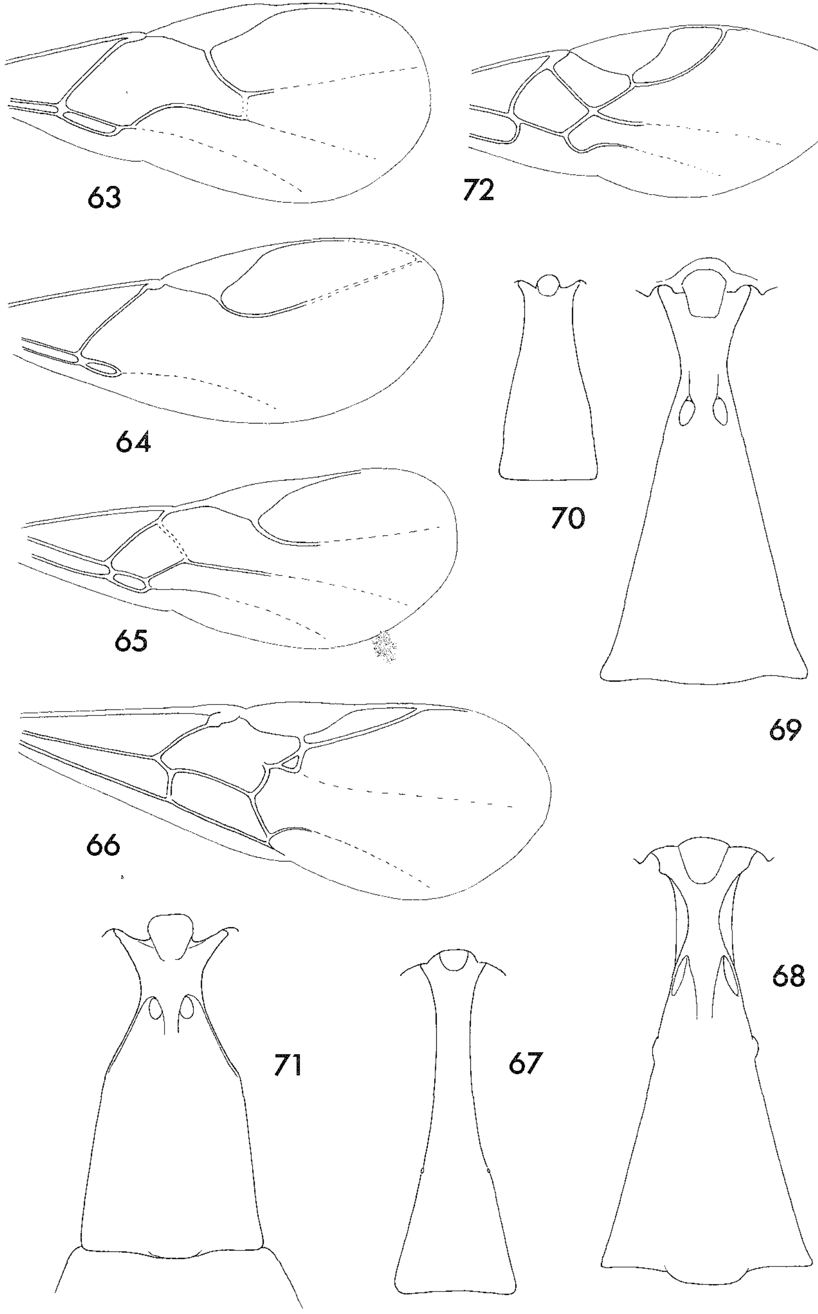

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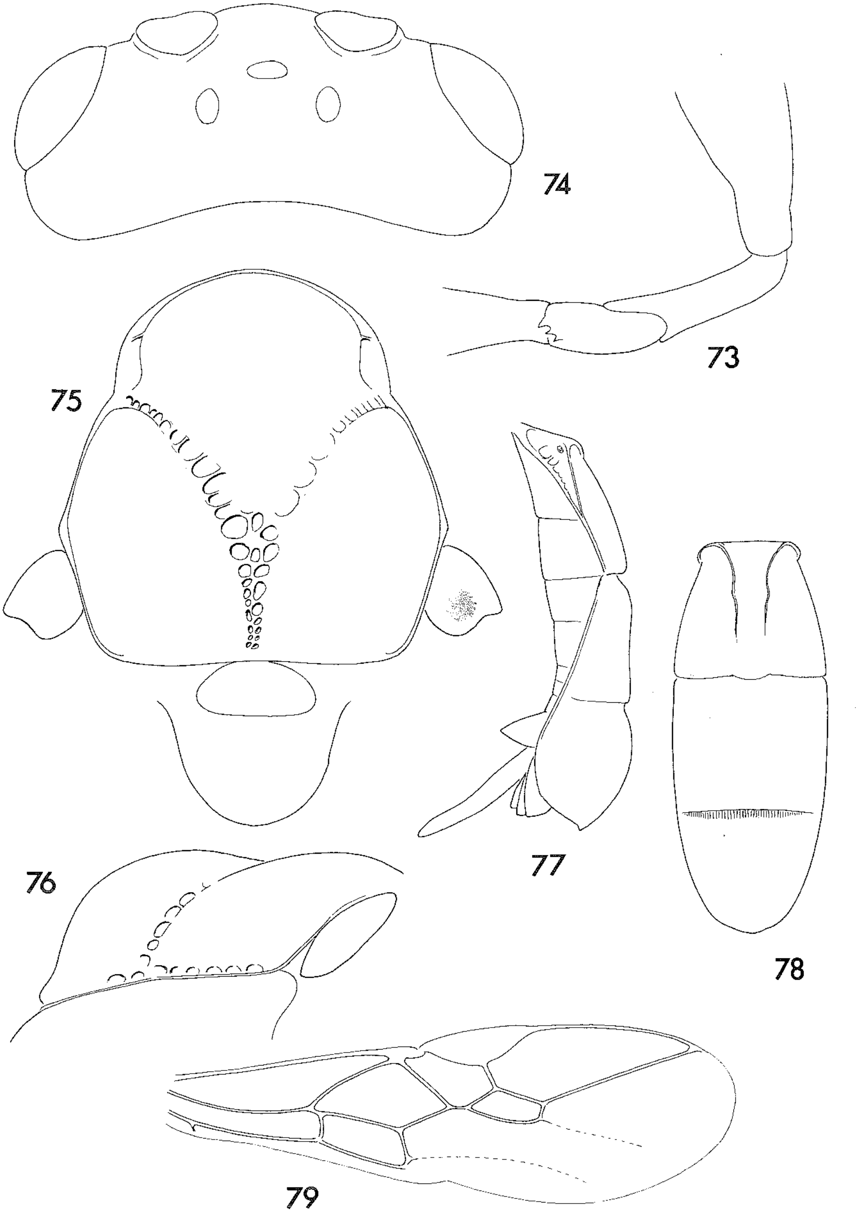

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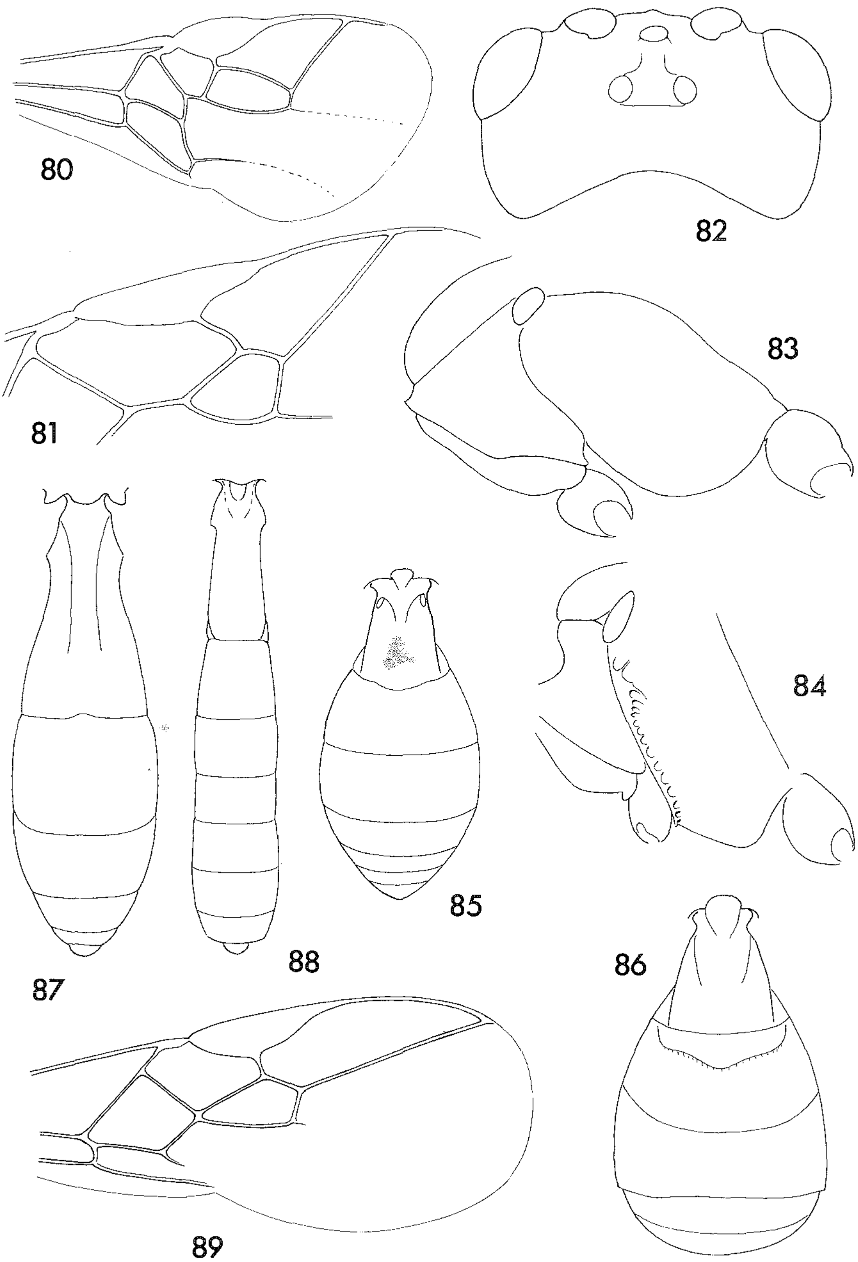

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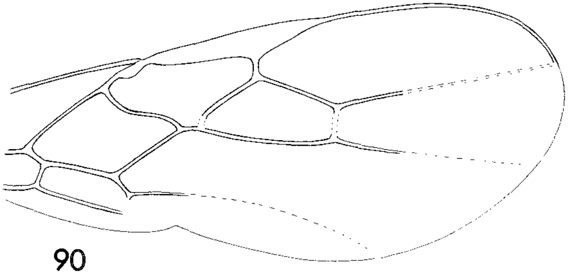

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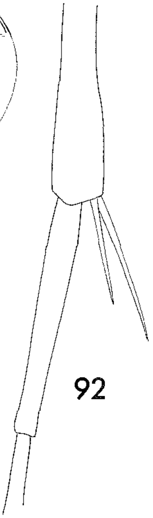

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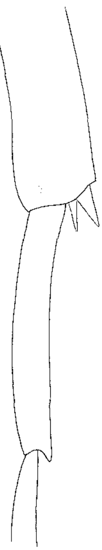

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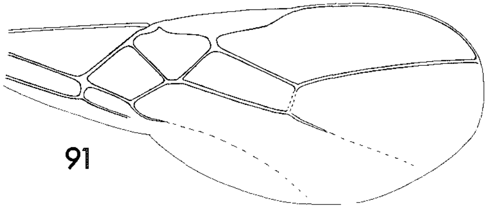

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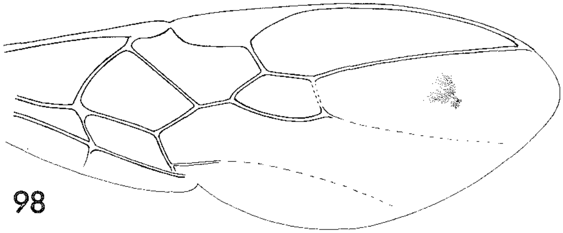

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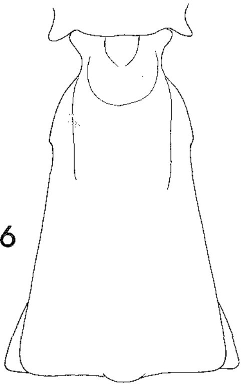

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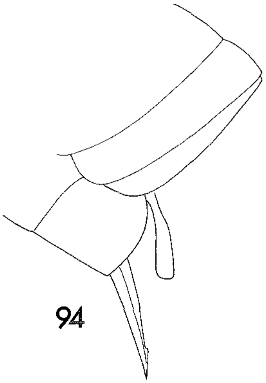

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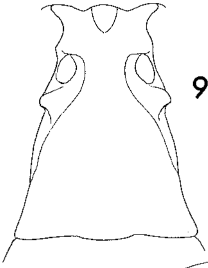

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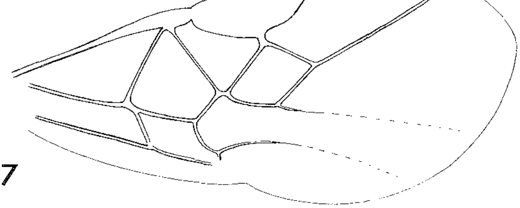

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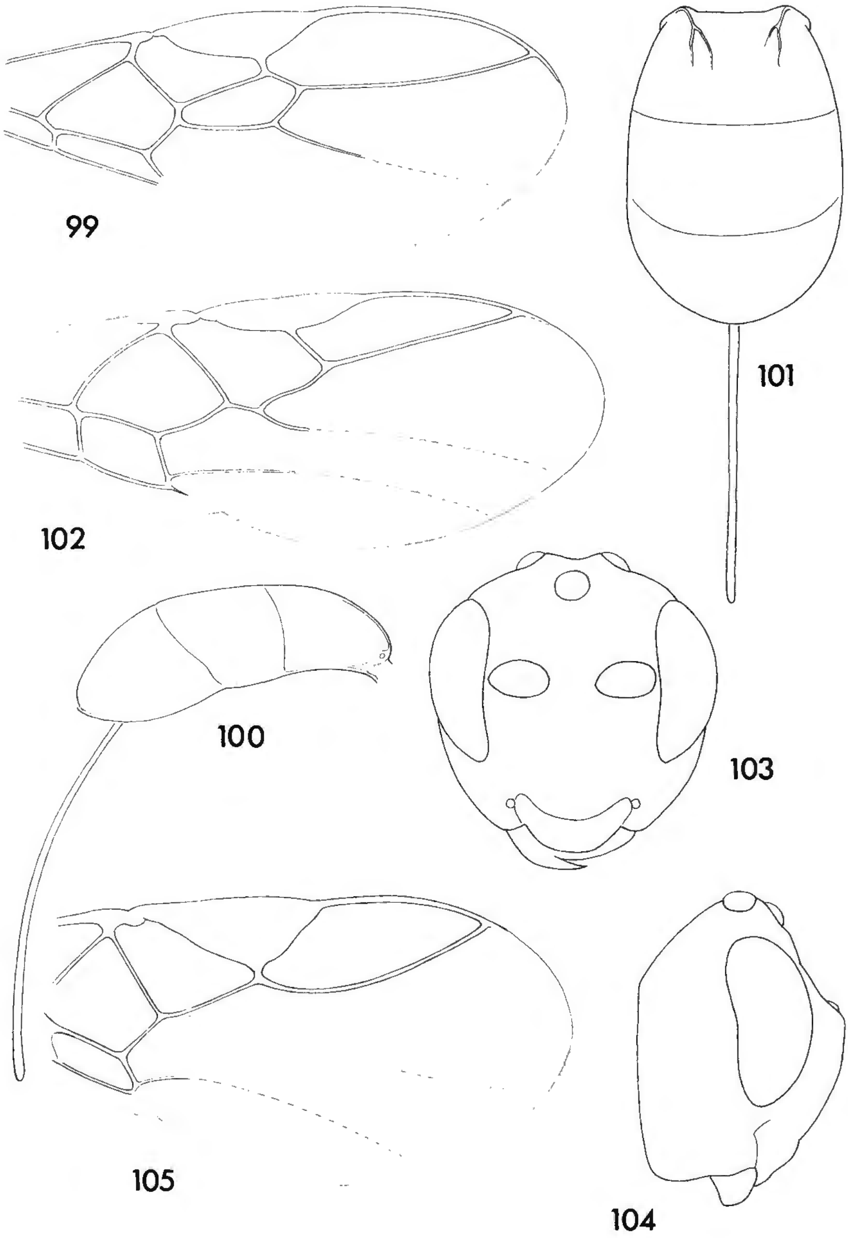

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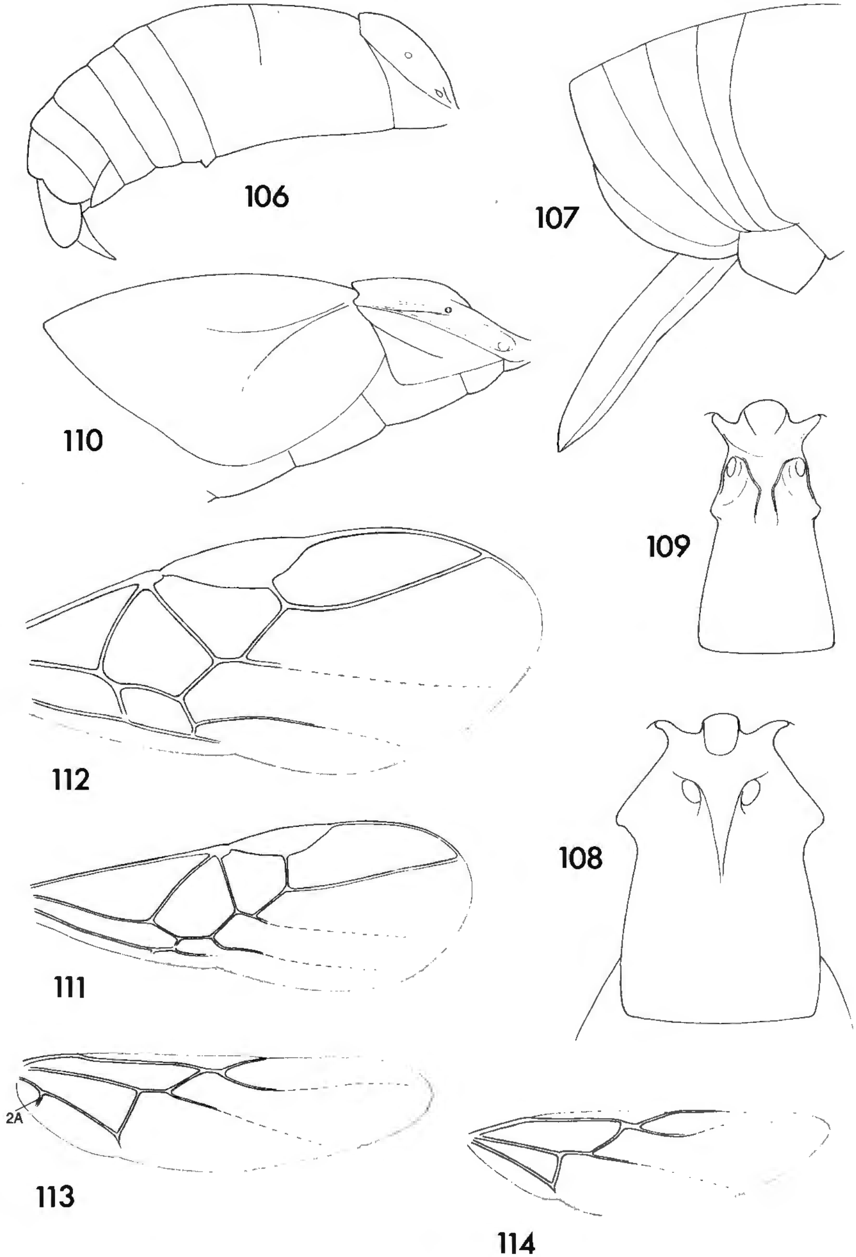

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Accounts of British subfamilies

Subfamily Adeliinae
(=Acaeliinae auctt.)

This is a small subfamily, with only about 20 described species worldwide. The sole European genus is *Adelius*, which has been widely known as *Acaelius* or *Acoelius* as a result of various confusions finally laid to rest by Mason (1985). Four species are recorded from Britain, though the genus has received little taxonomic study and it is probable that several more await recognition. They are either wholly black or partly reddish, and all are small and rather squat. They have a characteristic wing venation that could be confused only with that of Miracinae (cf. figs 51, 52), and the wings are partly infumate in the female sex. Although traditionally included in Microgastrinae (e.g. Nixon, 1965), with which there is a superficial resemblance, Adeliinae was given subfamily rank by van Achterberg (1976d) and was subsequently considered to be only distantly related to Microgastrinae (van Achterberg, 1984b).

In Britain, *Adelius* species are solitary koinobiont endoparasitoids of the larvae of Nepticulidae (Lepidoptera), destroying the host only after it has left its mine and formed a cocoon, from which the adult parasitoid emerges through a roughly circular hole chewed some way short of the apex. Nepticulid larvae in search of pupation sites penetrate a large variety of structures, including other leaf-mines, where they are easily overlooked, and this habit almost certainly accounts for all records in the literature of *Adelius* reared from non-nepticulid hosts, at least in Britain. A slight cocoon is formed within that of the host, in which most species overwinter. However, some species attack the generations of certain nepticulids that mine through the winter (e.g. *Etainia sericopeza* (Zeller)) and these presumably overwinter inside their hosts.

There are no detailed accounts of the biology of any *Adelius* species, but Čapek (1971 and personal communication) has judged that oviposition must be into the egg stage of the host. Various authors (e.g. Nixon, 1965) have noted a similarity of leg and antennal structure between *Adelius* and the subfamily Cheloninae but, if Čapek is correct, this may be simply convergence as a result of oviposition into host eggs. However, although van Achterberg (1984b) proposed a classification in which the two groups are widely separated, more recent studies indicate a close relationship between them (C. van Achterberg, personal communication).

Identification. There is at present no basis for reliable identification (van Achterberg, in prep., European species).

Subfamily Agathidinae

This moderately large subfamily, with at least 800 species worldwide, is relatively poorly represented in temperate areas so that in Britain we have only 24 species in three genera, *Agathis*, *Bassus* (= *Microdus*) and *Earinus*. Various nomenclatural difficulties beset the interpretation of the literature between about 1917 and 1948 (e.g. Muesebeck, 1927; Simmonds, 1947a) in which the subfamily was often called Braconinae, until the reinterpretation of the name *Bracon* by the International Commission on Zoological Nomenclature's Opinion 162 (1945) brought forward the name Agathidinae for this group. The more recent application (Sharkey, 1985) of the name *Bassus* to the genus formerly called *Microdus* may provoke a further change of the subfamily name to Bassinae. The venation of the forewing provides sufficient means to place the known British agathidines, which all have a small second submarginal cell as well as a short, narrow marginal cell (fig. 66). *Agathis*, but not our other two genera, also has a marked downwards elongation of the head and labio-maxillary complex, which is an adaptation for feeding at flowers shared by very few other braconid species in Britain.

Agathidines are solitary koinobiont endoparasitoids of moderately concealed lepidopteran larvae, evidently using their long ovipositors to probe for hosts in their frass-ridden feeding tunnels, mines or retreats. Species of *Agathis* and the closely related *Bassus* have been the subjects of detailed biological study, particularly in North America. They attack the host early in its life, usually in the first or second instar, and the minute egg is placed either inside (Odebiyi & Oatman, 1972, 1977) or attached to (Dondale, 1954; Quednau, 1970) a ganglion of the ventral nerve chain or sometimes one of the lateral lobes of the protocerebrum (Quednau, 1970). This process is accomplished with a single insertion of the ovipositor, and concurrent temporary paralysis has been observed (Flanders & Oatman, 1987). The egg increases in size before hatching and the caudate first-instar larva, which has a discernible tracheal system but no spiracles, floats freely in the haemocoel. It is equipped with 'fighting' mandibles and, after feeding, the larva remains in its first instar during the feeding period of the host, diapausing in this stage if the host diapauses partly grown (Thorpe, 1933; Dondale, 1954; Balduf, 1966; Quednau, 1970).

An unusual feature of first-instar agathidine larvae is that they are polypodeiform (Clausen, 1940; Hagen, 1964), bearing fleshy protuberances on eleven consecutive body segments starting with the second. These 'pseudopods' occur as single pairs on thoracic segments but as double pairs on abdominal ones. They are of uncertain function, perhaps locomotory. Broadly similar structures are seen in some Macrocentrinae and have (rarely) been reported in some Alysiinae; rather different fleshy outgrowths of the larval cuticle are also known to occur commonly in first-instar Opiinae and rarely in final-instar Euphorinae.

Odebiyi & Oatman (1972) concluded that there were only three larval instars in the agathidine they studied and considered that previous authors (e.g. Balduf, 1966; Quednau, 1970) had misinterpreted the fed form of the first instar as a second instar. Quednau (1970) noted that the cell mass of the trophamnion persists in the host and is apparently fed upon during early larval development, but other authors appear not to have noticed teratocytes as such, so these presumably do not arise. After the host has spun its cocoon, the final-instar parasitoid larva emerges from its body and completes its feeding externally (Nickels *et al.*, 1950; Dondale, 1954; Odebiyi & Oatman, 1972, 1977). The biology of a species of the non-British genus *Vipio* (= *Cremnops*) has also been described (Simmonds, 1947a, as *Bracon*), and differs principally in that the egg is deposited into the haemolymph and the host is successfully attacked in all instars. The development of *Earinus* remains unknown. Most British *Agathis* and *Bassus* species probably overwinter as first-instar larvae in their larval hosts, and make only frail cocoons from which they emerge by chewing rather irregular holes. *Earinus* species, on the other hand, overwinter in shining white cocoons that are much stronger, and emerge by cutting a neat, circular cap from the end.

British host records for agathidines (Nixon, 1986) concern lepidopteran larvae that mine or live otherwise constrained in buds or under tight silken runs in their early instars, with Gelechiidae, Coleophoridae and Torticidae being particularly prominent host groups for *Agathis* and *Bassus*, and *Agonopterix* (Oecophoridae) and genera such as *Agrochola* (Noctuidae) providing regularly for our two commonest *Earinus* species. Despite having an overall host range wide enough to embrace at least eight families of Lepidoptera in Britain, agathidines are specialised in ways that preclude large elements of the Lepidoptera from attack – notably caterpillars which, in early instars, live fully exposed or in closed mines – as the discovery of expelled frass seems to be a key stage in the ovipositional behaviour of Agathidinae.

Identification. Nixon (1986), European species.

Subfamily Alysiinae

(Figs 115–117)

This is a large subfamily containing well over 1000 described species worldwide, of which more than 200 in 40 genera have been recorded as British. Most species are rather small, and alysiines are more associated with moist habitats than is usual for braconids generally (Wharton, 1984). The subfamily is easily recognised by its major synapomorphy – the short, broad and outwardly directed 'exodont' mandibles (figs 17, 44, 45). These nearly always have three or more teeth and their tips do not meet, let alone overlap, even when they are closed. Alysiines are divided into two tribes, Alysiini and Dacnusini, which are about equally rich in species although the former has more than twice as many genera worldwide. The tribe Alysiini is probably paraphyletic with respect to the Dacnusini, but there are reasonable grounds for regarding both the tribe Dacnusini and the subfamily Alysiinae as holophyletic groups (Griffiths, 1964; Wharton, 1980). The simplest morphological difference between the two tribes is that Alysiini have three submarginal cells in the forewing while Dacnusini have only two. This is, however, one of the few braconid subfamilies in which apterous or brachypterous forms occur (*Chasmodon*, *Panerema* and *Atopandrium* in Britain). The lack of wings together with the extreme reduction of the thorax in two such genera (*Lodbrokia* and *Pseudopezomachus*, neither recorded from Britain) makes their tribal placement problematical. Griffiths (1964) and Wharton (1980) both summarise the history of the classification of the subfamily.

The two tribes have different emphases to their overall host ranges, but there are too few detailed accounts of the biology of particular species for any meaningful differences in their developmental biology to be discerned. All species are koinobiont endoparasitoids of cyclorrhaphous Diptera, and rearing records from other groups are almost certainly erroneous (Griffiths, 1964; Wharton, 1984). The host is usually attacked as a fairly young larva, though final-instar hosts are preferred by some species (Graham-Smith, 1919) and oviposition into the egg is known in a few species in several genera of Dacnusini (e.g. *Polemochartus* (Mook, 1961), *Coelinidea* and *Symphya* (cf. Clausen, 1954)). Larval hosts are sometimes temporarily paralysed during oviposition (e.g. Graham-Smith, 1919), though there appears to be only one insertion of the ovipositor.

The egg is usually placed at random in the haemocoel, though a tendency to attach it to the inner side of the integument of older hosts has been observed in at least one species (Flanders, 1973). Considerable swelling of the egg before it hatches has been noted by several authors (Haviland, 1922; Evans, 1933; Guppy & Meloche, 1987), and the functional trophamnion in some Dacnusini remains adhering to the first-instar larva until it moults (Haviland, 1922; Wright *et al.*, 1947; Guppy & Meloche, 1987). However, teratocytes as such do not seem to have been recorded and, once sloughed, the trophamnion is apparently degraded during the general histolysis that follows the host's pupation. In all cases the host continues to develop until the puparium stage is reached before being destroyed, typically with the parasitoid larva waiting in its mandibulate first-instar stage until this event, and subsequently completing its feeding rapidly. In rare cases pseudopods on the body segments of first-instar larvae have been reported (cf. Clausen, 1940). Most studies have recognised three larval instars altogether, though more have been described in some cases (e.g. Wright *et al.*, 1947).

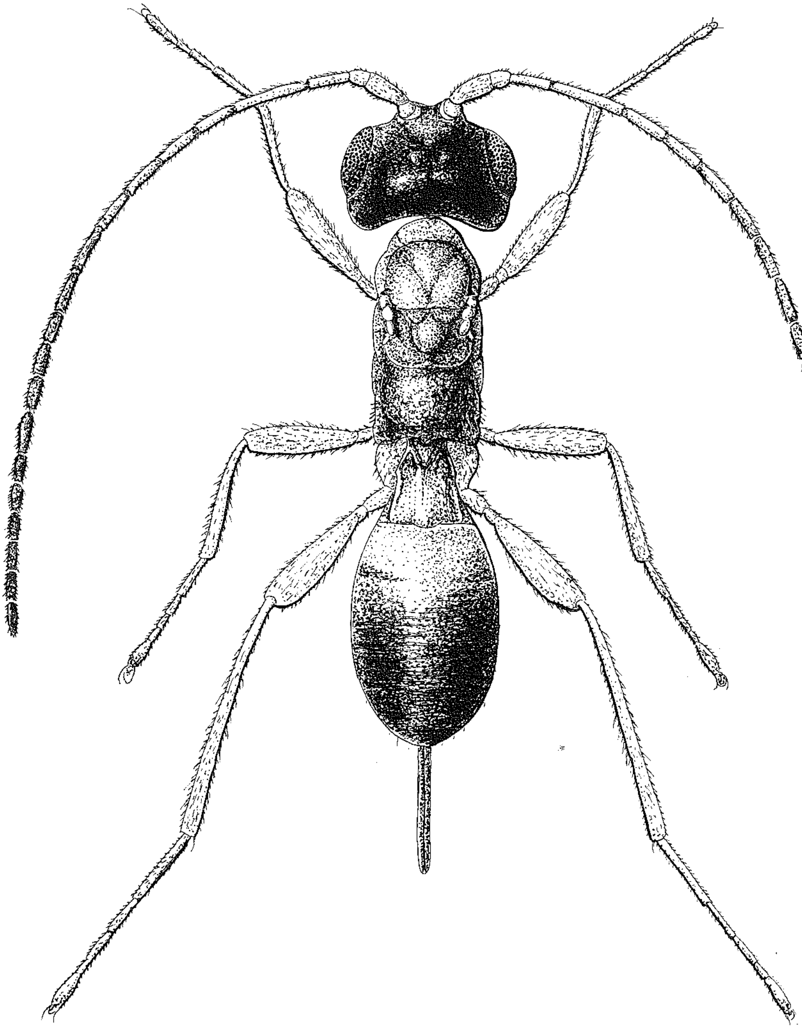

Fig. 115. *Chasmodon apterus* (Nees von Esenbeck), Alysiinae.

Several workers (e.g. Varley & Butler, 1933; other references in Wharton, 1984) have noted the precocious formation of the puparium of parasitised hosts, although its formation can also be delayed (Prince, 1976). Usually the parasitised host puparium is normal to all outward appearances (Griffiths, 1964) but van Achterberg and Bin (1981) recorded parasitised puparia formed without the horns characteristic of their healthy counterparts, and parasitised puparia are sometimes undersized (Wright *et al.*, 1947). The parasitoid pupates within the host puparium, oriented head to head. Cocoon formation, though evidently unusual at least in Dacnusini (Griffiths, 1964), is known in species of both tribes (Wharton, 1984; Guppy & Meloche, 1987). As in Opiinae, the meconium is voided at adult emergence, not at the time of pupation (Salkeld, 1967). For emergence, the specialised exodont mandibles of the adult are used to break the puparium more or less along the preformed fissures that would have yielded to the fly's ptilinum (Griffiths, 1964), though Wharton (1984) points out that the mandibles are involved also in ploughing through whatever substrate overlies the host puparium, and he also cites one species in which the mandibles are regularly used by prospecting females to tunnel towards hosts concealed in fungi. The genus *Aphaereta* contains both solitary and gregarious species, and the latter chew more randomly placed emergence holes through the host's puparium. Gregariousness has also been seen in a species of *Phaenocarpa* (van Achterberg, in prep.), but otherwise Alysiinae are known only as solitary parasitoids. The winter is normally passed as a mature larva in the host puparium, and some species can remain in diapause for more than one winter.

Wharton (1984) has reviewed the known biology of Alysiini, emphasising that much less information is available for this tribe than for the Dacnusini. Other informative accounts include those of Graham-Smith (1919), Myers (1927), Evans (1933), Chernoguz & Reznik (1987) and, for various aspects and consequences of host searching behaviour, an important series of papers by Vet and co-workers (1984–1985). In all, about twenty families of cyclorrhaphous Diptera are recorded as regular hosts, but most species of Alysiini attack those living in ephemeral and odoriferous substrates such as dung, carrion, fungi and rotting or fermenting vegetable material, and in some cases the adults exhibit profound morphological specialisation for exploring these substrates. Only relatively few genera (e.g. *Phaenocarpa, Dapsilarthra, Adelurola, Chasmodon, Alysia*) include species associated with phytophagous Diptera (mostly leaf-miners), these hosts being particularly exploited by Dacnusini instead. There are a few strong associations at the generic level with particular host taxa – for example, most *Dinotrema* species attack Phoridae – and host ranges of individual species are apparently usually narrow (Wharton 1984). Notable exceptions are some of the gregarious *Aphaereta* species: *A. pallipes* (Say), for example, is known from hosts in eight families found in a wide range of situations in North America (Wharton, 1984), and has recently been reared in Britain (M. R. Shaw, 1983a). It is known that the eggs of another gregarious species, *A. minuta* (Nees), hatch relatively late despite being laid into very small hosts (Evans, 1933), and the relationship between late hatching, host size at oviposition, gregariousness, and extent of host range in Alysiini would make an interesting study.

Occasionally the Diptera (e.g. some Phoridae and Sarcophagidae) parasitised by Alysiini may themselves be acting as parasitoids but, as explained in the introductory section on general biology, it is not especially helpful to regard Alysiini as true hyperparasitoids in these cases because their arrival is probably usually subsequent to the death of the first host and their orientation remains to the scene of decay, rather than to the life-history of the original host. A further illustration of the original preoccupation of Alysiini with organic decay (notwithstanding limited radiation to some endophytic host groups such as leaf-miners) may be their failure to exploit as hosts the predatory Syrphidae which, though unusually accessible to parasitoids

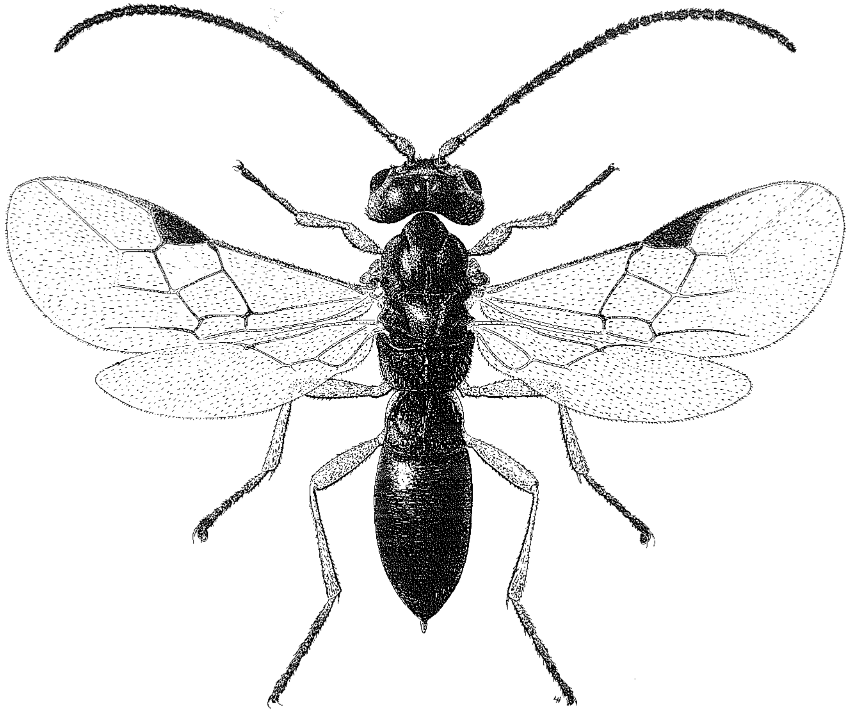

Fig. 116. *Alysia manducator* (Panzer), Alysiinae.

generally (cf. Shaw & Askew, 1979), may be simply too clean-living or mobile to have been adopted.

In contrast with Alysiini, Dacnusini have a rather narrowly defined host range centred upon the cyclorrhaphous Diptera that feed in the tissues of growing angiosperms (Griffiths, 1964). The vast majority of species (especially of *Exotela*, *Dacnusa* and most *Chorebus*) are specialist parasitoids of Agromyzidae, but some groups have well-defined associations with Ephydridae (*Chaenusa* and some *Chorebus* species parasitise *Hydrellia*) and Chloropidae (some of which are parasitised by species of *Coelinius*, *Coelinidea* and *Polemochartus*). A very few other stem-boring or leaf-mining Diptera in the families Drosophilidae, Psilidae and Cordyluridae are also exploited by host-specific Dacnusini. Griffiths (1964–1968, 1984), in his exceptionally comprehensive analysis of the western European Alysiinae associated with Agromyzidae, all of which are Dacnusini except for part of the genus *Dapsilarthra*, showed that most Dacnusini have extremely narrow host ranges but that there are also a few species that attack a wide range of agromyzids. In many cases, however, species limits in the Dacnusini are difficult to define, being complicated by host-correlated morphological variation (e.g. Godfray, 1984) and experimental approaches are needed to elucidate the extent to which speciation may have occurred. The classification of Dacnusini proposed by Griffiths relates their phylogeny very closely to that of their hosts but his views remain untested outside the western European fauna, as no other workers have researched the species of other faunistic areas in such depth.

Identification. Fischer (1971a) provides both a generic key and keys to species that cover much of the European fauna of Alysiini, but Wharton's (1980) key to and diagnoses of the North American genera will probably work better for all but the *Aspilota* group of genera (for which see van Achterberg, 1988a) and the few British species in the excluded genera *Atopandrium*, *Chasmodon*, *Idiolexis* and *Trachyusa*. In addition to Fischer's (1971a) work, keys that cover European species are available for parts of all of the following genera of Alysiini: *Alysia* (Fischer, 1967; Wharton, 1986, 1988a); *Tanycarpa* (van Achterberg, 1976a); *Dapsilarthra*, including *Mesocrina* (= *Pesudomesocrina*), and *Adelurola* (van Achterberg, 1983b); *Orthostigma* (Königsmann, 1969; van Achterberg & Ortega, 1983); *Aspilota* auctt. (Fischer, 1972a; Munk, in prep.; see also Wharton, 1985; and van Achterberg (1988a) has redefined the *Aspilota*-group of genera and provides partial keys to species occurring in Britain under the generic names *Aspilota*, *Dinotrema*, *Leptotrema* and *Pterusa*); *Aphaereta* (Fischer, 1966, 1967); *Synaldis* auctt. (Fischer, 1962, 1967); *Phaenocarpa* (Papp, 1968; Fischer, 1970, 1990); *Idiasta* (Königsmann, 1960; see also van Achterberg, 1974); *Anisocyrtra* (van Achterberg, 1986); *Trachyusa* (van Achterberg & O'Connor, 1990). Van Achterberg (1975) gives a key to genera of the apterous and brachypterous Alysiinae and to species of *Chasmodon*. In addition, Wharton's (1977) account of certain characters and terminology is of general value in the study of Alysiini. Nixon (1943–1954) and Griffiths (1964–1968, 1984) both give species-level revisions of British Dacnusini, and include keys to genera. Nixon's pioneering classification and nomenclature was substantially eclipsed by Griffiths's work, as was part of his species-level taxonomy. Although Nixon's keys may be found easier to use as a first step towards identification, for specimens reared from known hosts Griffiths's approach certainly offers the more reliable means and the better basis for further investigation. Other keys cover the British species in the following genera of Dacnusini: *Polemochartus* (Maetô, 1983); *Symphya* (Zaykov, 1982); and *Coloneura* (van Achterberg, 1976a). Godfray (1984) gives an account of intraspecific variation in relation to host species in *Exotela cyclogaster* Foerster.

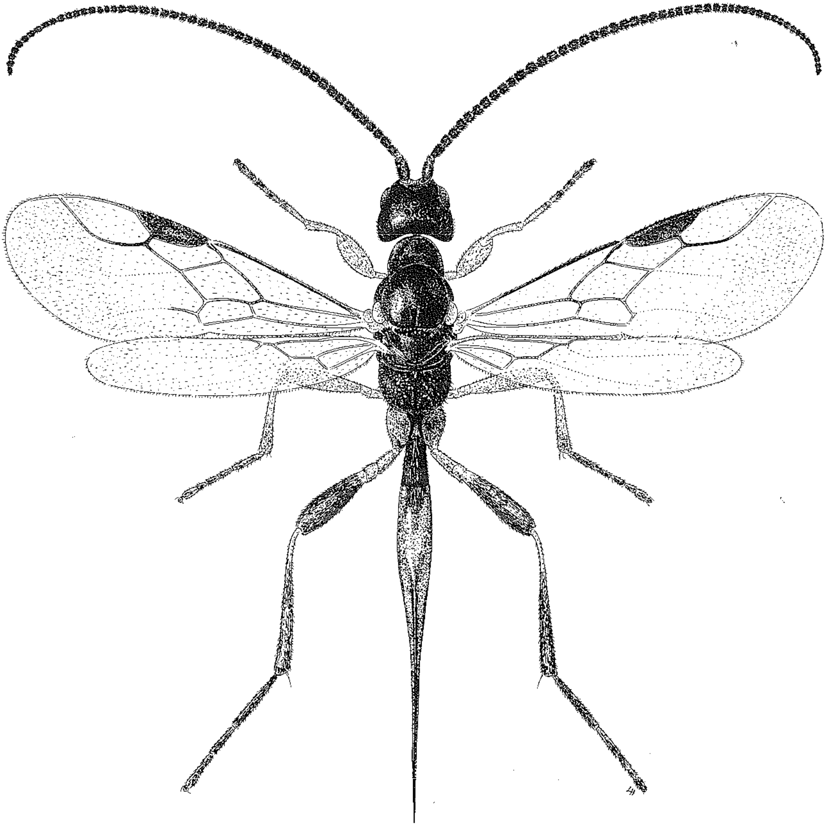

Fig. 117. *Coelinius anceps* (Curtis), Alysiinae.

Subfamily Aphidiinae

This medium-sized subfamily contains about 300 described species concentrated, like their host group, mainly in northern temperate regions. Almost 70 species in 16 genera have been recorded as British. All species attack aphids and the host range of the subfamily is thus distinct from that of any other ichneumonoid group. This fact and the presence of a flexible suture between the second and third tergites of the gaster, which is unique among braconids, has encouraged several workers to accord the group full family status, distinct from the Braconidae. Although widely acknowledged as arbitrary, this viewpoint has been adopted by the majority of specialists on the Aphidiinae during the past twenty years, and it was followed in the most recent British checklist (Huddleston, 1978). However, van Achterberg (1984b) has shown that it is without phylogenetic justification and he firmly concluded that Aphidiinae should be placed as a subfamily within the Braconidae. The hypothesis (Mackauer, 1968) that Aphidiinae may be closely related to Euphorinae did not gain general acceptance and was not upheld by van Achterberg (1984b). Some uncertainties in the suprageneric classification of aphidiines were outlined by O'Donnell (1989).

Aphidiines are small and weakly sclerotised insects, often having more or less profoundly reduced forewing venation (see figs 63–65) although in some genera (e.g. *Ephedrus*, fig. 62) the venation remains essentially complete. Tremblay (1978, 1981) discussed some evolutionary trends within the subfamily. All species are solitary koinobiont parasitoids of ovoviviparous aphids (Aphididae, sensu lato): the fully oviparous groups of Aphidoidea (Adelgidae and Phylloxeridae) are not known to be attacked. Aphids living exposed on plant surfaces are parasitised by the widest range of aphidiines, but a few genera specialise on concealed hosts: *Paralipsis*, for instance, attacks root aphids. At the species level, host ranges are often restricted to one or a few related aphid species or genera, but a few aphidiines attack a much wider range of aphids within more or less narrow habitat constraints (Mackauer & Starý, 1967; Starý & Rejmânek, 1981) and separate populations of a single species may be merely conditioned to narrow host preferences (Pungerl, 1984). Several species have been manipulated successfully in biological control programmes, especially in North America (Hagen & van den Bosch, 1968; Clausen, 1978) and the potential importance of aphidiines in the population dynamics of agricultural pests has led to their being comparatively well studied biologically (see Starý (1970) for a comprehensive review of the biology of Aphidiinae, and Starý (1987) for a guide to the literature arranged under subject fields). Various physiological and developmental abnormalities are exhibited by aphids parasitised by Aphidiinae (Spencer, 1926; Johnson, 1959, 1965), and their behaviour may also differ markedly from that of unparasitised individuals (Powell, 1980; McAllister & Roitberg, 1987, 1988; Brodeur & McNeil, 1989).

All stages of the host except the egg are usually susceptible to attack, but perhaps the majority of aphidiines oviposit most readily into middle nymphal instars. To oviposit, the female parasitoid curls her abdomen under her thorax, its apex projecting forwards under her head. This posture is also adopted by many Euphorinae and Meteorinae, but aphidiines have particularly flexible and telescopically extendible gasters. In some species of *Praon* the adult parasitoid pins the host to the substrate with its legs before ovipositing (Beirne, 1942a; Schlinger & Hall, 1960), and in *Trioxys*, which usually attacks hosts in very early instars (but see Singh & Srivastava, 1987), there is a pronged grasping structure at the apex of the gaster to restrain host movement (Schlinger & Hall, 1961). Oviposition is usually a simple jabbing process, rapidly accomplished and into a random site, but a species of *Monoctonus* is known to deposit its egg only among the host's massed thoracico-abdominal ganglia after a more precise and protracted insertion of the ovipositor through a ventral thoracic suture (Griffiths, 1960, 1961).

Aphidiine eggs swell considerably as embryonic development takes place and, when they hatch, the trophamnion persists for a while around the caudate first-instar larva before dissociating to liberate teratocytes into the aphid's haemolymph. These swell greatly by absorbing nutrients and are then eaten by the parasitoid larva, constituting practically its only nourishment before its final instar. The 'feeding' of the teratocytes no doubt contributes to the rapid degeneration of the aphid embryos that are developing within the host, but this starts so soon after parasitisation that it is presumably more than simply a question of nutrient diversion: inhibitory secretions, either from the adult female parasitoid or from her egg, seem also to be implicated in disrupting the development of all but very advanced embryos (Polaszek, 1986). In a different aphidiine/aphid system, however, Kring & Kring (1988) have shown that parasitism interferes principally with oogenesis and hardly at all with embryonic development or progeny deposition.

Any supernumary parasitoids, resulting from multiple or occasionally (in *Trioxys*: Schlinger & Hall, 1961) single attacks, are quickly destroyed by the best established larva, usually also apparently by physiological suppression (Spencer, 1926; Johnson, 1959; Schlinger & Hall, 1961). Hågvar (1988) showed that the egg stage can be effective in this competitive process. Although rare, or at any rate hard to observe, physical conflict between first instar larvae, which are variously tailed, adorned with integumentary spines and equipped with powerful mandibles (Beirne, 1942b; O'Donnell, 1989), has occasionally also been inferred (Vevai, 1942; Liu & Carver, 1985). However, O'Donnell (1989), in a comprehensive analysis of the functional morphology of first-instar aphidiines, has suggested that even the mandibles may be primarily used for locomotion.

O'Donnell (1987a,b) provided convincing evidence that there are only three larval instars in aphidiines, although four or even five have usually been reported in the literature (e.g. MacGill, 1923; Beirne, 1942a). The second instar lacks mandibles, feeding largely on teratocytes and also any host embryos and other mobile cellular material that can be sucked into the oesophagus (Schlinger & Hall, 1960). The third instar is the first to have spiracles and is again equipped with mandibles, using them to cut a ventral slit in the host's skin after all its contents have been consumed. Most genera spin a frail cocoon inside their host's skin, which hardens and darkens, attaching this 'mummy' to the substrate by silken threads via the ventral opening. However, the genera *Praon* (Schlinger & Hall, 1960) and *Dyscritulus* (Hincks, 1944) spin cocoons directly onto the substrate leaving the empty skin of the aphid more or less securely fixed on top.

In general, temperate aphidiines pass the winter as final-instar larvae (at least sometimes with retained meconium: Liu & Carver, 1985) in mummies and cocoons that are tougher and darker than those destined to hatch the same summer. Emergence is through a neatly cut circular hole. Many aphidiines are capable of numerous generations in a season, with life cycles as short as 2–3 weeks under good conditions. In common with most other koinobionts they have potentially high fecundities and, in addition, their spread is sometimes enhanced by the dispersal of parasitised alate aphids. As a result of these characteristics aphidiines can become very numerous by late summer by which time, however, they are usually themselves heavily attacked by secondary parasitoids, many of which belong to species or higher taxa completely specialising in attacking mummified aphids (Sullivan, 1987). No other group of Braconidae supports such a specialised hyperparasitoid fauna; testimony, perhaps, to the success of Aphidiinae as a group as well as to the ease with which parasitic wasps can locate aphid colonies through chemoreception (Rotheray, 1981; Bouchard & Cloutier, 1984).

Identification. Starý's (1966) keys to all genera and species found in Czechoslovakia include almost all of the British fauna; Mackauer (1959), European *Areopraon* and

Praon; Starý (1973), European *Aphidius*, but see also Liu & Carver (1982) and Pungerl (1983, 1986) who have reassessed the constancy of several traditional characters; Gärdenfors (1986), Palaearctic *Ephedrus*; van Achterberg (1989), European *Monoctonus* and world *Harkeria*; Powell (1982), species attacking cereal aphids in Britain, with a key to genera based on mummies; O'Donnell (1989), genera or groups of genera based on first-instar larvae; Finlayson (1990), tribes, genera and (some) species based on cephalic structures of final-instar larvae.

Subfamily Blacinae

As presently restricted (van Achterberg, 1988b) this is a relatively small subfamily with about 100 described species worldwide. The great majority, including just over 20 recorded from Britain, belong to the genus *Blacus*. The only other British Blacinae are a species of the allied genus *Blacometeorus* (van Achterberg, 1988b) and *Dyscoletes lancifer* (Haliday), one of only two species in its genus. In the past, *Blacus* and *Dyscoletes* have been united with various other groups, although with little pertinent justification. The status of the subfamily still seems questionable, and the British genera were only provisionally united at subfamily rank by van Achterberg (1984b) pending a better knowledge of their biological characteristics and larvae. All British species are rather small, slender, brown or blackish insects. In most British *Blacus* the ovipositor is shortly exserted, and only in one British species does it extend the full body's length beyond the apex of the gaster, but in *Dyscoletes* it is much longer. The latter genus has a distinctively-shaped second submarginal cell in the forewing (fig. 99) and many *Blacus* species have conspicuous posterolateral protuberances on the propodeum, but none of our genera is easy to recognise from superficial characteristics.

D. lancifer is an endoparasitoid of the larvae of the mecopteran *Boreus hyemalis* (Linnaeus) in which, apparently, it passes the winter (Aubrook, 1939). Other details of its biology remain unknown. *Blacus* species are common as adults in Britain, but remarkably poorly understood biologically. From Čapek's (1983) review of the published rearing records, many of which stem from isolated rearings along with numerous other insects under poorly controlled conditions, it can be concluded that species of *Blacus* are probably solitary koinobiont endoparasitoids of coleopteran larvae; the few records from Diptera and other insect orders are almost certainly erroneous. *Blacus* species are common in damp habitats such as woods and fens and, as they seem usually to have been reared from decaying vegetable substrates, small and mobile (perhaps predatory or fungivorous) beetle larvae may prove to be central to their host range. However, some species are recorded as parasitoids of phytophagous beetle larvae (Haeselbarth, 1973). At least one species is believed to overwinter as an adult (Marshall, 1889; Hancock, 1925; König, 1967) and some are nocturnal (Haeselbarth, 1973). Several regularly form evening swarms, composed largely of males, which females presumably approach or enter in order to mate (Southwood, 1957; König, 1967; van Achterberg, 1977).

Identification. Van Achterberg (1988b), world Blacinae; Haeselbarth (1973), European *Blacus*; Mason (1976), world *Dyscoletes*.

Subfamily Braconinae
(Fig. 118)

This is a large subfamily with well over 2000 described species worldwide. Its greatest success and diversity is seen in Old World tropical and subtropical regions (Quicke, 1987b), where many species are among the largest braconids and are brightly coloured. Over 50 species have been recorded as British, but almost all are rather small, blackish or partly orange insects belonging to the genus *Bracon* (the present account does not distinguish *Habrobracon* and *Pigeria* from *Bracon*, but as both have been accorded full generic status in recent works (respectively by Quicke, 1987b and van Achterberg, 1985a) we have included them as genera in the checklist). The genus *Coeloides*, distinctive by its modified antennal segments 3 and 4, contains a small number of moderately common parasitoids of bark beetles in Britain. Each of the remaining five genera long recorded as British (Kloet & Hinks, 1945; Huddleston, 1978) contains only a single supposedly British species, and it is considered extremely doubtful whether any except for *Baryproctus*, which may be extinct, has ever really occurred here (D. L. J. Quicke, personal communication). Indeed, we now omit *Cyanopterus* from the checklist on the strength of Morley's (1909a) retraction of his earlier record and his other remarks.

Various tribes currently placed in Rogadinae have been included in Braconinae in the past and, indeed, the relatively plesiomorphic subfamilies Braconinae, Rogadinae, Doryctinae and Histeromerinae remain difficult to disentangle satisfactorily. However, the British Braconinae are quite easily separated from these other groups that have a similarly strongly emarginate clypeus – the feature, properly called the hypoclypeal depression, that gives them all their characteristic 'open mouth' (=cyclostome) appearance (cf. fig. 27). Some of the Opiinae (q.v.) that most nearly exhibit this condition can also bear a resemblance to braconines. When they are alive, almost all braconines can readily be recognised by a characteristic 'woody' odour that they emit when handled or disturbed (D. L. J. Quicke, personal communication).

All British Braconinae have clearly exserted ovipositors and develop as ectoparasitoids of concealed hosts, usually concentrating attack on the actively feeding late larval instars. Most appear to be strict idiobionts, injecting venoms that induce long-term paralysis of the host before they oviposit on or near to it. The venoms are generally rather quick-acting (but see Genieys, 1925; Hagstrum & Smittle, 1977) and they have received considerable biochemical and physiological investigation (Beard, 1978; Piek, 1986). However, some species leave the host in a condition in which it can resume activity, becoming quiescent only some days later when, presumably, the venom takes full effect (Munro, 1917; De Leon, 1935). Similar adaptations are seen in some exothecine Rogadinae (M.R. Shaw, 1983b). Some, at least, of the non-British endoparasitic braconine subtribe Aspidobraconina, which emerge as adults from butterfly pupae (van Achterberg, 1984d; Quicke, 1987a, 1989), could possibly be genuine koinobionts as circumstantial evidence often suggests that the hosts had been attacked before pupation, although the morphology of the adults suggests at least an ancestry of adaptation for oviposition through the harder cuticle of pupae (Quicke, 1987a, b).

The smaller braconine genera recorded from Britain are mostly specialised towards fairly narrow host groups, *Coeloides*, *Atanycolus* and *Isomecus* (= *Vipio* auctt.) being associated with beetles (Čapek, 1970), and *Baryproctus* attacking chloropid Diptera (Quicke, 1987b). The host range of *Bracon* is much wider, most commonly involving Coleoptera and Lepidoptera, with Diptera (e.g. Rotheray, 1988) and phytophagous Hymenoptera (e.g. Salt, 1931; Carleton, 1939) also sometimes serving as hosts. The hosts all share a moderate degree of concealment, usually in living plant tissue, and typically include inhabitants of tree bark, stems of annual and biennial plants, galls and seed heads or vessels, but some are case-bearers. Leaf-rollers and endophytic hosts that are only weakly concealed such as leaf-miners, as well as those living fully concealed in hard wood, are much less regularly attacked. Some braconine genera (e.g. *Coeloides*) appear always to be solitary, but species of *Bracon* may be solitary or gregarious. Some *Bracon* species

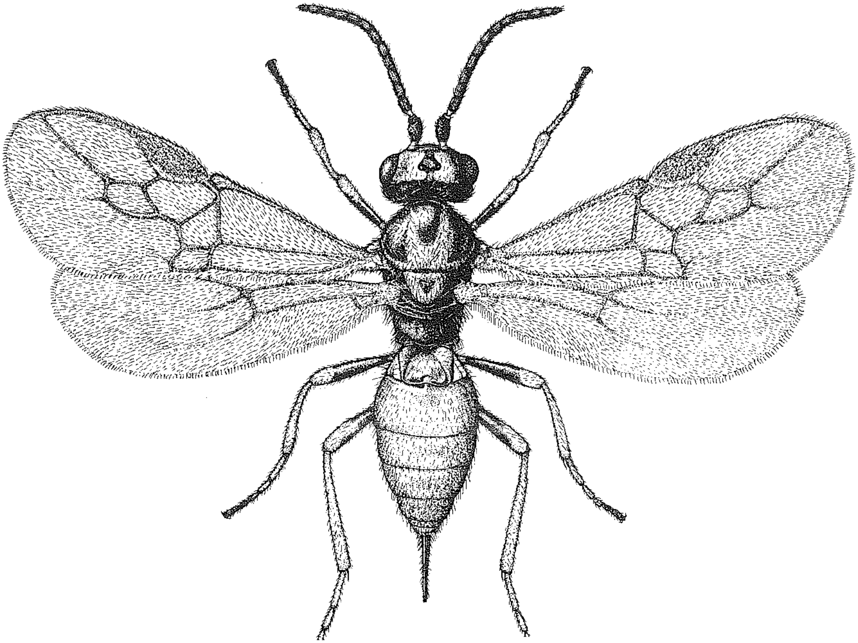

Fig. 118. *Habrobracon hebetor* (Say), Braconinae.

can undoubtedly develop on different hosts at different times of year (Puterka *et al.*, 1986a,b) or sometimes even on hosts of more than one order (Adams *et al.*, 1969; Puterka *et al*, 1986a,b; Kopelke, 1983) within a particular niche. However, most recorded host ranges seem to be quite narrow, as indeed is true for the majority of idiobiont ectoparasitoid braconids in contrast with the broader host ranges characteristic of many comparable ichneumonids. Various kinds of physiological (host suitability) restrictions have been noted in the host ranges of braconines, including nutritional constraints and the specificity of venom action (Genieys, 1925; Beard, 1972; Gerling & Rotary, 1973; Temerak, 1984).

Braconines are synovigenic, and often need several days or possibly even weeks after emergence to mature their relatively large eggs. *Bracon* species have often been found to host-feed as adults but, despite sometimes involving feeding tubes when the host is fully concealed and other complex behavioural interactions (Genieys, 1925; Glover & Chatterjee, 1936; Hagstrum & Smittle, 1977, 1978), the habit is not always obligatory (Laing & Caltagirone, 1969) and has not been mentioned in several accounts of the biology of *Coeloides* (De Leon, 1935; Russo, 1938; Ryan, 1962; Ryan & Rudinsky, 1962; Beaver, 1967). Oviposition is usually through the substrate concealing the host although, if this is flimsy, females of *Bracon* sometimes wriggle or bite their way to contact the host itself (Glover & Chatterjee, 1936). Eggs are normally laid on the host's body although the first-instar braconine larva is well adapted to travel short distances to locate its host if necessary: many accounts (though not all: De Leon, 1934; Sudheendrakumar *et al.*, 1982) draw attention to a spiny integument, prominent antennae and high activity. Sometimes, however, the egg shell is not completely cast before the larva starts to feed (Glover, 1934; Laing & Caltagirone, 1969).

Fighting between supernumary larvae is known in some solitary braconines (e.g. Adams *et al.*, 1969) but the mandibles of the first-instar larvae are not particularly well developed for this purpose and in several species gregariousness seems to be facultative. Most authors have recorded five larval instars for both *Coeloides* (e.g. Ryan, 1962; Beaver, 1967) and *Bracon* (e.g. Munro, 1917; Glover, 1934; Nelson & Farstad, 1953; Laing & Caltagirone, 1969). Although Munro (1917) detected a tracheal system open to spiracles only in the last two instars, it seems likely that these features are always present in all instars (Genieys, 1925; Glover, 1934; Nelson & Farstad, 1953; Bennett, 1960; Ryan, 1962). All instars have toothed mandibles, adapted for biting through the cuticle and scraping at the tissues of the host. The winter is generally passed as a cocooned final-instar larva, though at least one British species possibly overwinters as an adult (Hancock, 1925). The adults chew irregularly circular subapical holes to emerge from their cocoons, which are formed in situ beside the host remains. In some bivoltine *Bracon* species the overwintering cocoon is markedly more robust than that of the summer generation (Somsen & Luginbill, 1956; Adams *et al.*, 1969), but this may not be true of *Coeloides* species (Beaver, 1967) which make their cocoons more deeply concealed under bark.

Several braconines attack economically important hosts: for example, *Coeloides* and some *Bracon* species parasitise forestry pests, and there are other *Bracon* species that attack stored products pests such as flour moths. In warm temperate climates some *Bracon* species regularly parasitise weevil grubs and caterpillars damaging field crops like cotton and maize, including in a few cases more or less exposed noctuid larvae. Consequently several *Coeloides* and *Bracon* species have been quite well studied, and some interesting behaviour patterns are recorded. Both Ullyett (1945) and Laing & Caltagirone (1969) noted a tendency for *Bracon* species to paralyse all available hosts before returning to them to host-feed and oviposit (see also Hagstrum & Smittle, 1977, 1978), and Gerling (1971) found that oviposition on moribund hosts that had produced haemolymph-feeding parasitoids (*Microplitis*) occurred readily. Richerson & Borden (1972) and Richerson *et al.* (1972) produced evidence that detection of the infra-red radiation resulting from the metabolism of beetle larvae concealed beneath bark may help *Coeloides* species to find hosts. Ryan & Rudinsky (1962) provided a sequential photographic record of *Coeloides* probing for hosts and also reported, as did Beaver (1967), that there is a tendency in these solitary species for the larger host individuals to be preferred for female progeny. The mating strategy of a species of *Coeloides* is described by Dix & Franklin (1983). The ease with which certain *Bracon* (and especially *Habrobracon*) species can be maintained in laboratory culture has led to their being widely used for genetic research (see, for example, references under A.R. Whiting and P. Whiting in Shenefelt, 1965; and Martin, 1947) and, in this context, one species (of *Habrobracon*) has even been sent into space (cf. Matthews, 1974).

Identification. Quicke (1987b) keys Old World genera and presents the modern classification (see also Quicke, 1988). Most of the British genera can be recognised more simply from Mason (1978), Tobias (1971) or Quicke & Sharkey, (1989) but van Achterberg's (1985a) diagnosis of *Pigeria* should be consulted in conjunction with the first two of these. Haeselbarth (1967), Palaearctic *Coeloides*. There is no reliable key to the *Bracon* species found in Britain but Beyarslan & Fischer (1990) give a key to subgenera (their key to *Glabrobracon* species may be too simplified to be easy to use reliably).

(Subfamily Cardiochilinae)

Cardiochiles saltator (Fabricius), now classified in the subfamily Cardiochilinae (van Achterberg, 1984b), appears on the most recent British checklist (Huddleston, 1978) as a result of having been listed as British by Shenefelt (1973a). However, as there is no evidence that it has ever occurred in Britain it should be deleted, and we have excluded Cardiochilinae from the key as well as the checklist. Cardiochilines are solitary koinobiont endoparasitoids of lepidopteran larvae, particularly Pyralidae and Noctuidae feeding in compact sites such as buds. Further information about the biology and recognition of the subfamily can be sought through Huddleston & Walker (1988).

Subfamily Cenocoeliinae

This rather small subfamily (van Achterberg, 1984b) contains perhaps 70 described species in six genera worldwide, mainly subtropical and tropical in distribution and best represented in the New World. Although two species of Cenocoeliinae have been recorded as British (Huddleston, 1978) there is no good evidence that any species other than *Cenocoelius analis* (Nees von Esenbeck) has been found here, and even this has very rarely been collected. The subfamily is immediately recognisable within the Braconidae on account of the uniquely high insertion of the gaster on the propodeum (fig. 58), a feature otherwise shared with Evanioidea. Rohwer (1914) cited evidence that cenocoeliines are koinobiont endoparasitoids of wood or bark boring beetle larvae, killing the host only after it has prepared for pupation and completing their feeding externally. A cocoon is then spun within the host's pupation cell or gallery, and the adult emerges from its cocoon through an irregularly chewed hole (Čapek, 1970). As far as is known cenocoeliines are solitary parasitoids. Saffer (1982) remarked that in North America one species can overwinter either in its cocoon or in its host, and she described a rather broader host range for the group spanning several families of phytophagous beetles (Cerambycidae, Buprestidae, Scolytidae and Curculionidae), involving species that live in fruit and the stems of herbaceous plants as well as wood and bark. Saffer also briefly discussed the recorded host range of the one indisputably British species (see also Čapek *et al.*, 1982).

Identification. Marshall (1889) gives a description of the British species and Hellén (1958) distinguishes this from another N.W. European species.

Subfamily Cheloninae

(Fig. 119)

This is a fairly large subfamily with more than 700 described species worldwide. About 40 species in three genera have been recorded as British. Chelonines are rather robust and heavily sculptured insects. Although frequently having some pale markings, *Chelonus* and *Ascogaster* are predominantly blackish, while *Phanerotoma*, of which there are relatively few rather scarce species in Britain, is largely yellowish-brown. Chelonines are easily distinguished from other braconids by their possession of a gastral carapace (figs 55–57), formed by the fusion of the first three tergites, together with a complete postpectal carina (fig. 53) and three submarginal cells in the forewing (fig. 54). In *Phanerotoma* the carapace (figs 55, 56) bears two crenulate transverse furrows, marking the boundaries between the first three tergites, but there is no articulation at these junctions and in *Chelonus* (fig. 57) and *Ascogaster* even the furrows are completely absent (except in occasional aberrant specimens). A more or less developed gastral carapace is present in several genera in other subfamilies, e.g. *Symphya* (Alysiinae), having exodont mandibles; *Triaspis* and *Schizoprymnus* (Helconinae), with no postpectal carina and only two submarginal cells; and *Acampsis* (Sigalphinae), in which there is an articulation between the first two tergites and the carapace has a characteristic shape (figs 77, 78).

All chelonines are solitary egg-larval endoparasitoids of Lepidoptera, ovipositing into the host egg but not killing the host until the end of its larval life, after it has prepared a pupation retreat. Like most egg-larval koinobionts, chelonines mainly exploit host groups that have concealed larvae. In Britain, they are associated almost entirely with ditrysian ‘microlepidoptera’ – though the most primitive groups, and those in which body size is small, are the least attacked. Elsewhere in the world a few *Chelonus* species are important and well-studied parasitoids of certain ‘macrolepidoptera’, such as the noctuid genera *Heliothis* (Marsh, 1978) and *Spodoptera* (Ingram, 1981; Soteres *et al.*, 1984), and even in Britain one or two species of *Ascogaster* have occasionally been reared from geometrids. *Ascogaster* is, however, largely restricted to attacking tortricoids or tortricoid-like hosts (Evenhuis, 1969; S.R. Shaw, 1983; Huddleston, 1984; Jones, 1985). While *Chelonus* has a very much more diffuse overall host range than *Ascogaster*, the British species of *Phanerotoma* seem to be narrowly specialised to small groups of Pyralidae, Gelechiidae and Tortricidae (van Achterberg, 1990a; see also Jones, 1985).

Because chelonines are associated with several economically important groups of Lepidoptera, quite a lot has been published on their biology. The relatively minor developmental variation that exists between species does not usually correspond to clear differences between genera. Many, though certainly not all (e.g. Pierce & Holloway, 1912; Evenhuis, 1969) of their hosts lay batches of eggs, and chelonine fecundity is generally high with a potentially rapid oviposition output (Vance, 1932a; Rechav, 1978; Kainoh & Tamaki, 1982). Host-feeding does not usually occur, though it is reported in at least one case (Clausen, 1940). Host-derived kairomones, from scales shed while depositing eggs, from adult excrement, and from the reproductive organs of the female moth, are important for host location (Vinson, 1975a; Kainoh *et al.*, 1982; Chiri & Legner, 1986). However, the responses to such

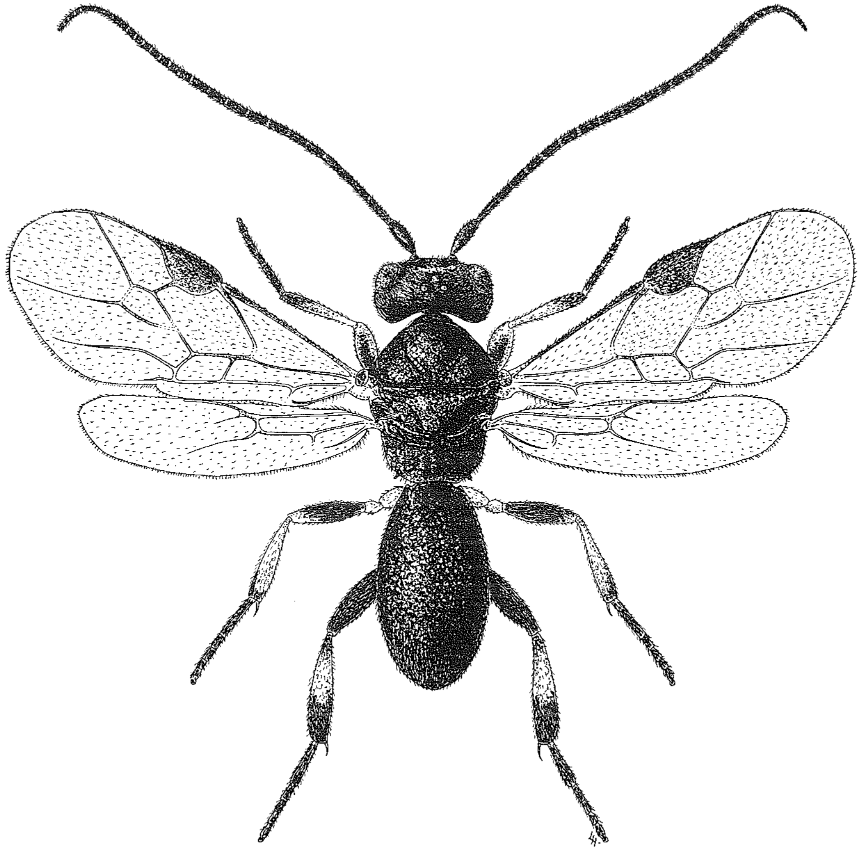

Fig. 119. *Chelonus gravenhorstii* (Nees von Esenbeck), Cheloninae.

kairomones may be rather non-specific (Chiri & Legner, 1986), perhaps commensurate with the potential for a relatively wide host range (e.g. Broodryk, 1969a) due to oviposition into the physiologically poorly defended egg stage. Several authors (e.g. Ullyett, 1949; Kawakami & Kainoh, 1985) have found that superparasitism tends to be avoided.

Some accounts suggest that host eggs can be attacked successfully only at rather precise developmental stages (e.g. early: Rosenberg, 1934; late: Ullyett, 1949) but other workers, sometimes studying the same species (e.g. Boyce, 1936), have found that eggs are usually at least moderately susceptible through most of their development, although as they approach maturity their suitability usually declines (Kainoh & Tamaki, 1982; Powers & Oatman, 1984; D. Jones, 1987; but see Ullyett, 1949; Paul *et al.*, 1980). In species of all three of the genera found in Britain the precise oviposition site depends on the stage of development reached by the host egg at the time (Wishart & van Steenburg, 1934; Boyce, 1936; Hawlitzky, 1979). In older eggs, in which rotation of the embryo has already occurred, oviposition is straight into the haemolymph of the developing embryo. The chance of successful parasitisation then usually seems to correspond roughly to how much time before host eclosion the parasitoid has to hatch and establish itself, although Ullyett (1949) considered that the host was first to hatch under his culture conditions and both Kawakami & Kainoh (1986) and D. Jones (1987) found that most unsuccessful parasitoids were not killed until the host had reached its second larval instar. In fresh eggs, on the other hand, the parasitoid egg is placed into the yolk (Wishart & van Steenburg, 1934) or just under the chorion, in which case the first-instar larva penetrates the yolk after hatching (Rechav & Orion, 1975). However it has arrived there, in most cases studied the parasitoid larva (or possibly egg: Hawlitzky, 1979) is able to pass from the yolk into the developing host embryo only up to the time that the dorsal closure of the latter occurs, and any larvae that fail to do so are lost. However, Narayanan *et al.* (1961) explicitly state that in their study the first-instar parasitoid larva remained external to the host embryo until the latter was mature, boring into it just before it hatched.

Expansion of the parasitoid egg before it hatches has been observed (Narayanan *et al.*, 1961; Rechav & Orion, 1975), and the serosal cells that at first still partly surround the newly hatched larva (Vance, 1932a) persist to become teratocytes (Bühler *et al.*, 1985). Most authors have recognised only three larval instars, and development is similar in the three British genera (e.g. Bennett, 1960; Powers & Oatman, 1984; Kawakami, 1985). First-instar chelonine larvae have large heads and sclerotised mandibles, with which they eliminate competitors (see Kawakami & Kainoh, 1985 for photographs); they are at first caudate but, as they develop and grow, they become vesiculate. The parasitoid remains in its first instar virtually throughout the feeding period of the host, overwintering thus if the host larva overwinters, although it undergoes appreciable development and growth.

As the host ceases feeding and starts to prepare for pupation the parasitoid moults to its second instar, by which time it has a clearly developed, though still closed, tracheal system and mandibles greatly reduced in size (possibly even absent: Cox, 1932; but see Boyce, 1936). Moulting to the third-instar takes place very soon, by which time the host is a cocooned prepupa. The anal vesicle tends to hold up the exuviae of earlier instars. The third-instar larva, which has large, serrate mandibles and open spiracles, then orientates head to head within the host, almost completely emerges from it, and feeds externally until only the host's cuticle remains (see Broodryk, 1969a for a photographic record of this process). The parasitoid then spins its satiny white cocoon within that of the host. Species that do not overwinter as first-instar larvae do so as cocooned prepupae. The adult emerges through an irregular, subapical chewed hole.

Hosts parasitised by Cheloninae exhibit some interesting developmental abnormalities, apparently suffering endocrine disruption (D. Jones, 1985, 1987). Several studies involving noctuid and other moderately large hosts of *Chelonus* (Bradley & Arbuthnot, 1938; Rechav & Orion, 1975; Ingram, 1981: and see references in Jones, 1985) have revealed that parasitised caterpillars spin their cocoons precociously – that is, one or more instars before healthy individuals would do so. In other studies, involving smaller microlepidopteran hosts of *Chelonus*, *Phanerotoma* and probably also *Ascogaster* (Rosenberg, 1934; Boyce, 1936; Bennett, 1960; Hawlitzky, 1979; Powers & Oatman, 1984), the full number of host larval instars have been recorded, although there is a progressive loss of host size increment (reflected as head capsule width) in successive instars: in certain cases, this stunting may happen to one of the hosts of a given chelonine much more than to another (Cox, 1932). It has also been found that if a host is attacked by a chelonine but for some reason no parasitoid develops, then it will attain the prepupal stage but still exhibit the stunting expected of a parasitised individual and subsequently die in an arrested stage of development. Although it is not entirely clear why this happens (Bühler *et al.*, 1985; D. Jones, 1987), the effects are manifested even if the parasitoid egg dies (Ferran & Daumal, 1973) and, indeed, the causative factor has been traced to material injected after the bulk of the venom but before the egg (Leluk & Jones, 1989). A factor in the venom is also known to cause castration of the host, but only if it is introduced early in the process of embryogenesis (Reed-Larsen & Brown, 1990). Chelonines have 'virus-like particles' (i.e. polydnaviruses) in their venom (Stoltz & Vinson, 1979), but it is not yet clear whether, or how, these relate to the various distortions of normal host development outlined above.

It seems probable that control over host development has been instrumental in allowing some chelonines, ancestrally associated with relatively small 'microlepidoptera', to switch to co-occurring host groups of a physically larger size. They have done this without themselves becoming appreciably larger, or becoming gregarious: remaining solitary sustains the aggressive behaviour by the first-instar larva that gives egg-larval parasitoids such a strong advantage in interspecific competitions. It may be critical, however, that the parasitoid should not be too small in relation to the host, or else partly consumed host remains would be left to putrefy and threaten the health of the parasitoid cocoon, which is always spun alongside them. The *Chelonus* species that attack relatively large hosts, such as noctuids, induce them to spin cocoons precociously, resulting in such a dramatically undersized prepupa that it can be consumed entirely. Delayed-action venoms, able both to arrest hosts in a prepupal state and to switch them to this stage precociously, are known also in Rogadinae (M.R. Shaw, 1981, 1983b), although the effects are not exactly analogous in that rather distantly related subfamily.

Identification: Huddleston (1984), Palaearctic *Ascogaster*; van Achterberg (1990a), western Palaearctic genera, and species of Phanerotomini; Huddleston (in prep.), Palaearctic *Chelonus*.

Subfamily Doryctinae

(Fig. 120)

This is a moderately large subfamily with about 1000 described species worldwide, best represented in tropical and subtropical regions, particularly in the New World. In Britain there are only about 20 species in eight genera, but four tribes are represented. Doryctines are generally considered to be the most ancient group of extant Braconidae (Čapek, 1970; van Achterberg, 1984b): as might then be expected, present day doryctines are rather diverse in structure and the definition of the subfamily has always caused problems in the absence of clear synapomorphies

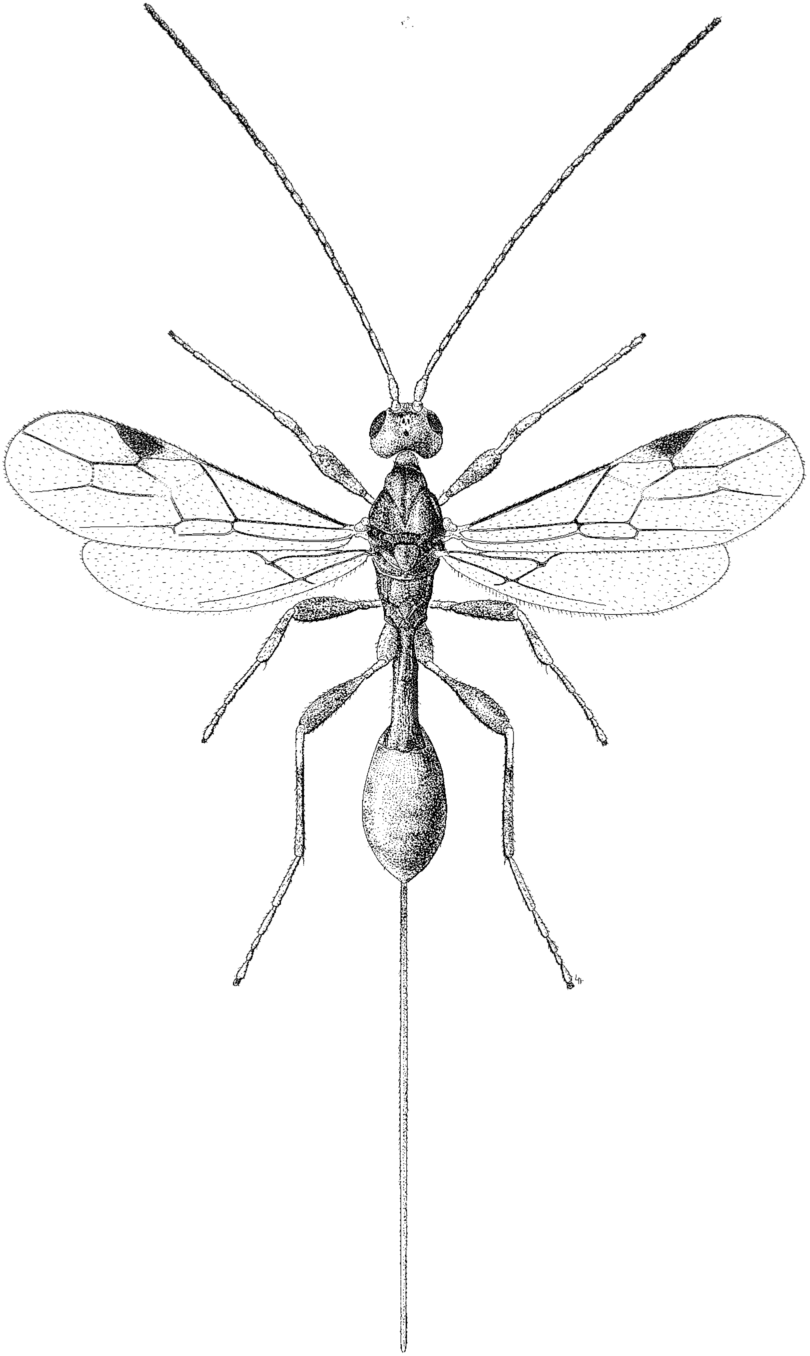

Fig. 120. *Spathius exarator* (Linnaeus), Doryctinae.

(Marsh, 1965, 1970; van Achterberg, 1984b; Shaw & Edgerly, 1985). In Britain they can be distinguished from other cyclostome braconids (see section on Braconinae) by their possession of a row of well-differentiated spines on the fore tibia (fig. 43), although this character is sometimes difficult to see on small specimens and is weakly present in *Coeloides* (Braconinae). In addition, they differ from braconines in having a well-developed occipital carina, and from rogadines in their usually cubic or subconical heads (cf. figs 29, 30).

The four tribes represented in Britain do not closely resemble one another: Doryctini and Spathiini have three submarginal cells in the forewing while Ecphylini and Hecabolini have only two, and Spathiini differ from the rest in having a petiolate gaster with the first tergite narrow for the whole of its length. Species of *Dendrosoter* are rather bizarre in appearance, having pronounced head sculpture and ornamentation and, in males, a thickened wing venation and a pterostigma in the hindwing. Although not regarded as closely related, males of *Hecabolus* also exhibit this last feature. In Britain, females of one species of *Spathius* are apterous, and elsewhere certain species are known to be polymorphic in this respect in one or both sexes (e.g. Ayyar, 1941).

The only known instance of phytophagy in the Braconidae occurs in Doryctinae (Macedo & Monteiro, 1989) and the Neotropical genus *Sericobracon*, remarkable for being an internal parasitoid of paralysed adult Embioptera (Shaw & Edgerly, 1985), was described as a doryctine. Otherwise, the biology of the subfamily is apparently relatively unspecialised. Although detailed biological studies are on the whole lacking, the majority of the genera that occur in Britain are recorded as ectoparasitoids of beetle larvae that live beneath bark or in dead wood (Starý, 1957; Čapek, 1970; Hedqvist, 1976). Less often the wood-inhabiting larvae of other orders have been cited as supposed hosts. Mostly the hosts appear to be attacked as well-grown and actively feeding larvae, though *Ecphylus silesiacus* (Ratzeburg) also parasitises early instars; a habit that undoubtedly contributes to the exceptional variability of this species (Russo, 1938; Marsh, 1965).

Species of the genera *Dendrosoter* (Hanson, 1937; Russo, 1938; Beaver, 1967; Mendel, 1986), *Ecphylus* (Russo, 1938; Beaver, 1965, 1967; Matthews, 1969), *Spathius* (Russo, 1938; Lyngnes, 1955, 1960) and *Doryctes* (Beaver, 1965, 1967) are best known biologically: solitary parasitism seems to be the rule, although one British species of *Spathius* is certainly gregarious (M.R. Shaw, 1988a) and gregarious development is known also in *Doryctes* (Watanabe, 1961). The adult females use the ovipositor to penetrate the substrate to oviposit on or near the host. In most cases the host is probably stung and paralysed first, but Robert (1961) noted that host activity continued for a while after parasitisation by a species of *Spathius*. The first-instar larvae are spiculate, active and, like later instars, have spiracles and toothed mandibles. Russo (1938) described the first- and final-instar larvae, cocoons and pupae of several species, but there is little published information on the number of larval instars. Larval development is fairly rapid; some species are plurivoltine and in all cases the winter is passed as a final-instar larva in its cocoon, which is spun in situ and from which the adult emerges through an irregularly chewed hole (Russo, 1938; Beaver, 1967). Interesting observations on mating strategies in *Dendrosoter* have been made by Mendel (1986); see also Dix & Franklin (1983), who noted similar behaviour in the braconine genus *Coeloides*.

Some non-British genera of Doryctini have a rather different host spectrum, being gregarious ectoparasitoids of stem-inhabiting hosts. *Heterospilus*, recorded from Britain by Morley (1937, as *Synodus*) in error and accordingly here deleted from the British list, has a particularly wide host range (Marsh, 1982), especially involving larval Coleoptera and Lepidoptera but including also symphytan Hymenoptera (Hill & Smith, 1931). A few tropical genera (*Rhaconotus*: Cherian & Israel, 1941; *Allorhogas*: Melton & Browning, 1986) parasitise a range of pyralid Lepidoptera. In all of these, oviposition is through the plant tissue and eggs are laid in a loose batch, generally near the head end of the host larva. An exotic solitary species, *Heterospilus prosopidis* Viereck, parasitising bruchid larvae in pulses, has been much studied as a laboratory animal (see references in Shenefelt & Marsh, 1976), but published perceptions (Jones, 1982; Wellings *et al.*, 1986; King, 1989) that it is a koinobiont endoparasitoid are without foundation (e.g. Bridwell, 1918). Although all doryctines are idiobionts, some are known to be dependent on the paralysed condition of the host and are unable to develop satisfactorily if it has been killed artificially (Ayyar, 1941; Cherian & Israel, 1941). Apparently, then, realised host ranges at the species level may be limited to potential host species that are not killed outright by the venom, as seems also to be the case with some Braconinae (q.v.).

Identification. Marsh (1965) gives a key to genera that includes all British Doryctinae except *Wachsmannia*; Huddleston & Fergusson (in prep.) give a full treatment of the British fauna.

Subfamily Euphorinae

(Fig. 121)

Here we are following the classification of S.R. Shaw (1985, 1988), which excluded meteorines from Euphorinae, rather than that of van Achterberg (1984b), which included them. This should, however, be recognised as a somewhat arbitrary decision. In this limited sense, Euphorinae is a medium-sized subfamily, including about 375 described species in 35 genera arranged into ten tribes (Shaw, 1985). Over 60 species in 16 genera, representing nine of the tribes, have been recorded from Britain. In the British fauna, euphorines can be recognised by the combination of having two submarginal cells in the forewing (fig. 72) and, usually, a petiolate first gastral tergite (fig. 67). In Centistini, however, the gaster is not petiolate (fig. 108): this tribe can be recognised by the broad and downwardly directed ovipositor with broad sheaths (figs 106, 107) (though in some centistines the ovipositor is very short). In a few other genera (e.g. *Leiophron*) the petiolation of the gaster is rather indistinct (fig. 70), but in these cases the radius (2Rs + 3Rs) is characteristically upcurved to run close to the pterostigma (fig. 72). Reduced wing venation is a characteristic of several genera of Euphorinae.

All euphorines are koinobiont endoparasitoids and, as with most koinobionts, at the species level host ranges are normally rather narrow. Indeed, several studies suggest that in many euphorines they may be exceptionally narrow, and this may be correlated with the high incidence of thelytoky in most genera. However, the host spectrum of the subfamily as a whole is remarkably broad, involving (worldwide) at least six orders of insects: Coleoptera, Hemiptera, Psocoptera, Hymenoptera, Neuroptera and, in just one recorded case, Orthoptera (cf. S.R. Shaw, 1985, 1988). Species attacking the first four of these orders occur in Britain. The endopterygote hosts are attacked as adults (at least predominantly), while the exopterygote ones are attacked either as adults or, much more often, in the nymphal stage and then killed as final-instar nymphs or sometimes adults. The endopterygote host groups used by euphorines tend to have overwintering, or at any rate long-lived, adults that engage in considerable feeding.

The majority of euphorines are solitary parasitoids, but gregarious development occurs in some species of at least three genera, notably *Microctonus* (McColloch, 1918; Wade & St George, 1923; Loan, 1967; Loan *et al.*, 1969; Luff, 1976; Loan & Holliday, 1979; Doyen, 1984) but also *Perilitus* (Waloff, 1961) and *Syntretus* (Alford, 1968). The generic classification of Euphorinae proposed by Shaw (1985) was deliberately constructed without reference to their early stages or biology, partly in order to facilitate ecological hypotheses relating to the evolution of the group (S.R. Shaw, 1988). This approach has suggested that the original hosts of Euphorinae were chrysomelid beetles, and that parasitism of the adult rather than the larval stage was a switch first promoted by the co-occurrence of host adults and larvae on the same pabulum. In a similar fashion, subsequent permeations from existing hosts into completely unrelated new host groups co-occurring in the same niche, in addition to more conventional radiations onto phylogenetically related hosts, were invoked to account for the pattern of host utilisation now seen in the subfamily (S.R. Shaw, 1988).

Parasitism of adult beetles is practised by British species of Euphorinae in at least ten genera, in the tribes Perilitini, Dinocampini, Townesilitini, Microctonini, Centistini and Cosmophorini. The best known and studied attack species of Curculionidae (e.g. Jackson, 1928; Loan & Holdaway, 1961a,b; Drea, 1968; Drea *et al.*, 1972; Gerdin & Hedqvist, 1985), Chrysomelidae (e.g. Waloff, 1961; Loan, 1967; Wylie, 1984, 1985; Wylie & Loan, 1984) and Coccinellidae (e.g. Ogloblin, 1913, 1924; Balduf, 1926; Bryden & Bishop, 1945; Walker, 1962; Iperti, 1964; Sluss, 1968; Obryki *et al.*, 1985) of agricultural significance, but Carabidae (e.g. Luff, 1976, 1977), Scolytidae (cf. Shaw, 1989; also Shenefelt, 1960), Staphylinidae (cf. Lipkow, 1965) and probably still other families (cf. Shaw, 1985) are attacked by others. *Cosmophorus*, with one British species (Shaw, 1989), is regarded (Čapek, 1970; Shaw, 1985) as the most specialised of all: its hosts are scolytid bark beetles, which are held in the female's huge mandibles as she oviposits into them in their constraining burrows, evidently with the additional help of a temporarily paralysing venom (Seitner & Nötzl, 1925; Loan & Matthews, 1973). Other extreme morphological structures probably used during oviposition include the raptorial antennae of female *Streblocera* (although the act has never been recorded for this rarely seen genus), of which a non-British species had been reared from a chrysomelid (Watanabe, 1942). *Allurus* and *Centistes* species use their legs to grasp the host when ovipositing (Loan, 1964, 1972) and some species of *Townesilitus* (Haeselbarth & Loan, 1983; Wylie & Loan, 1984), *Pygostolus* (Loan & Holdaway, 1961a) and *Perilitus* (Gerdin & Hedqvist, 1985) leap onto the elytra of the host in order to oviposit. However, most stalk their beetle hosts on foot before attempting to jab them, with the abdomen curled under the thorax so that the ovipositor projects forwards under the face (as photographed by Loan & Holdaway, 1961b; Iperti, 1964; Loan, 1967), and several authors (Balduf, 1926; Bryden & Bishop, 1945; Waloff, 1961; Loan, 1967; Sluss, 1968; Weiss *et al.*, 1978) have drawn attention to the importance of movement and other visual cues in promoting the parasitoid's oviposition sequence.

In general, euphorines ovipositing into mobile and well-armoured beetles face considerable difficulties in inserting the ovipositor through an unsclerotised membranous area, and various interesting behavioural sequences are described in the literature (e.g. Balduf, 1926; Jackson, 1928; Waloff, 1961; Weiss *et al.*, 1978; Doyen, 1984). Although oviposition between abdominal sclerites, often near the anus, is probably the most usual, some species exhibit a well-pronounced preference for oviposition into other sites, such as the mouth (Wylie, 1985), the base of an antenna (Freeman, 1967; Loan, 1974a), or between particular thoracic or head sclerites (Waloff, 1961; Loan, 1964; Gerdin & Hedqvist, 1985). Others are evidently more plastic in their behaviour (e.g. Loan, 1967; Sluss, 1968; Drea *et al.*, 1972; Wylie and Loan, 1984). Wherever the egg is placed there may be a tendency for it to drift towards the abdomen in the haemolymph (Wylie, 1985), and in any case the first-instar larva usually rapidly moves to the abdominal cavity, where subsequent development takes place (e.g. Loan, 1964).

The egg swells in the host's haemolymph – in some cases enormously, though there is considerable variation between species (Loan, 1963a) – and teratocytes are liberated when it hatches. Initially these may have a secretory function (Sluss, 1968; Sluss & Leutenegger, 1968) but at least in some cases (e.g. Ogloblin, 1924; Jackson,

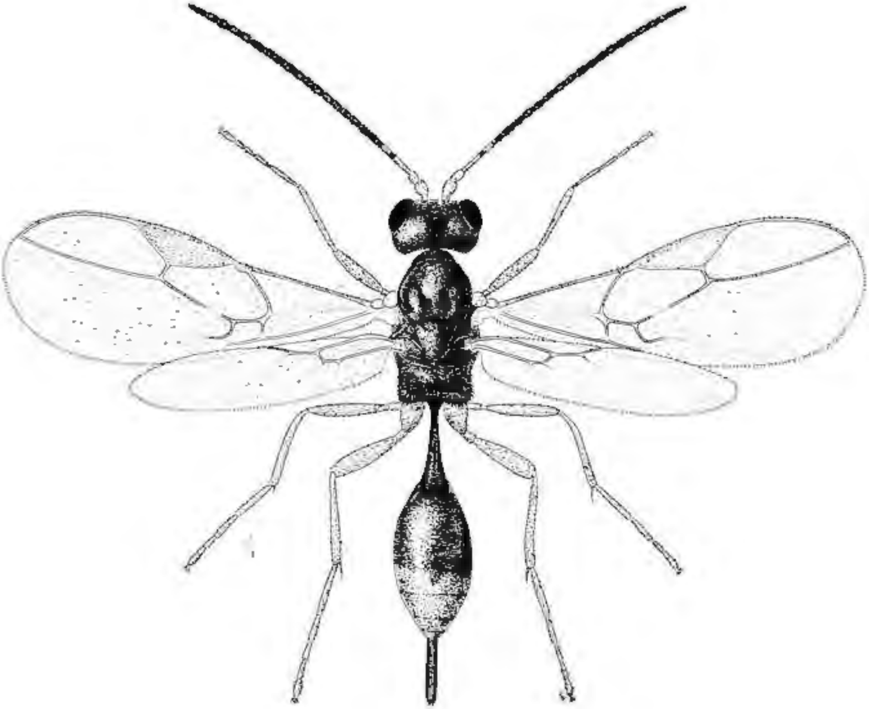

Fig. 121. *Syntretus vernalis* (Wesmael), Euphorinae.

1928; Loan, 1964) they are later consumed by the developing larvae: in some other cases (Drea *et al.*, 1972) their occasional absence has been noted. The caudate first-instar larva is equipped with large, falcate mandibles and has a closed tracheal system (e.g. Loan, 1963a). It is usually this stage that overwinters, though one species of *Perilitus* is reported to overwinter as a final-instar larva inside its diapausing host (Waloff, 1961): possibly because the first instar is of short duration, this species is also abnormal within its genus in being facultatively gregarious. Most authors have recorded five larval instars; the mandibles of the second are indistinct (or possibly absent: Loan & Holdaway, 1961b). In several cases the moult to the fifth instar has been observed to take place only as the larva leaves the host (Loan & Holdaway, 1961a,b,; Loan, 1963a), which it normally does through a lesion between apical abdominal sclerites that may thus be left plugged by the exuviae.

The effect of the parasitoid on the host depends to some extent on the relative sizes of host and parasitoid. In one famous series of experiments (Timberlake, 1916), in which *Dinocampus coccinellae* (Schrank) was developing in a particularly large ladybird host, some host individuals not only survived successful parasitism to resume feeding and reproducing (see also Walker, 1962; Sluss, 1968), but could even serve as host again! In some *Microctonus* and *Pygostolus*, however, female hosts are rendered sterile very soon after the egg is laid, though male hosts may remain apparently fertile (Jackson, 1928; Loan & Holdaway, 1961a,b). In other cases even males are usually castrated fairly quickly (Drea, 1968). By the time the parasitoid is fully grown the hosts of most euphorines are more or less paralysed and so weakened that they die either soon after the parasitoid leaves or, sometimes, even before this happens (Loan *et al.*, 1969).

Pupation is in a cocoon that is normally spun in soil or litter, but *Pygostolus* species construct their cocoons on twigs or leaves (Loan & Holdaway, 1961a; Blackith & Blackith, 1986) and *Dinocampus coccinellae* spins up beneath and between the legs of the ladybird that harboured it (Balduf, 1926). Emergence is by cutting a neat circular cap from the apex of these exposed cocoons, but in some of the species pupating in the soil the hole is evidently rather less regular (Loan, 1964) or even not apical (Loan *et al.*, 1969). It is usual for the euphorines that attack beetles to have two, or sometimes perhaps more, annual generations on a single generation of their univoltine hosts. Plurivoltinism of this type may be facilitated to some extent by the parasitoid causing its host to break winter diapause early (Wylie, 1982). In several genera, e.g. *Dinocampus* (Sluss, 1968; Obrycki *et al.*, 1985), *Perilitus* (Waloff, 1961) and *Microctonus* (Loan, 1963b; Drea, 1968; Drea *et al.*, 1972) certain species are known to be able to attack larval or pupal stages of their hosts successfully, in one case apparently to the exclusion of adults (Drea *et al.*, 1972), though development of the parasitoid is always delayed until the host becomes adult. One euphorine, *Pygostolus sticticus* (Fabricius), that attacks weevils (Blackith & Blackith, 1986) is so regularly recorded from various microlepidopteran larvae that its host range perhaps merits experimental investigation.

The biological notes given above relate to euphorines that parasitise beetles, but three of the tribes recognised by Shaw (1985), Loxocephalini, Syntretini and Euphorini, contain British genera with different host associations. In contrast to species parasitising beetles, univoltinism seems to be almost universal among these parasitoids. The rare and little-known *Loxocephalus* appears to be associated with nests of *Formica* ants (Morley, 1909b), but it is not clear in what capacity. The genus *Syntretus*, of which several species have been recorded from Britain, is parasitic on adults of apocritan Hymenoptera, one British species being a gregarious parasitoid of various bumble bees (Alford, 1968) and another developing singly in the abdomens of ichneumonids (Cole, 1959). It might be argued that the latter species provides a rare instance of a hyperparasitic braconid, as its behaviour falls within the definition, if not quite the spirit, of pseudohyperparasitism (Shaw & Askew, 1976).

A few species of *Euphoriella* attack mid to late nymphal instars of Psocoptera, which are killed either as late instar nymphs or, less often, as adults (New, 1970; see also Sommerman, 1956). However, the majority of the British euphorines that do not parasitise beetles are parasitoids of bugs. The rare and little-known genus *Wesmaelia* attacks nymphs of nabids (Muesebeck, 1963), and small exotic genera parasitise pentatomids (Čapek & Davidová-Vilímová, 1978) and tingids (Loan *et al.*, 1971), but the closely related genera *Leiophron* and *Peristenus* have undergone much more extensive radiations as parasitoids of mirid bugs. Leston (1961) recorded parasitism in the nymphs of 51 species of British mirids, involving five host subfamilies, and it seems that in general the host ranges of the euphorine species attacking nymphal exopterygote insects are rather broader than is usual for those attacking adult beetles (e.g. Waloff, 1967; New, 1970).

The general and developmental biology is recorded in detail for British species of *Syntretus* (Alford, 1968), *Euphoriella* (New, 1970) and, especially, *Peristenus* and *Leiophron* (e.g. Brindley, 1939; Loan, 1965; Waloff, 1967; Glen, 1977). Some species lift the host off the ground in order to ovipost (Waloff, 1967; Glen, 1977), and the process may also be facilitated by temporarily paralysing it (Waloff, 1967). In general, development of the early stages is very similar to other euphorines, though only four larval instars are recorded for some (e.g. New, 1970). The final-instar larvae of both North American species of *Holdawayella* are remarkable in having large abdominal appendages of uncertain function (Loan *et al.*, 1971): comparable structures have been seen in the genus *Syntretomorpha* (Walker, Joshi & Verma, 1990), which Shaw (1985) regarded as only remotely related. There are clear statements indicating the consumption of teratocytes or their contents (e.g. Loan, 1965; Waloff, 1967; Alford, 1968), and also recording the parasitoid's moult from fourth to fifth instar at the time it leaves the host in some cases (e.g. Loan, 1965; see also Principi *et al.*, 1979) but not all (New, 1970). The multi-enveloped cocoon is formed in the ground, and in most species it persists for much of the year as the parasitoid overwinters in it. In cases in which sufficient detail is known the adult is fully formed before the onset of winter (Alford, 1968; New, 1970; Loan, 1980; Wheeler & Loan, 1984) though, in at least some species, with unexpanded wings (Alford, 1968). This is an unusual means of overwintering for Braconidae, and may have originated with a need for adult activity particularly early in the season.

For biological information on European genera of Euphorinae not yet found in Britain, in addition to those already mentioned, the reader is referred to Séméria (1976) and Principi *et al.* (1979) for *Chrysopophthorus*; Čapek & Davidová-Vilímová (1978) for *Aridelus*; Čapek & Capecki (1979) and Deyrup (1981) for *Cryptoxilos*; and Smith (1953) for *Marshiella*. The genus *Holdawayella*, studied in North America by Loan *et al.* (1971), has also been recorded from Europe (Čapek, 1989).

Identification. Shaw (1985), key to genera including all known from Britain; Loan (1974b), European *Leiophron* and *Peristenus*; Richards (1960), some species of *Perilitus* and related genera; Čapek & Šnoflák (1959), European *Streblocera*; Čapek (1958), European *Cosmophorus*; Haeselbarth (1971), European *Pygostolus*; Haeselbarth (1988), Palaearctic *Townesilitus*.

Subfamily Gnamptodontinae
(= Gnaptodontinae auctt.)

This small subfamily of about 35 species worldwide is represented in Europe by the cosmopolitan genus *Gnamptodon* (for which the widely used spelling *Gnaptodon* (cf. van Achterberg, 1984a) is formally rejected in Opinion 1424, 1987). Two rather infrequently encountered species occur in Britain. The genus has traditionally been included in the Opiinae, but its placement has always been problematical and, indeed, van Achterberg (1976d) transferred it to the Rogadinae before according the group subfamily status (van Achterberg, 1983c). Gnamptodontines are small insects, less than 2 mm long, having a characteristic curved groove on tergite 2 that delimits a transverse basal area (fig. 86).

So far as is known all species are solitary koinobiont parasitoids of monotrysian Lepidoptera of the leaf-mining family Nepticulidae. However, although rearings have been quite plentiful, the biology of *Gnamptodon* has not been studied in detail. Parasitised host individuals collected as actively mining larvae later vacate their mines in the usual way and spin normal cocoons, inside which the parasitoid kills the prepupal host and constructs its own flimsy cocoon. On this strong circumstantial evidence *Gnamptodon* species have been presumed to be endoparasitoids (e.g. Čapek, 1970), and, indeed, the consistently cleaned out and crumpled appearance of the nepticulid larval skins seen by us suggests that this is so. However, in view of the possibly close relationship of Gnamptodontinae with Rogadinae, in which ectoparasitism is inconspicuously retained by some koinobiont genera (M. R. Shaw, 1983b), this inference does require extremely careful confirmation (see also van Achterberg, 1983c). The parasitoid overwinters in the host cocoon, emerging through an irregularly circular chewed subapical hole. Present evidence suggests that both British species may be strictly univoltine. Van Achterberg (1984e) discussed the host-plant associations of the European species.

Identification. Van Achterberg (1983c), Palaearctic species.

Subfamily Helconinae

(Fig. 122)

As currently recognised (van Achterberg, 1984b), this is a moderately large subfamily containing over 400 described species worldwide. Just over 40 species in ten genera, grouped into three tribes, have been recorded as British. So far as is known all are solitary parasitoids, although biological information is lacking for most of the species. The current concept of the subfamily restricts it to groups that are koinobiont endoparasitoids of beetle larvae, and excludes several formerly included genera that attack other host groups (cf. Huddleston, 1978). Nevertheless, Helconinae is still a heterogeneous assemblage and not well characterised by synapomorphies: like other groups based largely on plesiomorphic character-states, it is unlikely to be strictly holophylectic. Indeed, the retention of relatively primitive character-states and the use of endophytic coleopteran larvae, widely presumed to be the archaic host group for Braconidae, has encouraged the view that helconines are close to the ancestry of a major lineage of koinobiont endoparasitic Braconidae – from which many other subfamilies presumably arose as diversification onto other host groups took place. (Note, however, that koinobiont endoparasitoids independently arose from ectoparasitoids of other host groups in the cyclostome subfamily Rogadinae or close relatives (M. R. Shaw, 1983b; van Achterberg, 1984b)). Mason (1974) unravelled some of the considerable nomenclatural and conceptual confusion that has bedevilled this part of the classification, and van Achterberg (1983a) suggested possible relationships between the tribes remaining in Helconinae.

Species of the tribe Helconini are fairly easily recognised by the shape of the second submarginal cell (fig. 98). They are among the largest of British Braconidae, but are very seldom collected. Their hosts appear to be the larvae of cerambycids, and perhaps other wood-boring beetles, but little is known of their developmental biology. The tribe Diospilini, which, like Helconini, has three submarginal cells in the forewing (fig. 97), contains species recorded from less deeply concealed

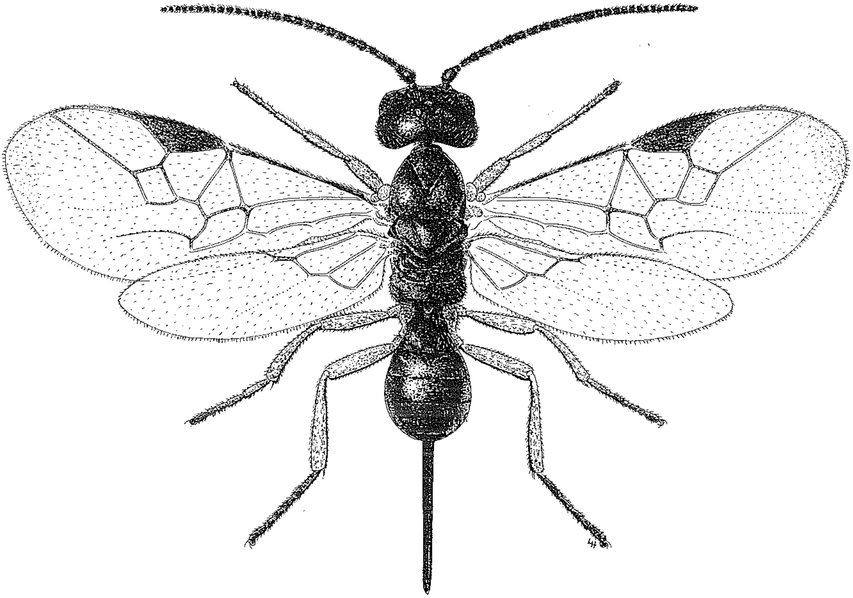

Fig. 122. *Diospilus* sp., Helconinae.

phytophagous beetles such as Curculionidae and Nitidulidae. The biology of one species of *Diospilus* parasitising *Meligethes* larvae has been investigated by Osborne (1960). He recorded that the egg has a pedicel which is sometimes embedded in the host's gut wall, that the egg swells greatly before hatching, that a trophamnion consisting of a single layer of cells surrounds the embryo, that the apneustic first-instar larva has a large head armed with sharp, falcate mandibles and develops an anal vesicle, and that the final instar larva has weak mandibles and completes its feeding externally after the host has constructed its pupation chamber, in which the parasitoid cocoon is eventually formed. Eggs were found in larval hosts, though Osborne (1960) did not record which host stage is attacked. However, is seems that egg-larval parasitism occurs in at least one *Diospilus* species (Parrott & Glasgow, 1916).

Some species of Brachistini are very well known to be egg-larval parasitoids (Clausen, 1954; Haeselbarth, 1962; Parnell, 1964; Čapek, 1971; Alauzet, 1987) and this habit may prevail throughout the tribe. In Brachistini there are only two submarginal cells in the forewing (fig. 112), and the gaster is generally relatively short and broad. In two genera (*Triaspis* and *Schizoprymnus*) the first three tergites are modified into an unarticulated carapace concealing the remaining segments. Two transverse furrows mark the boundaries of these tergites in *Triaspis*, but not in *Schizoprymnus*. In both genera the ovipositor is normally clearly exserted and this feature, as well as their substantially different wing venation (cf. figs 54, 112), provides a ready means of distinguishing them from British species of other genera (e.g. of Cheloninae) having an abdominal carapace. Most species for which hosts are known are parasitoids of weevils or Bruchidae. The most complete biological studies are on *Eubazus semirugosus* (Nees von Esenbeck) (=*Brachistes atricornis* auctt.), a parasitoid of *Pissodes* (Curculionidae) that is bivoltine in at least part of its range (Haeselbarth, 1962; Alauzet, 1987). The winter is passed as a first-instar larva, which is armed with large mandibles and develops an anal vesicle, inside the overwintering host. Altogether there are three larval instars, and the last emerges from the host in its pupation chamber to feed externally. Haeselbarth (1962) notes that parasitised hosts are induced to construct abnormal pupal cells, from which the adult parasitoid can more easily eclose. Less extensive observations have been published on *Triaspis* species (Beirne, 1946; Berry, 1947; Obrtel, 1960; Parnell, 1964), from some of which it is evident that the final-instar larvae again feed externally, and the adults emerge from the cocoon through a jagged chewed hole.

Identification. Hellén (1958) provides a key to genera and species of much of the European fauna of 'Helconinae' sensu lato; Mason (1974), genera of Brachistini; van Achterberg (1987a), European Helconini; Šnoflák (1952), European *Triaspis*; van Achterberg (1990c), subgenera of *Eubazus* and related genera, and species of *Foersteria*.

Subfamily Histeromerinae

The subfamily consists of just two described species of *Histeromerus*; one Nearctic but the other Palaearctic and found, albeit rarely, in Britain. *Histeromerus* exhibits many plesiomorphous character states, and has usually been included in the Doryctinae (e.g. Shenefelt & Marsh, 1976; Huddleston, 1978). However, van Achterberg (1976d) placed the genus in the Braconinae on the basis of some presumed synapomorphies, but more recently (1984b) accorded it subfamily rank on account of its extremely isolated position. *Histeromerus* is easy to recognise from its distinctive head and front and hind legs (figs 38–42).

Histeromerus has been recorded as a parasitoid of wood- or fungus-inhabiting beetle larvae or pupae of various families, and it is likely to prove to be an idiobiont ectoparasitoid. It is a gregarious parasitoid of large beetles, but is also recorded (van Achterberg, 1984b) from some beetle species that are so small that solitary parasitism might be inferred. Adult females of *Histeromerus* have sometimes been found apparently searching for hosts deep inside beetle-infested decaying wood. Fragmentary biological information accompanying British captures of *H. mystacinus* Wesmael has been given by Bignell (1901, 1902), Donisthorpe (1929, 1940), Morley (1935) and Hincks (1952). It seems extremely improbable that *Histeromerus* is ever truly endoparasitic, although the wording of Donisthorpe's accounts, taken together with comments by Elliott & Morley (1907), and with Hincks's (1952) capture of a female apparently ovipositing *into* an active elaterid larva, may appear to suggest it. It seems more likely, as no reared parasitoids appear to have resulted, that Hincks's female was simply trying, unsuccessfully, to paralyse the host, and Donisthorpe's host pupae had probably been attacked as pharate adults, the host cuticle then supporting deep excavation by the parasitoid larvae through the lesions they made. Bignell's (1901, 1902) observation is fully consistent with idiobiotic ectoparasitic development, despite an alternative interpretation by Elliott & Morley (1907). Nevertheless, the conclusive evidence is still lacking.

Identification. *Histeromerus mystacinus* is the only European species and can therefore be identified from the key to subfamilies.

Subfamily Homolobinae

As defined by van Achterberg (1979c) this is a relatively small subfamily with about 60 described species worldwide. Four species of *Homolobus* and two of *Charmon* are known from Britain. The history of both the nomenclature and the higher classification of these genera is complex. *Homolobus* was traditionally known as *Zele* and generally included in the Macrocentrinae (e.g. by Nixon, 1938; Eady & Clark, 1964), but van Achterberg (1976d) first transferred it to Helconinae and then (van Achterberg, 1979c), finding that the name *Zele* properly applies to a group related to *Meteorus* (then in Euphorinae), called up the available name *Homolobus* for *Zele* auctt., at the same time erecting the subfamily Homolobinae. The name *Charmon* was shown by Mason (1974) to apply to species traditionally but incorrectly referred to the genus '*Eubadizon*', which was an unjustified emendation of *Eubadizus*, itself an unjustified emendation of *Eubazus*. Mason (1974) tentatively placed *Charmon* in the Orgilini, at that time part of Helconinae, but van Achterberg (1979c) included *Charmon*, in the tribe Charmontini, in his new subfamily Homolobinae.

Except that testaceous, crepuscular and nocturnal species (Huddleston & Gauld, 1988) predominate in both genera, there is little in the superficial appearance of *Charmon* and *Homolobus* to suggest a close relationship. *Homolobus* species are rather large and have short, almost concealed, ovipositors (fig. 94) and three submarginal cells in the forewing. They parasitise caterpillars that feed exposed at night, especially Geometridae and Noctuidae. *Charmon* species are much more slender and have long ovipositors and only two submarginal cells. They attack microlepidopteran larvae that feed in weakly concealed sites such as spinnings, buds, etc. Although the host lists given by van Achterberg (1979c) are heavily dominated by Tortricidae, it is our impression that *Charmon* species have abnormally wide host ranges encompassing several families, with Gelechiidae a particularly regular component. Both genera are solitary koinobiont endoparasitoids and kill the host in its pupation chamber, in which the parasitoid cocoon is spun. Both genera overwinter as cocoons and eclose by detaching a cap. In *Homolobus* this is cleanly but inexactly cut, while in *Charmon* the cap is more apical and circular but less sharp. Allen (1982) has recorded an ectoparasitic feeding phase by the final-instar larva of *Homolobus* (but his statement that the host's skin is also consumed is not borne out by our own observations). Otherwise, details of their developmental biology are scant, though Kolaib (1987) noted three larval instars in *Homolobus*, of which the second and third have an anal vesicle, and also records a final external feeding phase.

Identification. Van Achterberg (1979c) monographs the subfamily.

Subfamily Ichneutinae

This is a small subfamily of about 20 species worldwide, principally Holarctic in distribution. Three tribes are recognised, though their placement together is tentative (van Achterberg, 1976d, 1984b). The most divergent (Muesebeckiini, which does not occur in Europe) is poorly known biologically: indeed *Paraligoneurus*, the only genus for which host records exist, is recorded from both nepticulid Lepidoptera and agromyzid Diptera (cf. Shenefelt, 1973a). These two leaf-mining families make quite similar mines, but the former host group is made the more credible by Čapek's (1970) statement that pupation takes place in the lepidopteran host cocoon. The other two tribes, Ichneutini and Proteropini, parasitise Symphyta and are of particular interest in being the only braconids known to be endoparasitoids of larval Hymenoptera. Though both tribes are represented, only two species of *Ichneutes* and the sole species of *Proterops* are recorded from Brtain. They are medium-sized and rather stout braconids, with characteristic wing venation (figs 80, 81). Species of *Ichneutes* are dark and heavily sculptured, at least on the propodeum and the first tergite, and they have strongly lobed and bent tarsal claws. *Proterops*, on the other hand, is conspicuously smooth and shining, with a bright yellowish gaster and unlobed claws that are only slightly curved.

Ichneutes species are solitary koinobiont endoparasitoids of tenthredinid sawflies, and are able to exploit endophytic as well as exposed feeders. Those that parasitise leaf-mining or gall-forming tenthredinids oviposit into the host's egg (Nägeli, 1936; Zinnert, 1969), a strategy employed also by some *Ichneutes* species whose hosts feed exposed on foliage, although others oviposit only into early-instar larvae (Zinnert, 1969). The host is killed after it has constructed its cocoon, in which the ichneutine pupates. One species is reported by Zinnert (1969) to overwinter either as a pupa or as a first-instar larva in its prepupal (eonymph) host. *Proterops* is an uncommon solitary koinobiont endoparasitoid of argid sawflies (Pschorn-Walcher & Kriegl, 1965), but its developmental biology is not known in greater detail. Although parasitising sawfly hosts must have been a successful host switch at the time it took place, it seems strangely unsuccessful now: there are very few, and mostly only uncommon, ichneutine species in relation to the considerable species-richness and abundance of the phytophagous sawfly fauna seen in north temperate areas. Detailed studies on the developmental biology of ichneutines could be of great interest as they might elucidate the origin of the group as well as the reason for its apparent lack of success.

Identification. Hellén (1958), European species; Haeselbarth (in prep.), European *Ichneutes*.

Subfamily Macrocentrinae

(Fig. 123)

This is a medium-sized subfamily with about 150 described species worldwide. Eighteen species of *Macrocentrus* and one of *Austrozele* are known to occur in

Britain. Macrocentrines are all koinobiont endoparasitoids of lepidopteran larvae, and the adults can easily be recognised by the presence of several teeth on the apex of the hind trochantellus (fig. 73): these are absent in other braconids although in the homolobine genus *Homolobus* (which superficially resembles *Austrozele*) the apex of the hind trochantellus is sometimes produced into a single dentate process. Species of *Macrocentrus* are slender insects, 4–10 mm long (excluding the ovipositor), and many are long-legged, giving them a delicate appearance. They have moderately to very long ovipositors and the second of their three submarginal cells has a characteristic shape (fig. 79). Some are blackish-brown but many are predominantly testaceous and nocturnal (Huddleston & Gauld, 1988).

The majority of the British species of *Macrocentrus* are gregarious: a few of these attack noctuids that feed on roots or inside stems, but the most frequently encountered attack Pyralidae and Tortricidae feeding in shoots, spun or rolled leaves, or other concealed sites including in one case resinous galls. The solitary species form a distinct group and are, on the whole, larger. They attack various concealed microlepidopteran larvae including Sesiidae, Oecophoridae, Gelechiidae and Tortricidae. The single British species of *Austrozele* appears to be rare and is not yet formally described. It is almost certainly nocturnal and has been reared as a solitary parasitoid of the hypenine noctuid *Hypena crassalis* (Fabricius), a species whose larva feeds exposed on *Vaccinium myrtillus* by night but rests concealed during the day.

Macrocentrus is an interesting genus biologically because some – presumably all – of the gregarious species develop by polyembryony (Parker, 1931a; Paillot, 1937; Cranham & Danthanarayana, 1966). Polyembryony, whereby an entire single-sex brood develops from only one alecithal (=hydropic, sensu Flanders, 1942) egg by repeated division to give rise to many independent embryos, occurs in several unrelated groups of Hymenoptera (Ivanova-Kasas, 1972; Gauld & Bolton, 1988) though not elsewhere in the Braconidae. Some of the processes leading to polyembryonic development also take place in at least one of the solitary species of *Macrocentrus*, but only one of the resulting morulae continues to become an embryo (Daniel, 1932; Finney *et al.*, 1947). As Parker (1931b) remarks, the initial stages of polyembryony are similar to the processes leading to the less extreme development of teratocytes (which do not continue to divide) from the trophamnion.

Parker (1931a), Wishart (1946) and Dittrick & Chiang (1982) all describe the biology of *M. cingulum* Reinhard (cf. van Achterberg & Haeselbarth, 1983), a polyembryonic species that parasitises pyralids and occurs in Britain. The host is most easily attacked in situ in its middle instars and oviposition is into any part of the haemocoel. The egg overwinters in the primary and secondary germ stages inside the overwintering host: not until spring do these germs continue to develop to become tertiary germs, morulae and embryos, and eventually first-instar larvae. These have abdominal pseudopods in two pairs on each of the first twelve body segments, an evident tracheal system but no spiracles, a small anal vesicle, and well-developed sharply pointed mandibles. The most advanced hatch and consume various trophamniotic fragments, including developing embryos and germs of various sizes and even to some extent one another. They also cause considerable mechanical damage to various tissues, producing debris that they consume as second-instar larvae, when they apparently lack mandibles. Depending on the size of the brood, the third-instar larvae, in which mandibles reappear, can almost fully destroy the host before emerging from it, moulting to the final instar more or less concurrently, to complete their feeding externally.

Perhaps because brood sizes and the quantity of food available to each larva are poorly controlled, the final external feeding phase seems not to be absolutely obligatory, for Parker (1931a) obtained normal, if undersized, cocoons and adults from larvae that he removed as they emerged from the host. Although the later stages of embryonic development are delayed until the host has reached its final

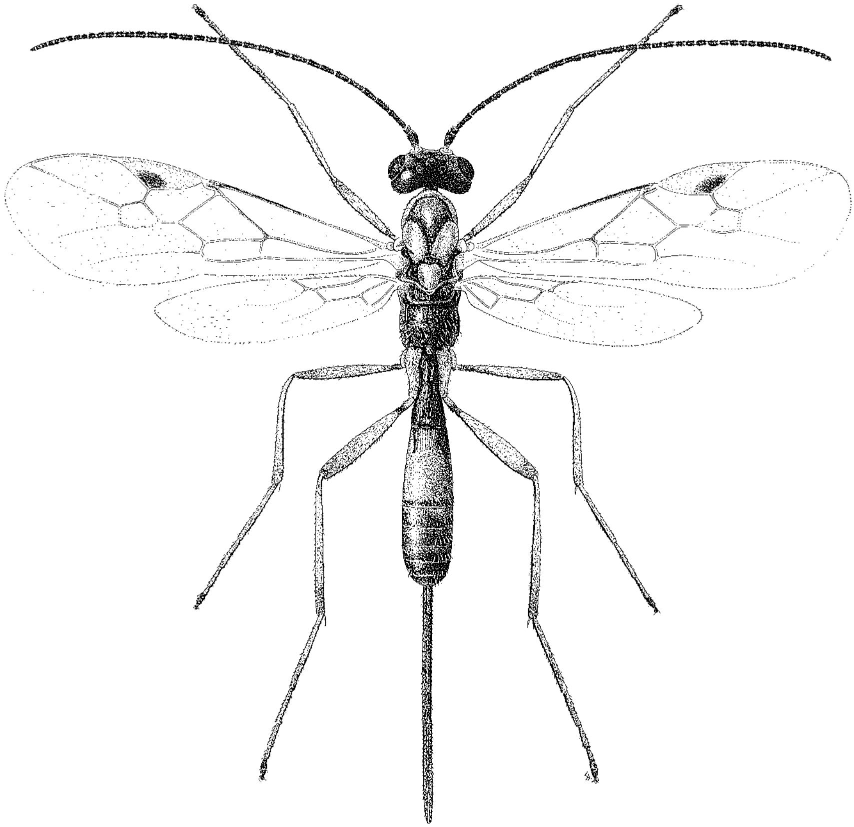

Fig. 123. *Macrocentrus collaris* (Spinola), Macrocentrinae.

instar (Dittrick & Chiang, 1982), the same poor control over the host's vigour may explain why hosts are often killed as final-instar larvae rather than as prepupae in prepared pupation sites, and this may limit host ranges to species that rest (as opposed to merely pupating) in the concealment needed for the parasitoids' final ectophagous phase. The gregarious species usually spin their individual, elongate, brownish cocoons arranged within a communally-spun, outer envelope: in some cases the resulting mass is loosely ordered and more or less fusiform, but in at least one species the cocoons are accurately aligned in a honeycomb-like, closely packed array. All macrocentrines cut a neat, circular cap from the extremity of the cocoon to emerge. Mixed-sex broods of gregarious *Macrocentrus* species are quite often reared: in our experience this occurs especially when the level of parasitism in the host population is high, when it is evidently the result of multiple oviposition (see also Parker, 1931a).

The biology of a multivoltine solitary species of *Macrocentrus* has been studied by Fink (1926), Stearns (1928), Daniel (1932), Finney *et al.* (1947) and Putman (1963). The egg swells greatly in the hosts' haemolymph but initial stages of polyembryonic development are arrested so that only one larva results. The first-instar larva lacks pseudopods (in contrast to *M. cingulum*). The winter is passed as a mature and presumably aggressive first-instar larva within the diapausing host, and the first moult is delayed until the host is cocooned. The resulting second-instar larva is described as having small mandibles, but in other respects subsequent development is similar to that of gregarious species. Both Fink (1926) and Stearns (1928) reported that male progeny of unmated females were smaller in size than males from mated females, but neither author advanced a satisfactory explanation of this phenomenon.

Identification. Eady & Clark (1964), European *Macrocentrus*, but see also van Achterberg & Haeselbarth (1983) whose revision of the group comprising the solitary species includes additions; van Achterberg (in prep.), *Austrozele*, and Palaearctic *Macrocentrus*.

Subfamily Meteorinae

Most modern workers (e.g. Tobias, 1966; Čapek, 1970; van Achterberg, 1976d, 1979c, 1984b; Loan, 1983) have followed Muesebeck (1936a) in classifying meteorines within Euphorinae; but here we follow S. R. Shaw's (1985, 1988) more recent resurrection of Meteorinae as a distinct subfamily, although recognising that this is a somewhat arbitrary decision likely to be overturned by future workers (C. van Achterberg, personal communication).

The subfamily Meteorinae, as recognised here, is of medium size and consists chiefly of the large, cosmopolitan genus *Meteorus* with about 175 described species (cf. S. R. Shaw, 1988), of which 29 have been found in Britain (Huddleston, 1980; M. R. Shaw, 1988b). The small Holarctic and Neotropical genus *Zele* (=*Zemiotes*), with five British species, is also included (cf. van Achterberg, 1979c, 1984b), even though Mason (1973) and Shaw (1985) argue that *Zele* exhibits mainly plesiomorphic character states and therefore cannot be regarded as related to *Meteorus*. The placement of such taxa will always be problematical in classification systems that admit only holophyletic groupings, recognised solely by synapomorphies, as these techniques of phylogenetic analysis will all too easily exclude them from whatever group they have been placed in. As that result is clearly unsatisfactory, and in the absence of profound autapomorphies, we follow the most recent author prepared to place the genus positively (van Achterberg, 1979c, 1984b; see also Maetô, 1990, who has suggested that *Meteorus* is paraphyletic with respect to *Zele*). In the British fauna meteorines, as here construed, are easily recognised from the combination of petiolate gaster (figs 68, 69, 71) and subtrapezoidal or almost quadrate second submarginal cell, and *Zele* differs from *Meteorus* most obviously in the more even distribution of hairs on at least the apical halves of the gastral tergites (reduced more or less to a single row per tergite in *Meteorus*) and in the distal widening of the marginal cell of the hind wing (Huddleston, 1980).

Most species of *Meteorus*, and all *Zele*, are koinobiont endoparasitoids of lepidopteran larvae, but some species of *Meteorus* exclusively attack larval Coleoptera. Even among the *Meteorus* that attack Lepidoptera there are several distinct trends. The species most frequently encountered are solitary and oviposit into macrolepidopteran caterpillars that live exposed on vegetation. Before the host is fully grown the parasitoid larva emerges, typically close to an abdominal spiracle, and immediately (Lyle, 1914) or after moving away for a short distance (Muesebeck, 1918) suspends itself from the substrate and starts to spin an ovoid, more or less brownish cocoon at the end of a silken thread about 1–8 (exceptionally up to 20) cm long. Madel (1963) gives a stepwise photographic record of the process, and it is from this characteristic pensile cocoon that the genus takes its name.

No doubt these pensile cocoons are inaccessible to some potential enemies but, perhaps surprisingly, they are very prone to attack from idiobiont parasitoids (e.g. Muesebeck, 1918; Proper, 1934; Lejeune & Silver, 1961), and this vulnerability, perhaps together with a susceptibility to wind damage, may explain why pupation and emergence of the adult always take place quite rapidly. Thus it seems that all *Meteorus* species making pensile cocoons overwinter as first-instar larvae inside caterpillars rather than in their cocoons. Many are certainly multivoltine: in some cases the regular hosts are also multivoltine, and at least one species has successive generations on first young and then older larvae of the same host generation (Muesebeck, 1918; Burgess & Crossman, 1929; Lejeune & Silver, 1961; see also Ingram, 1981), but in many species there is a seasonal alternation of hosts (e.g. Madel, 1963). A few species attack tortricid larvae living concealed in leaf spinnings, in which case the parasitoid emerges from the host larva in its retreat and a much thinner and more cylindrical, non-pensile cocoon is made concealed in situ. Except when the host is killed in an early instar, most species attacking lepidopteran hosts still feeding on vegetation leave the host individual able to roam for a few days after the parasitoid has left it, desiccation in at least some cases being delayed by the cast exuviae of the parasitoid larva, which are left plugging the exit wound (Madel, 1963). Several host larvae of one *Meteorus* species were found capable of resuming feeding for a time (Shaw, 1981b), but this does not usually occur in others: indeed, in one study (Askari, *et al.*, 1977) surrogate hosts ceased feeding from the time that the parasitoid eggs first hatched.

A few of the *Meteorus* species that parasitise large lepidopteran larvae that rest or pupate in subterranean situations are gregarious, with brood sizes of up to 40, and they make their ovoid, non-pensile cocoons in untidy heaps, perhaps normally in the host's pupation chamber. Separate gregarious species attack Noctuidae (Marshall, 1887; Lyle, 1914) and Hepialidae (King, 1933). Yet other *Meteorus* species attack detritivorous and fungivorous microlepidopteran larvae feeding concealed in mosses, bracket fungi on trees, and various organic remains: these are solitary species and make their cocoons in situ, although it has not been recorded whether or not the hosts are prepupal by the time they are killed, as is the case in a North American species that parasitises concealed pyralid larvae (Simmonds, 1947b). Huddleston (1980) outlined some correlations between the biology and morphology of *Meteorus* species, pointing out that the species attacking concealed microlepidopteran larvae share some morphological characters with those that attack beetle larvae.

Except that one species is now known to attack the leaf-mining larva of a chrysomelid, killing the host in its subterranean pupation chamber (M. R. Shaw, 1988b), the majority of *Meteorus* species associated with beetles parasitise either those that live in wood or tree bark or, in other cases, those that live in arboreal bracket fungi. This may suggest that, in Meteorinae as apparently in Euphorinae (S. R. Shaw, 1988), permeation of a novel host group has occurred as a result of its close cohabitation with the original hosts. Čapek's (1970) belief that the *Meteorus* species that parasitise beetle larvae represent the most advanced in the group would imply that Lepidoptera were the first hosts used, but Mason (1973) argues that the original hosts were Coleoptera with the corollary that the genus *Zele* is viewed as only distantly related rather than in some way ancestral. Maetô (1990) suggested that host switching from Coleoptera to Lepidoptera may have occurred more than once.

Among the biological studies on *Meteorus* already referred to, Madel's (1963) works stands out as particularly detailed, and includes photographic records of several key processes. In addition, Askari & Coppel (1978) have provided photographs of courting and mating behaviour (for which see also Simmonds, 1947b). Oviposition into exposed hosts is typically accomplished by bending the petiolate gaster under the thorax and advancing on the host with the ovipositor thrust forward under the face (as also in some Euphorinae and in Aphidiinae). Species having concealed hosts tend to have smaller eyes and no doubt depend more strongly on cues other than vision (Huddleston, 1980), and Strickland (1923) has noted a much less extreme oviposition posture. The egg expands greatly in the host's haemocoel, and the first-instar larva is caudate, with the falcate mandibles to be expected of species overwintering in this stage. A tracheal system is weakly evident from the first instar, but open spiracles are present only in the final instar. Most authors record three instars, the middle one having weak mandibles, and in some species (Strickland, 1923; Madel, 1963) the third and final instar is only reached as the parasitoid leaves the host, though in others (Simmonds, 1947b; Askari *et al.*, 1977) the second instar is of short duration and the third has a major feeding role before eclosing. In the final instar the mandibles are small and not serrate, in contrast with those of many braconids whose final instars feed externally. Madel (1963) states that the larva is a haemolymph feeder throughout its life, but surprisingly there is no mention of this being mediated by teratocytes in several studies that would appear to have been sufficient to detect them (Simmonds, 1947b; Madel, 1963; Askari *et al.*, 1977), so perhaps they do not occur.

The host range of *Zele* species, adults of which are predominantly crepuscular or nocturnal (Huddleston & Gauld, 1988), is centred on Pyralidae, Noctuidae and Geometridae. All *Zele* appear to be solitary parasitoids and some of the species are rather large. At least one British species is bivoltine, with an alternation of hosts, but others are univoltine. They all overwinter as prepupae in fusiform, felted cocoons that they spin in the hosts' pupation chambers, and pupation by the host in concealment is probably a crucial determinant of host range (compare the *Meteorus* species that make pensile cocoons, in which overwintering host larvae are more important).

The developmental biology of *Zele* is known chiefly through the work of Parker (1931b), though he comments that the host involved may not have been entirely suitable. As in *Meteorus*, oviposition into various sizes of larvae can be successful, and the egg swells greatly before hatching. In contrast, however, the presence of teratocytes and their considerable growth was noted. Teratocytes were not seen to be consumed, though the great reduction (or possible absence) of mandibles in the second instar suggests that they may be. Direct feeding on the fat-body appeared to be extensive, as judged by areas of apparent damage. The host was incompletely consumed by the time the parasitoid larva eclosed, but no external feeding was seen: substantial host remains found with cocoons of various British species also suggest that external feeding is absent, despite the concealed sites in which the hosts are invariably killed.

As in Euphorinae, the existence of a non-feeding instar in some meteorines (Strickland, 1923; Madel, 1963) suggests that a final ectophagous phase has been lost in this group, as has occurred in the majority of microgastrines. (The statement by Tobias (1967) that an ectophagous phase occurs in *Meteorus* resulted from a misinterpretation of the source literature). Both *Meteorus* and *Zele* emerge from the cocoon by cutting a neat cap from the anterior end; in *Zele* the cut is occasionally a bit lopsided.

Identification. Huddleston (1980), W. Palaearctic *Meteorus*; van Achterberg (1979c, 1984c), world *Zele*.

Subfamily Microgastrinae

(Fig. 124)

With about 1300 described species worldwide, Microgastrinae (as recognised by Mason, 1981; van Achterberg, 1984b; = Microgasterini sensu Nixon, 1965) is one of the largest subfamilies of the Braconidae and more than 250 species have been recorded as British. Microgastrines are all koinobiont endoparasitoids of lepidopteran larvae and the vast majority of known hosts belong to the Ditrysia. They have radiated extensively in association with this large and varied host group, so that microgastrines are among the most important components of the parasitoid complexes of most groups of ditrysian Lepidoptera in all zoogeographic regions. The British species are mostly rather small, dark insects. Microgastrines are characterised by their invariably 18-segmented antennae (though basal flagellar segments are sometimes constricted centrally so that each may appear as two). They generally also have a short gaster and large hind coxae. The small second submarginal cell ('open' in *Apanteles* sensu lato) is a character otherwise seen only in Agathidinae, which differ markedly in having a short and narrow marginal cell (cf. figs 47, 66).

The generic and tribal classification of Microgastrinae has always presented considerable problems, largely because of the size and world-wide distribution of the group and the high incidence of morphological convergence and character reduction (see Nixon, 1965 and Mason, 1981 for brief historical accounts). In particular, the enormous number of species having the second submarginal cell open (i.e. the traditional genus *Apanteles*, estimated by Mason (1981) to total between 5000 and 10,000 species worldwide) presents a formidable classification problem in both practical and phylogenetic terms. In the relatively recent past, it has been approached in two ways. In the first place, Nixon's (1965) pioneering reclassification of the subfamily on a world basis results (if allowance is made for later restrictions in subfamilial limits) in an arrangement of the British species in five genera (cf. Microgasterini in Huddleston, 1978), three-quarters of them in the huge but easily recognised traditional genus *Apanteles*. Nixon's work was inspired particularly by the need to identify species, and he divided the traditional genus *Apanteles* into 44 species-groups (which he considered to be more or less 'natural' but without defining that term as holophyletic) that could be recognised and keyed reasonably clearly, as a prelude to a major aim of providing keys to the species of especially N.W. Europe including the British Isles.

Nixon (1965, 1972) appreciated that the traditional *Apanteles* was polyphyletic, but he refrained from formally splitting the genus on the grounds that his (albeit extensive) knowledge of the group was insufficient for him to recognise additional genera that would be durable and thereby more useful than the informal and less rigid species-groups he employed. Nevertheless, he saw the need for more genera to be recognised eventually and, in the second major approach to the systematics of Microgastrinae in recent years, Mason (1981) sought a more precise phylogenetic

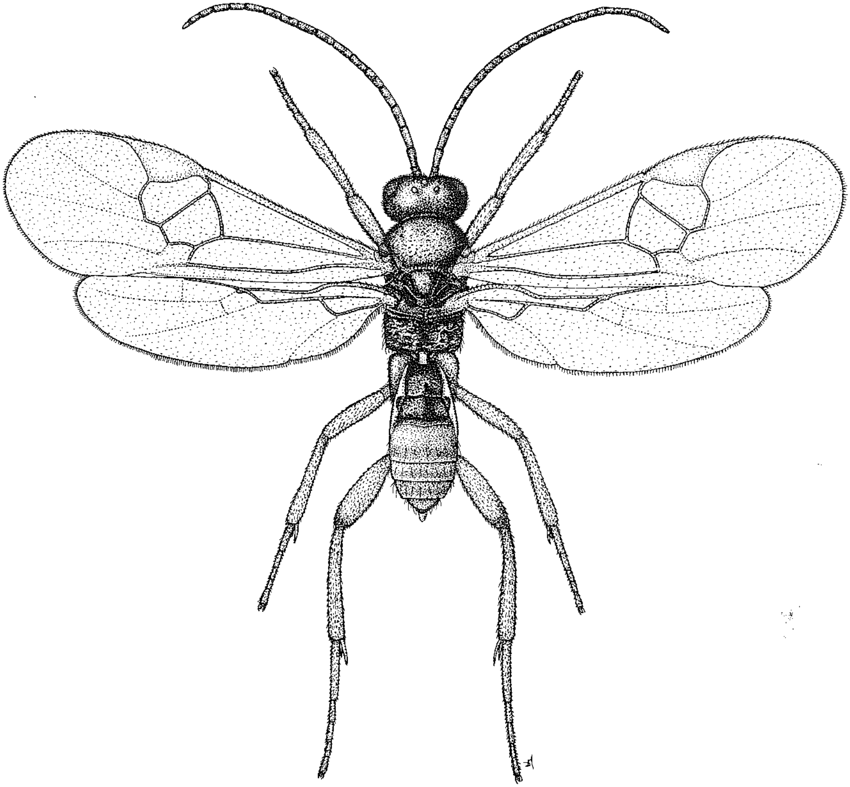

Fig. 124. *Apanteles glomeratus* (Linnaeus) (= *Cotesia glomerata* (Linnaeus)), Microgastrinae.

justification for many additional genera. Although it was also aimed at resolving the particular difficulties presented by the traditional genus *Apanteles*, Mason's approach was a more scientifically oriented attempt to derive a natural classification for the subfamily as a whole, in that it employed formal phylogenetic techniques. Mason's (1981) analysis led him to recognise 50 extant genera of Microgastrinae arranged in five tribes, compared with Nixon's 19 genera in one tribe. Although in many cases Nixon's species-groups are more or less co-extensive with the newly defined genera, Mason has erected a hypothesis about the evolutionary relationships between them that is much more positive, and therefore more open to criticism, than anything proposed by Nixon.

Although few objectively expressed criticisms have yet been raised in print (but see Walker, Kitching & Austin, 1990, published while our work was in press), Mason's scheme has been largely rejected by Tobias (1986) and many systematists would concur with Austin (1989, 1990) that Mason's classification should represent no more than a first hypothesis – which is, indeed, the spirit in which Mason presented it – as several important assumptions of his seem questionable and many relationships are still unclear. However, Mason's classification has been widely adopted by applied biologists, and it is rather unfortunate that such a large number of generic names are being taken up so enthusiastically in advance of further critical analysis of the group by systematists, which remains a clear need. In the present work we have opted to continue to use Nixon's classification rather than Mason's for further reasons that are essentially practical: (1) keys at species level to the British fauna are all organised along Nixon's lines; (2) not all British species run smoothly to genus in Mason's key (even though new generic placements have now been published by Papp (1988)); (3) some of the biological literature on unidentified species of *Apanteles* sensu lato would still be unplaceable in Mason's classification, and (4) to follow Mason would not, on balance, simplify our presentation of information. However, we include both alternatives in the checklist of genera.

In Britain most more or less exposed lepidopteran larvae are subject to attack from at least one species of microgastrine, and it is not unusual for two or even more to parasitise a given host population. While these parasitoids sometimes each have a wider host range, a few Lepidoptera support more than one apparently monophagous microgastrine species: a situation rarely paralleled by other ichneumonoid subfamilies. Although the greatest radiations of microgastrines have been in association with exposed caterpillars of macrolepidoptera, endophytic hosts are only a little less prone to attack. Some microgastrines have long ovipositors with which to reach hosts concealed in relatively soft substrates such as flower heads, leaf rolls and fungi, and others are specialised to attack leaf-mining hosts. In addition, many Lepidoptera whose late-instar larvae are deeply endophytic are sought early in their life when they are more accessible. However, far fewer species of the more primitive groups of Lepidoptera (Zeugloptera, Dacnonypha and Monotrysia) are attacked, and some of those that are have clearly been incorporated into the host range of a particular microgastrine species that parasitises an ecologically similar group: for example, some species regularly attacking leaf-mining Gracillariidae can also be reared from Tischeriidae.

In general, microgastrines, like most koinobionts, have fairly narrow host ranges though a few plurivoltine species attacking arboreal caterpillars in particular use rather disparate hosts successively as the season progresses. Most species oviposit into early or middle-instar hosts, but a few species of *Protomicroplitis* (Zorin, 1930, as *Microgaster*) and in the *glomeratus*-group of *Apanteles* (Johansson, 1951; Tadić, 1958; Wilbert, 1960) are known to oviposit into host embryos: although this behaviour may be only facultative in some cases (Johansson, 1951; Wilbert, 1960), in others the tip of the ovipositor sheath is modified in a way suggesting that attacking the host egg is usual (cf. *Rasivalva* of Mason, 1981, and *Apanteles hyphantriae* Riley).

Other unusual oviposition behaviour has occasionally been noted: for example Yeargan & Braman (1986) record and illustrate a case in which the female habitually attacks hosts after sliding down the escape threads they use to drop temporarily from leaf edges.

Gregarious development has apparently arisen on many occasions within Microgastrinae, and it occurs in most genera and in most species-groups of *Apanteles* (except those that attack only very small hosts), though often in a minority of species. In gregarious species all the eggs are usually squirted into the host with one insertion of the ovipositor, though some species are said to make repeated insertions (De Saeger, 1937). Broods are typically of about 10–40, though in some species considerably smaller or larger broods are normal. Le Masurier (1987) analysed brood size in gregarious *Apanteles* species in relation to host size, Kitano (1976) recorded the incidence of sibmating in a gregarious species, and Whitfield (1987) noted swarming behaviour in a solitary species.

The winter is generally passed as a cocooned prepupa or else as a first- or, in some of the gregarious species, perhaps as a second-instar larva (cf. Laing & Levin, 1982) in the host. Most microgastrines can overwinter in only one way, but in a few species of the *Apanteles glomeratus*-group both modes are seen in the same species (e.g. Parker, 1935; Allen, 1958; Laing & Levin, 1982), and in *Apanteles glomeratus* (Linnaeus) itself the overwintering stage depends on the species of host being parasitised.

The host associations of *Microgaster* species (cf. Opinion 1510, 1988), which are relatively large microgastrines with clearly exserted ovipositors and undoubtedly towards the ancestral end of the subfamily, are limited by host biology in an interesting way. Most are solitary parasitoids attacking the early instars of moderately large, silk-spinning microlepidoptera, for example tortricids and oecophorids, and they kill the host either as a prepupa or, often, in sites such as leaf-spinnings that the late-instar host larva makes in which to rest or feed. The *Microgaster* larva kills the host and issues from it to complete its feeding externally (e.g. Vance, 1932b), depending for shelter on the host's retreat. The host range of the genus extends to some species of nymphalid and hesperiid butterflies, but only to those whose larvae make suitable retreats in which the final ectophagous development of the parasitoid can take place. Just one species, attacking abnormally large hosts for the genus, is gregarious. The cocoon is always white and moderately stout: some species overwinter within it, but others overwinter in host larvae.

A number of *Microplitis* species are also relatively large but, in contrast with *Microgaster*, *Microplitis* species are among the most advanced microgastrines. They are wholly endoparasitic, have almost concealed ovipositors, and predominantly attack exposed macrolepidoptera. Most British species parasitise noctuids, though a few specialise on other families such as Sphingidae, Notodontidae or Geometridae. Many of their hosts live fully exposed on vegetation throughout their larval stages and are killed by solitary species as partly grown larvae. Because *Microplitis* species are essentially haemolymph and fat-body feeders, in many cases these hosts remain alive for several days after the parasitoid larva has emerged, which usually takes place from a central or posterior abdominal segment. The cocoon is then formed either beneath the quiescent host or as a projecting, longitudinally fluted lozenge which may eventually be brushed off as the dying larva moves around. Cocoons formed beneath quiescent hosts may hatch before the host has died or they may outlast it and persist through the winter. In either case the cocoon probably derives some protection from the moribund host, either because it is cryptic or aposematic or, perhaps, just because the stricken host would be a better target for a passing predator. Overwintering cocoons are usually very tough, either strongly fluted or else dark brown and parchment-like. Cocoons whose occupants are destined to emerge within a week or two are usually thinner and less fluted, and of a lighter grey colour or, in several species, a quite striking green. Probably the winter is passed in the cocoon stage by all British *Microplitis*, and plurivoltine species have dimorphic cocoons. A few species are gregarious and typically kill the host as a prepupa, but even these feed only on the haemolymph and fat-body and leave much of the host unconsumed.

Protomicroplitis species, of which Nixon (1965) recognised several disparate species-groups, are also predominantly haemolymph and fat-body feeders and, like *Microplitis* (to which they are not very closely related) and certain groups of *Apanteles* (to some of which they are), they often have interesting cocoon-forming strategies and sometimes an association with the host that persists after the emergence of the parasitoid larva. The commonest British species attack macrolepidoptera. One solitary species attacking conifer-feeding geometrids always forms its yellow-brown cocoon at of the very tip of a needle, in contrast to the host's usual resting place towards the needle base. Gregarious species attacking large geometrids cause the host to arch as they emerge, and a neat honeycomb of pinkish brown cocoons is formed in the semicircular space between the host and the twig on which it rested. A majority of the solitary species make plain white cocoons, sometimes in semi-concealment.

In overall terms it is difficult to say more than that other British microgastrines, which are mostly *Apanteles* sensu lato, have host relations that range between the extremes represented by *Microgaster* on the one hand and *Microplitis* and *Protomicroplitis* on the other. Cocoon structure is very varied: while species that kill the host in a concealed site usually form relatively simple white cocoons, similar to those of *Microgaster* though on the whole less robust, some of the species that spin their cocoons in exposed sites produce much more elaborate and sometimes highly characteristic structures. Some entire species-groups of *Apanteles* (for example the relatively primitive *ater*-, *metacarpalis*- and *laevigatus*-groups) are associated with more or less concealed microlepidoptera, make rather featureless white cocoons in the host's pupation or resting site, and are almost invariably solitary: the host is usually fully consumed save for its cuticle and in several species, at least, this is accomplished through a final ectophagous stage (e.g. Basinger, 1938). Leaf-miners are attacked by the invariably solitary members of the *circumscriptus*- and *carbonarius*-groups: in some of the former the cocoon is suspended, hammock-like, from threads at either end in tentiform mines, keeping it clear of the leaf epidermis and no doubt helping to limit attack from eulophid pseudohyperparasitoids, while in the *carbonarius*-group the host is not killed until it has made its own cryptic cocoon remote from the feeding site.

Others, such as the *vitripennis*-group, use larger and more exposed hosts, usually macrolepidoptera: the parasitoids are haemolymph and fat-body feeders and, if solitary, kill the host before it is fully grown and form simple white or yellow cocoons exposed on leaves, although gregarious species more often kill the host as a prepupa in concealment. The winter is very often passed as an early, probably first, instar larva in the host and some of the commonest species are plurivoltine, using different species of univoltine hosts occupying similar niches (usually on tree leaves but sometimes in the herb layer) at different seasons, involving quite broad host ranges overall. The same tendency is seen in a few species of the *glomeratus*-, *popularis*- and *ultor*-groups, and this alternation of hosts is one way in which rapidly developing species can exploit purely aestival, exposed, univoltine macrolepidopteran larvae, which constitute a very plentiful resource, without reducing to a univoltine way of life with a very long cocoon stage.

In the *glomeratus*-group several locally monophagous species achieve plurivoltinism in association with univoltine hosts in a different way. The host is generally one that feeds in late summer, overwinters, and feeds again the following year, and the parasitoids have successive generations on the single host generation, using the host also as an overwintering vehicle. In some of these species the parasitoid is solitary at all times (e.g. Parker, 1935) and in others it is first invariably solitary and then gregarious (e.g. Wilbert, 1960), but in most known cases there is a small brood of perhaps one to five individuals in early-instar hosts and subsequently one or occasionally two further generations involving larger broods as the available hosts get bigger. At least one species accelerates the host's breaking of winter diapause (Parker, 1935), presumably improving the synchrony between the resulting adult parasitoids and healthy hosts coming out of hibernation, and in some gregarious species the cocoon masses vary appreciably according to season: Porter (1983) found that in one species unemerged adults of the final brood from one host cycle aestivate in their more substantial cocoon mass to await the new host generation.

The *glomeratus*-group is the largest species-group of *Apanteles* in Britain and about two-thirds of its species are gregarious. The great majority, but not all, parasitise macrolepidoptera and most species feed only on the haemolymph and fat-body, vacating the incompletely consumed host in a fairly exposed situation. Cocoons in the *glomeratus*-group range in colour from white to various shades of yellow or occasionally pink or brownish, but it is in their structure that they vary most strikingly. Several species produce simple, ovoid cocoons, either singly or untidily heaped around the host remains and connected to one another by only a few strands of silk. Some gregarious species spin cocoons individually sprouting from the host's body as the larvae emerge, and these may fall from the wandering host leaving the brood scattered rather than aggregated. In others, however, the larvae emerge absolutely synchronously and align in a tight group, spinning copiously as they do so to form an array of closely packed cocoons surrounded by loose, fluffy silk, the whole structure ending up as a large ball up to an inch across. Such cocoon masses are common in low vegetation in summer, where the risk from pseudohyperparasitoids is particularly great. Some species in the *vitripennis*- and *pallipes*-groups produce very similar silken balls and, as the stricken host subsequently crawls out of and away from these masses, such cocoons are often mistaken for spider's egg sacs. A few of the solitary species in the *glomeratus*-group spin cocoons under an outer net or sheet, or with a dorsal tuft, passing the winter in these relatively robust structures. Only in a very few cases are overwintering cocoons fluted. Isolated species of *Apanteles* in smaller species-groups produce cocoons in honeycomb-like masses, rather like those of some *Protomicroplitis*, either exposed or in one case below ground, and one solitary species is remarkable for spinning its exposed cocoon raised from the substrate on a pedicel. Several species of the *glomeratus*- and *vitripennis*-groups parasitising low-feeding hosts limit pseudohyperparasitism by causing the hosts to climb up vegetation before the parasitoids erupt (e.g. Strickland, 1923; Calkins, 1977; Stamp, 1981; Sato *et al.*, 1983). Cocoon formation is typically started while the parasitoids' caudal segments are still within the host, and it is also typical of these groups that just before they emerge the parasitoid larvae moult to their third instars and leave their exuviae plugging the emergence holes.

Several microgastrines are important parasitoids of pest Lepidoptera and consequently biological studies on the group have been fairly plentiful, though they mainly involve relatively advanced microgastrines such as *Microplitis* or the *glomeratus*- and *vitripennis*-groups of *Apanteles*. *Apanteles glomeratus*, in particular, has been subjected to considerable study in laboratory culture (see Laing & Levin, 1982 for a review of literature to that date). In several studies the hosts of microgastrines have been found to suffer a brief spell of temporary paralysis when attacked. Eggs laid into the host haemocoel have in some cases been found to adhere loosely to internal organs by the terminal parts of their pedicels (King *et al.*, 1969), and they swell considerably before hatching (e.g. Vance, 1931; Fallis, 1942; Allen, 1958; Sato, 1980; Arthur & Mason, 1986). Teratocytes are liberated as the egg hatches (e.g. Tower, 1915), though in some cases the serosal cells surround the first-instar larva for several weeks (Vance, 1931). The teratocytes absorb nutrients and are almost certainly later consumed (Arakawa & Kitano, 1989), but they have been considered also to have secretory functions by several authors (cf. Stoltz, 1986).

Four larval instars may occur in some *Microplitis* (e.g. Hegazi & Führer, 1985; Strand *et al.*, 1988) and the same has been reported in at least one species of *Apanteles* (Porter, 1983). However, most studies on *Apanteles* and other microgastrines, including some *Microplitis* (Lewis, 1970; Puttler & Thewke, 1970), have revealed only three. First-instar larvae are mandibulate and aggressive at least in solitary species, though other means of suppressing competitors seem also to exist (Muesebeck, 1918; Hegazi & Führer, 1985). The larvae are caudate at first, but soon develop an anal vesicle, which may have a respiratory function (Muesebeck, 1918; Gatenby, 1919) though Edson & Vinson (1976, 1977) doubted this and considered it to be an organ for excretion and nutrient absorption. The vesicle, which persists until the third instar is reached, when it invaginates, has been seen to hold up the exuviae of earlier instars in several studies. Second-instar larvae have greatly reduced mandibles, but generally appear to feed on the fat-body in addition to haemolymph.

The final instar has more powerful and usually at least partly serrate mandibles, which are used to scrape through the host integument and, in groups with a final ectophagous phase and strongly serrate mandibles, to consume the remaining tissues. Open spiracles and a developed tracheal system are not present until the third instar. As outlined above, cocoon structure is extremely varied within the group, but in all cases a neatly circular cap is cut by the emerging adult. The loss of the final ectophagous phase, retained only by the more primitive groups of microgastrines, has left the more advanced groups with a non-feeding final larval instar which has presumably been able to specialise in cocoon construction. However, in a few *Microplitis* (Lewis, 1970; Arthur & Mason, 1986 – but contrast Puttler & Thewke, 1970) and in at least one group of wholly endoparasitic *Apanteles* (Muesebeck, 1918) the final instar does appear to feed internally for a time.

Many detailed studies on the physiological interactions between microgastrines and their hosts have been published in recent years. As well as investigations of the physiological effects of actual parasitism on the host, considerable attention has been focussed on the regulatory and protective functions of venoms, including the virus-like particles (some now classified as the virus family Polydnaviridae) that are produced in the female's reproductive tract and injected along with the eggs. Reviews and leading references not included in Laing & Levin (1982) include Stoltz & Vinson (1979); Beckage (1985); Osman *et al.* (1985); Kitano (1986); Stoltz (1986); Beckage *et al.* (1987); Styler *et al.* (1987); Tanaka (1987a,b); Hegazi *et al.* (1988); Stoltz, Guzo *et al.* (1988); and Strand *et al.*, (1988).

Identification. Nixon (1965), key to world genera and species groups, and keys to species of *Hypomicrogaster* and groups of *Protomicroplitis* occurring in Europe; Nixon (1968), world *Microgaster*; Nixon (1970), N.W. European *Microplitis*; Nixon (1972, 1973, 1974, 1976), N.W. European species of *Apanteles* sensu lato [the 1973 paper includes a key to N.W. European species-groups]. Wilkinson's detailed work on the taxonomy of individual species of *Apanteles*, beautifully illustrated by Terzi, is fully referenced in Nixon's papers. More recently Papp (1976b–1988) has keyed and discussed European *Apanteles*, including many species described by himself and by Russian authors, and he has proposed a large number of synonymies, particularly of Nixon's species. Papp has also treated European *Microgaster* (1976a) and *Microplitis* (1984c, as *Microgaster*). Mason (1981), reclassification of the subfamily and key to redefined genera.

Subfamily Miracinae

This is a small subfamily containing only about 15 described species worldwide. It had traditionally been included within Microgastrinae (e.g. Nixon, 1965; Čapek, 1970; Huddleston, 1978) until given subfamily status by van Achterberg (1984b), who proposed a placement far removed from the restricted Microgastrinae. Only a single species, *Mirax rufilabris* Haliday, has been formally recognised as British, although we have seen material that supports Richards's (1957) suggestion that further species may be present. They are small, squat and fairly dark insects, easily recognised by their characteristic wing venation (fig. 51) and 14-segmented antennae. *Mirax* species are solitary koinobiont endoparasitoids; in Britain, only nepticulid Lepidoptera (especially those mining low plants) appear to be hosts, but some tropical species parasitise *Leucoptera* (Lyonetiidae) (Wilkinson, 1936; Muesebeck, 1937) and in North America several groups of leaf-mining Lepidoptera are attacked (e.g. Walley, 1941; Whitfield & Wagner, in press). The winter is passed in the host's cocoon, from which (at least if it is a nepticulid) the adult parasitoid emerges through a neatly cut, circular hole some distance from the apex. We know of no detailed studies on the developmental biology of miracines.

Identification. Papp (1984a, 1989), W. Palaearctic *Mirax*.

Subfamily Neoneurinae

This is a small, Holarctic subfamily consisting of about ten rarely collected species in three genera. Three species of *Neoneurus* are recorded from Britain but only one, *N. auctus* (Thomson), can be recognised with certainty. Neoneurines are small, dark insects that superficially resemble microgastrines, although their characteristic wing venation (fig. 59) at once distinguishes them from all other Braconidae. Tobias (1966) placed the group within Euphorinae, largely on the grounds of development within the adult stage of the host, but although some affinity was supported by Čapek (1970) this placement has not been accepted by most subsequent workers (cf. Shaw, 1985), and van Achterberg (1984b) placed Neoneurinae close to Microgastrinae and far removed from Euphorinae.

The non-British (cf. Nixon, 1934) genus *Elasmosoma* has been recorded as ovipositing into the abdomens of adult worker ants of the genus *Formica* (Olivier, 1893; Pierre, 1893; Wasmann, 1897; Kariya, 1932) and field observations on *Neoneurus* species suggest that this genus also has a relationship with ants. Having emerged from its host, the fully grown parasitoid larva evidently spins its cocoon without straying from the host remains, for Wasmann (1897) reared a specimen of *Elasmosoma* from a cocoon found attached externally to the excavated abdomen of a dead worker in an observation colony of a *Formica* species. Čapek (1970) evidently saw a larva of *Neoneurus auctus*, but he does not record associated data.

Identification. Huddleston (1976), keys to genera (and to *Elasmosoma*). There is no modern treatment of *Neoneurus*.

Subfamily Opiinae

(Fig. 125)

This is a large subfamily containing over 1300 described species worldwide. About 100 species in four genera are recorded from Britain, almost all belonging to the cosmopolitan genus *Opius* sensu lato. Most opiines are small, squat and weakly

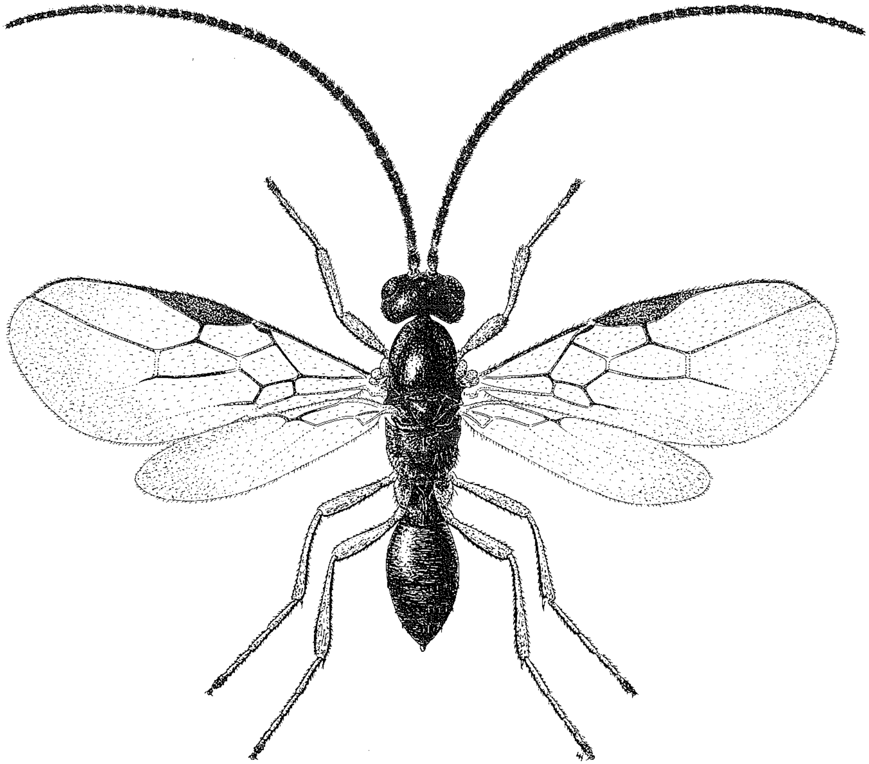

Fig. 125. *Biosteres* sp., Opiinae.

sculptured. They are usually rather uniformly brown or blackish but a few are more brightly marked with orange or yellow. The clypeus is often broadly emarginate so that there is a space between it and the mandibles when closed (fig. 28). This opening is usually relatively narrow, but in extreme cases it can lead to confusion with the 'cyclostome' subfamilies, and in particular Braconinae and Exothecini (Rogadinae) with which all opiines (except *Ademon*) share the lack of a prepectal carina. Opiines differ, however, in that the labrum remains more or less flat rather than being strongly concave. They can also be distinguished from braconines by their longer sub-basal cell in the hindwing (usually at least half as long as the basal cell in opiines but never more than a third as long in braconines) but they are not separable from exothecines on this character. In comparison with exothecines most opiines have distinctly broader and more triangular forewings, in which a long and apically narrowed second submarginal cell and sometimes a narrow and protracted pterostigma may also be diagnostic. The genus *Ademon*, with one British representative, is the least characteristic of the Opiinae, as it has both a discernible prepectal carina and granulate sculpture on the second and third tergites and completely lacks the broad-winged, hunched facies typical of the subfamily. A useful supplementary character for recognising *Ademon* is the incomplete vein 3Rs in the forewing (fig. 90).

Opiines are regarded by most workers as being closely related to the alysiines, these two groups probably having a common ancestry somewhere within the cyclostome group that includes the subfamilies Rogadinae, Doryctinae and Braconinae. However, in many features of their morphology and general biology opiines appear to be closer to the cyclostome group than are alysiines, suggesting that Opiinae (for which clear autapomorphies have always been elusive) may be paraphyletic with respect to Alysiinae. The internal classification of Opiinae has been much bedevilled by the use of inappropriate characters, as was thoroughly discussed by Wharton (1988b), who proposed considerable reorganisation. Much still remains to be done to establish generic limits, and in this subfamily the biological literature is therefore particularly difficult to relate to meaningful generic names.

All opiines are solitary koinobiont endoparasitoids of phytophagous cyclorrhaphan Diptera. Published biological and taxonomic information on the subfamily has been indexed by Fischer (1971b), although the generic concepts employed are outdated, and much of the subsequent literature can be traced via Wharton (1988b). In Britain most opiines are associated with leaf-miners, but in warmer climates the subfamily has important associations with Tephritidae, especially those infesting fruit, giving Opiinae a relatively high status with respect to biological pest control. Most British *Opius* are small and parasitise leaf-mining Agromyzidae, though a number of larger species attack leaf-mining Anthomyiidae (*Pegomya* and *Cheirosia*) and Tephritidae. The opiines attacking agromyzids generally have broader individual host ranges than the dacnusiine alysiines attacking the same host group. They include a group with long ovipositors parasitising hosts in seed heads but, in contrast with dacnusiines, opiines do not appear to have evolved specialised forms that parasitise stem-boring hosts (H.C.J. Godfray, personal communication). Similar restrictions, at least in Britain, occur in other host groups: for example the only anthomyiids attacked seem to be the leaf-mining *Pegomya* and *Cheirosia* species, and the many tephritids feeding in various ways in the capitula of Compositae seem not to be parasitised whereas the leaf-miners and the small numbers of species living in berries generally are. The dozen or so British species of *Biosteres*, as restricted by Wharton (1988b), are large opiines and probably entirely associated with leaf-mining Anthomyiidae of the genus *Pegomya*. The small genera *Eurytenes* and *Ademon* each contain only a single British species: the former has been reared particularly from agromyzids mining grasses and sedges, while *Ademon* parasitises *Hydrellia* species (Ephydridae) mining in submerged aquatic vegetation, and is reputed to use its long legs to swim under the surface of the water (see references in Fischer, 1971b).

Most of the information on the developmental biology of opiines has arisen from studies on tropical or subtropical species associated with tephritids developing in fruit in the New World (cf. Wharton & Marsh, 1978), and these are probably not even congeneric with any British opiines. However, one study of a British *Opius* species parasitising a leaf-mining agromyzid (Cameron, 1941) revealed such similarity that the following summary seems likely to be general. A few opiines are known to oviposit into the host egg (van den Bosch & Haramoto, 1951; Prokopy & Webster, 1978) but in general oviposition is into the host larva, sometimes while it is still young but quite often only rather late in its life. Some species invest female eggs preferentially in the larger hosts encountered (Avilla & Albajes, 1984), a habit commonly seen in idiobiont parasitoids but much less usually observed in koinobionts, and probably connected with an ancestry of very late attack on the host. The obligatory pre-oviposition period noted in some species (Willard, 1920) and the temporary paralysis of the host at the time of oviposition (Glas & Vet, 1983) also suggest that opiines may not be very far removed from an ancestry of idiobiosis and, no doubt, ectoparasitism. Orientation to the host can be facilitated by marking pheromones left by the female flies (Prokopy & Webster, 1978) or by fermentation products (Greany *et al.*, 1977), but visual cues followed by vibrotaxis (Glas & Vet, 1983) are perhaps often sufficient.

The egg is deposited just below the host's cuticle (Pemberton & Willard, 1918b; Lathrop & Newton, 1933) and is sometimes attached to the cuticle by one end (Willard, 1920). There is some indication that venoms modifying the host's physiology may also be injected (Yao, 1987), but there is apparently only one insertion of the ovipositor. The egg swells before hatching, and a mass of serosal cells at first surrounds the first-instar larva but they later disappear without developing into teratocytes (Pemberton & Willard, 1918b; Willard, 1920; Cameron, 1941). The first-instar larva generally bears fleshly processes on the first, and sometimes also the third (Kellin & Picado, 1913), body segments and has a discernible, though closed, tracheal system. It also has powerful mandibles which are undoubtedly used for fighting (Pemberton & Willard, 1918a), though other means of suppressing competitors are also employed (Lawrence, 1988). The first instar always persists until the hormonal changes accompanying host pupation trigger the parasitoid's moult to the second instar (Lawrence, 1982, 1986).

The second- and third-instar larvae apparently lack a tracheal system and have much reduced mandibles, feeding largely on fat globules and other semi-liquids arising from the host's internal histolysis. The fourth, final, instar has a tracheal system with functional spiracles and well-developed, untoothed mandibles, which are used to clean out the host's puparium, in which the parasitoid will pupate, oriented head to head, without either spinning a cocoon or voiding meconium. Except for those that can overwinter as a first-instar larva in a growing host (e.g. Cameron, 1941), temperate species pass the winter in the host puparium as a post-feeding final-instar larva: in some cases two or more winters are regularly passed (Lathrop & Newton, 1933), and it is of interest that this habit is not uncommon among tephritids. Emergence takes place through an irregularly chewed hole and, as in Alysiinae, the adult voids the meconium that has been retained throughout development (Pemberton & Willard, 1918b).

Identification. Fischer (1972b, 1986), Palaearctic species. Wharton (1987, 1988b) has proposed much rearrangement of the generic and suprageneric classification, and gives valuable information on the character states involved.

Subfamily Orgilinae

This is a medium-sized subfamily containing nearly 250 described species worldwide. The vast majority, including all those found in Britain, belong to the genus *Orgilus*, and so far as is known all species are solitary koinobiont endoparasitoids. Although the genus is cosmopolitan, *Orgilus* species are concentrated in the Holarctic region. Twelve of the 76 Palaearctic species recognised by Taeger (1989) are known to occur in Britain, though few of them commonly. They are dark and small to medium-sized braconids, with a rather elongate yet robust build, enlarged hind legs and narrow wings. Among groups with only two submarginal cells they may be distinguished by their narrow heads with strongly protuberant face and clypeus (figs 103, 104). Although a few species attack arboreal hosts to which they presumably fly, most parasitise hosts in low vegetation and probably search mainly on foot; in fact females of a few species are brachypterous. Van Achterberg (1987b) discusses the systematics of the subfamily, which he places closest to Helconinae.

The hosts are microlepidopteran larvae with a partly endophytic way of life – especially those with leaf-mining or tunnelling early instars, whose activities are given away by extruded frass. The females tend to probe such workings with their exserted ovipositors rather than pierce plant tissue directly in their search for hosts (Flanders & Oatman, 1982). Coleophoridae and Gelechiidae have provided the most host records, though other families such as Tortricidae and Oecophoridae are also parasitised. In most cases hosts are attacked in early (Juillet, 1960; Flanders & Oatman, 1982) or middle (Johnson & Smith, 1980) instars, though some studies have shown that attack on late-instar hosts can be successful (Broodryk, 1969b; Oatman *et al.*, 1969).

The egg is laid at random in the haemocoel and swells subsequently, when there is a tendency for it to adhere to internal organs (Broodryk, 1969b; Flanders & Oatman, 1982). Serosal cell masses surround the newly hatched larva but soon disperse (Broodryk, 1969b): teratocytes have not been noted and so presumably do not develop. The first-instar larva, which is the overwintering stage in most or possibly all temperate species, has large fighting mandibles but is not necessarily an effective inter-specific competitor (Schröder, 1974). At first it is caudate but it gradually becomes vesiculate towards the first moult, and a closed tracheal system has been discerned in at least one study (Oatman *et al.*, 1969). Although parasitism by *Orgilus* disrupts the host's development (Syme & Green, 1972) and reduces its size (Flanders & Oatman, 1982), the moult to the second instar does not take place until around the time that the host completes its feeding to seek a pupation site. The second-instar larva has much reduced but functional mandibles and feeds on the fat-body (Broodryk, 1969b). Oatman *et al.* (1969) present evidence that there are only three larval instars, and the final one, which is armed with serrate mandibles, emerges from the prepupal host to complete its feeding externally (Broodryk, 1969b; Flanders & Oatman, 1982). The whitish cocoon is spun in situ and the adult emerges from it through an irregularly chewed hole.

Identification. Taeger (1989), Palaearctic *Orgilus*.

Subfamily Rogadinae

(Fig. 126)

This is a moderately large subfamily, containing about 800 described species in around 90 genera. In Britain there are approximately 70 species treated in 15 genera that can be arranged provisionally in six tribes. (We have deleted the genus *Compressaria* from the checklist on C. van Achterberg's advice that this poorly

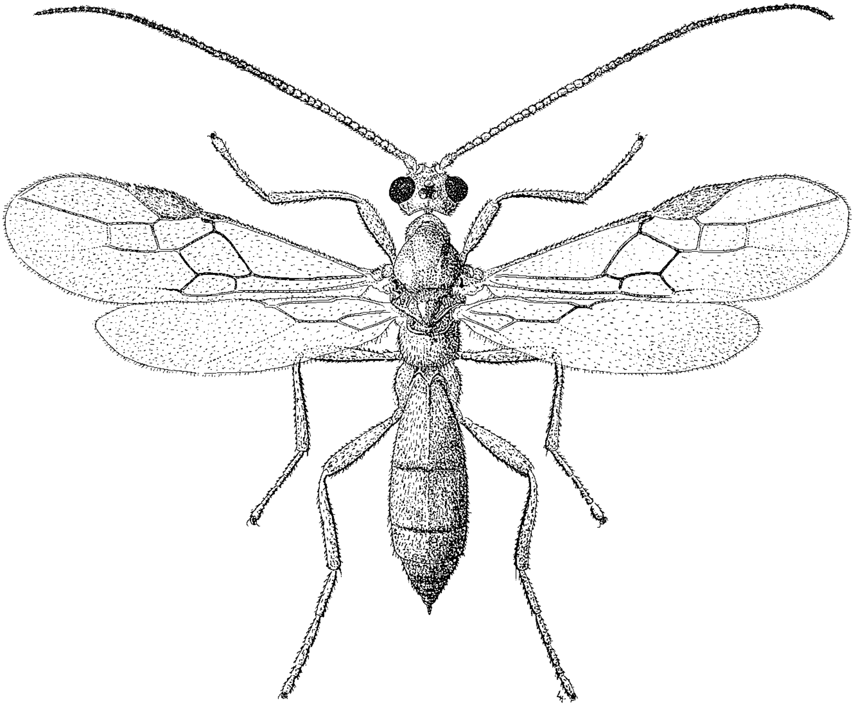

Fig. 126. *Aleiodes pallidator* (Thunberg), Rogadinae.

understood name will be synonymised within Opiinae). As currently interpreted the subfamily is exceptionally heterogenous, even among the cyclostome groups. This is partly because it has been used as a 'dumping ground', in that problematical taxa, excluded from other cyclostome or related subfamilies as these were being critically redefined by synapomorphies, have often been provisionally assigned to the Rogadinae with little justification other than that they were not relevant to the study in hand (e.g. Marsh, 1965; Quicke, 1987b; Wharton, 1988b). This understandable practice is a reflection of less effort having been made to define Rogadinae on the same grounds: being the last of the major cyclostome (or related) subfamilies to come under modern specialist review, it has been left with its boundaries undefended during an active period in the higher classification of the Braconidae. In its broadest interpretation, which is the one that we follow here, the subfamily Rogadinae is likely to be at least paraphyletic, and it is sometimes particularly difficult to assign included forms to it when sorting unfamiliar braconids at the subfamily level. Although recent authors have started to reject some elements from Rogadinae, suggesting alternative placements in an effort to narrow the subfamilial limits (e.g. Belokobylskij, 1984; see also Čapek, 1970), the real need in order to accommodate these problematical groups optimally is for rigorous phylogenetic analysis encompassing all of the basal groups of cyclostome, and indeed other, braconids. In the meantime a pragmatic approach is appropriate, and we are continuing to accept the provisional placement in Rogadinae of cyclostome groups that have not been positively incorporated elsewhere during recent reclassifications of other subfamilies. In Britain a braconid having a 'cyclostome' strongly emarginate clypeus and concave labrum, an occipital carina clearly discernible at least laterally and three submarginal cells in the forewing (sometimes two cells or apterous in *Pambolus*), and lacking spines in a row or cluster on the outer aspect of the front tibia, will probably be a rogadine (but see also notes under Braconinae, Doryctinae, Gnamptodontinae and Opiinae).

Even in a narrower sense, which might for example exclude Hormiini, Pambolini and Acrisini, the subfamily Rogadinae exhibits immense biological diversity. While the more advanced rogadines (i.e. Rogadini) have radiated greatly as endoparasitoids of more or less exposed Lepidoptera, the subfamily also includes species that are ectoparasitoids variously of Lepidoptera, Diptera, Coleoptera and Hymenoptera, and there is little doubt that the subfamily had its origins among more concealed hosts, developing some important affinities for leaf-miners in particular. Life-histories range almost on a continuum from idiobiont ectoparasitism to koinobiont endoparasitism, making the subfamily Rogadinae particularly interesting biologically. Indeed, the mechanisms underlying the transition, or perhaps several transitions, from ectoparasitism to endoparasitism that must have occurred within the group can be understood, at least in broad terms, from a consideration of the biology and host relations of even a small number of extant genera of Exothecini, Rhyssalini and Rogadini (M.R. Shaw, 1983b, using nomenclature now in part superseded).

Hormiini, Pambolini and Acrisini are all very small tribes in the British fauna, and none of the included species is at all common. Biological information is on the whole scanty, though there is a photographically illustrated account of *Chremylus* as a gregarious ectoparasitoid of case-bearing tineid moths (Mason, 1948). A remarkable exotic genus (*Cedria*, placed in Hormiini) overwinters as an adult and is celebrated for its maternal care (Beeson & Chatterjee, 1935; Clausen, 1940; Mathur, 1959) which is in rather marked contrast to a North American species of *Hormius* that has been recorded as a gregarious external parasitoid of a web-inhabiting tortricid, the female in this case merely ovipositing into the host's web and leaving the first-instar larva to contact the host (Basinger, 1938). Although poorly documented, the British species of *Hormius* also seems to attack microlepidopteran larvae more or less concealed by silk. *Acrisis* has been reared from conifer cones and twigs (Čapek, 1975; C. van Achterberg, personal communication): its host and means of development are not clear, though circumstantial evidence has led to the suggestion that this genus may parasitise Cecidomyiidae (Tobias, 1983). *Chremylus* and *Pambolus* (and also *Rhyssalus*) have been reared from beetle-infested wood, but infrequently and with little or no unequivocal evidence as to the identity of the actual host. A European *Pambolus* species has been reported more than once from Chrysomelidae but again the circumstantial details are not recorded (Leonardi, 1926).

The tribe Exothecini (cf. van Achterberg, 1983e) is better known and is ectoparasitic (M. R. Shaw, 1983b, refuting Beirne, 1946) mainly on late-instar leaf-miners, though *Shawiana* includes a parasitoid of gall-forming sawflies. The egg is often laid merely into the host's enclosure rather than being placed on the host itself. The host range of *Colastes* is particularly broad because one abundant species, *C. braconius* Haliday, will parasitise practically any suitably sized leaf-miner, arboreal or on low plants, including Lepidoptera, Coleoptera, Diptera and (more rarely) Hymenoptera. This breadth is all the more remarkable because host ranges within the subfamily are typically very narrow, even among the near-idiobionts, and indeed other species of *Colastes* are very much more host-specialised and attack only narrow groups of either Lepidoptera or Diptera (e.g. Godfray & McGavin, 1985). Species of *Xenarcha* and *Shawiana* are mainly associated with sawflies, though one species of *Shawiana* attacks leaf-mining beetles. All Exothecini appear to be solitary and they are typically more or less idiobionts, though in *Xenarcha* considerable host growth takes place after attack, and even in the other genera there is normally some temporary recovery of activity following initial paralysis (M. R. Shaw, 1983b). Most but not all species are more or less plurivoltine, and they overwinter as prepupae in their papery or tough, spindle-shaped cocoons which are normally formed in the feeding site. Cocoons of *Shawiana* in captivity have very occasionally overwintered twice.

Two genera of British Rhyssalini have been investigated biologically, but the host associations of the other, rarer, genera remain unclear. *Oncophanes* is a mainly arboreal gregarious ectoparasitoid of late-instar Tortricidae and other microlepidopteran larvae living in leaf-rolls or spinnings, and *Rhysipolis* is a solitary ectoparasitoid of late-instar leaf-miners that change leaves and/or later feed or pupate in other constructions (M. R. Shaw, 1983b). The studied species of both are more or less plurivoltine and overwinter as prepupae in their cocoons. The single British species of *Oncophanes* is a straightforward idiobiont, even to the extent of having a host range abnormally wide for the subfamily, using a venom that permanently paralyses the host and laying eggs only loosely (though very regularly) placed upon it. *Rhysipolis* species, on the other hand, are koinobionts, in particular taking advantage of their hosts' behaviour after the time of attack and, as might be expected, each having a very narrow host range. In *Rhysipolis* the egg is stuck firmly to an intersegmental membrane and the venom employed causes only temporary paralysis, though the host's recovery and resumption of feeding belie the power of the venom, which soon switches the host to a prepupal state and arrests its further development whatever its nominal instar. The parasitoid, which may have partially hatched from its egg while the host was still actively feeding, completes its development in the seclusion of the host cocoon.

The majority of the British Rogadinae fall into the wholly endoparasitic tribe Rogadini, which includes some rather large species. Perhaps the most characteristic feature of Rogadini is that pupation takes place, with or without an inner silken cocoon, inside the dead host's larval skin, which hardens and darkens to become a regularly and often characteristically shaped structure sometimes termed a 'mummy'. The small genus *Clinocentrus* attacks fairly well-grown web-inhabiting or otherwise semi-concealed microlepidoptera from a wide span of families overall, though each *Clinocentrus* species has a very narrow host range. Both univoltine and plurivoltine species are known and they develop as solitary koinobionts, killing their hosts as prepupae with the aid of venoms whose actions are indistinguishable from those of venoms used by ectoparasitic *Rhysipolis* species (M. R. Shaw, 1981a, 1983b). Even the egg placement of *Clinocentrus* reflects an *Oncophanes*- or *Rhysipolis*-like ancestry.

Rogas is represented in Britain by one extremely rare, or probably extinct, species that has been reared solitarily from Limacodidae and Papilionidae: a North American species has been studied as a solitary parasitoid of a zygaenid (Smith *et al.*, 1955). *Aleiodes* (in which we include *Petalodes*: van Achterberg & M. R. Shaw, in prep.) is by far the largest genus in this tribe and attacks macrolepidoptera, usually in second or early third instars. In most cases the host is killed when only partly grown and the mummy is stuck to the foodplant (or often another substrate, following a well characterised behavioural change by the stricken host) by means of a gluey fluid through an antero-ventral slit cut in the host integument by the fully grown parasitoid larva. In a few species the mummy is concealed loose in silk or in the host's pupation site, as in *Clinocentrus*, but the expulsion of fluid always takes place in both *Clinocentrus* (through a sub-caudal slit) and *Aleiodes*, even though it can be so unnoticeable subsequently that its existence has sometimes incorrectly been denied (e.g. by Dowden, 1938). It is of interest that host ranges in *Aleiodes* are often clearly dependent on habitat and sometimes then on the physical characteristics, rather than the relatedness, of the potential hosts found there. Indeed, in some instances the host range of the genus flows back, as it were, into more primitive Lepidoptera such as Pterophoridae and Zygaenidae from ecologically and physically similar but otherwise unrelated hosts like Lycaenidae (M. R. Shaw, 1983b).

In contrast to *Clinocentrus*, the venom of most if not all *Aleiodes* species functions only to cause temporary paralysis to facilitate oviposition (though even this is dispensed with in a few species attacking arboreal hosts), and paralysed caterpillars experimentally intercepted before oviposition takes place recover fully to produce viable adults (M. R. Shaw, 1983b). This ability of *Aleiodes* to occupy hosts through several host moults, unlike other British rogadines, is one of the adaptations that suggests the 'advanced' position of the genus within the subfamily, and it provides the potential to overwinter as an early-instar larva in a growing host. Several species of *Aleiodes* do this, often achieving bivoltinism by making use of different groups of univoltine hosts successively. However, many other *Aleiodes*, including most of the larger and more heavily built species, are associated only with Lepidoptera that overwinter in the pupal stage, in which case they overwinter as prepupae (as do all other British rogadine genera so far as is known), and are usually univoltine. Just a few *Aleiodes* are unusual among British Braconidae in overwintering as adults (but see also Blacinae and Braconinae): so far as is known all of these attack rather abundant arboreal geometrid hosts that overwinter as eggs and feed as larvae in early spring. Presumably overwintering as an adult is a necessary adaptation to exploit such early host species, whose own overwintering strategy has no doubt evolved at least in part to escape parasitism by the more typical parasitoids that are held up by overwintering as prepupae or in living hosts. At least one British species that overwinters as an early-instar larva causes its host to break diapause late (Askew & Shaw, 1986), so helping the parasitoid population to keep in synchrony with that of its only host species.

All British Rogadini are solitary, so far as is known, but gregarious development and adult emergence from enlarged communal mummies through individual holes occurs in some European (van Achterberg & M. R. Shaw, in prep.) and North American (Mason, 1979) *Aleiodes*, as well as in various exotic genera (e.g. Beeson & Chatterjee, 1935; Watanabe, 1962). Egg-larval parasitism is not yet known among Rogadini but, in view of their host associations and other adaptations, it might be expected to have arisen occasionally in *Aleiodes* or related genera, as it has for example in the subfamily Microgastrinae.

Most Rogadinae, even if endoparasitic, lay large and fully yolked eggs. Host-feeding is widespread and may be obligatory in all the ectoparasitic genera. In these, host-feeding is usually destructive, but if the host is much larger than the female parasitoid, as in *Oncophanes*, host-feeding and oviposition can take place on the same host individual (M. R. Shaw, 1983b). Host-feeding is uncommon and usually at most facultative in Rogadini (M. R. Shaw, 1983b), generally being non-destructive and taking place during, or after, oviposition into the same host (e.g. Ahmad, 1943). In a few exotic species of *Aleiodes*, however, it is recorded as being heavy and destructive (e.g. Chatterjee, 1943; Lentz & Pedigo, 1974). Even in endoparasitic Rogadinae actual oviposition usually takes place following a separately administered sting, so that in most endoparasitic species there are two insertions of the ovipositor with a gap of about 30 seconds or more between them. Exceptions occur in some *Rogas* (Smith *et al.*, 1955) and *Aleiodes* attacking fully exposed arboreal hosts: dispensing with the preoviposition paralysis in these cases presumably reduces the risk of hosts falling from their pabulum and starving.

Despite some reports to the contrary (e.g. Viggiani, 1962), there are probably five larval instars in all ectoparasitic genera (e.g. Dowden, 1941; Mason, 1948; Eichorn & Pschorn-Walcher, 1973), and most authors record five for *Rogas* (Smith *et al.*, 1955) and *Aleiodes* (e.g. Dowden, 1938; Ahmad, 1943) although only three have been distinguished in some studies (e.g. Boldaruev, 1958). In ectoparasitic rogadines the first-instar larva, which in some but not all genera has to find its paralysed host (M. R. Shaw, 1983b), has long antennae and cuticular spines, and all instars have open spiracles (e.g. Dowden, 1941; Viggiani, 1962). In *Aleiodes*, on the other hand, the first instar lacks setae, the tracheal system does not develop until the second instar, and functional spiracles appear only in the final instar (Dowden, 1938; Ahmad, 1943). Interestingly, *Rogas* is intermediate in having a developed tracheal system in the first instar (Smith *et al.*, 1955). As in ectoparasitic species, the first-instar larvae of the endoparasitoids have somewhat hooked mandibles but these are not especially enlarged, even in species that overwinter as first-instar larvae in the host (e.g. Dowden, 1938). The mandibles of the final-instar larvae are simple, in contrast to the partially serrate structures seen in ectoparasitic rogadines (Čapek, 1970). Emergence from the cocoon, or host mummy, is via a chewed subapical hole: it is of interest that adult *Rogas* (Smith *et al.*, 1955) and *Aleiodes* practically always emerge at the caudal end and through the dorsum of the host's skin, while *Clinocentrus* species nearly always emerge from the capital end but with no particular dorso-ventral bias.

Identification. Van Achterberg (1983d), Palaearctic genera of Exothecini and N.W. European species of *Shawiana* and *Xenarcha*; Papp (1975), European species of *Colastes*, with some *Shawiana* (as *Colastes*); van Achterberg & M. R. Shaw (in prep.), European *Aleiodes*.

Subfamily Sigalphinae

This is a small subfamily containing about ten species worldwide. Two genera, *Acampsis* and *Sigalphus*, have been recorded from Britain, each represented by a single species. However, we have been unable to trace any British specimens of *Sigalphus* and, like others before us (Marshall, 1885; Lyle, 1923), we doubt that it has ever occurred here. We have accordingly omitted it from the checklist, but we do include notes on its biology in this section. Sigalphines have a gastral carapace (fig. 78) and on this account were traditionally regarded as chelonines, but in contrast with Cheloninae their carapace is articulated between the first and second tergites (fig. 77). Van Achterberg (1976d) first placed Sigalphini in the Meteorideinae and subsequently (van Achterberg, 1984b) accorded the group subfamily rank, placing Sigalphinae far from both Meteorideinae and Cheloninae. The name *Sigalphus* was at one time misapplied to the helconine genus correctly known as *Triaspis*, and *Sphaeropyx* was in use for the genus now called *Sigalphus*.

Acampsis alternipes (Nees von Esenbeck) is seldom collected, perhaps because it flies early in the year. It has been reared from the geometrid genus *Alsophila*, both in Czechoslovakia (Čapek, 1975) and in England. According to Čapek (1975) the parasitoid larva leaves the final-instar host and descends on a thread to form a robust, silvery white cocoon in the litter. The adult emerges through an irregularly chewed hole the following spring. In Europe *Sigalphus irrorator* (Fabricius), which is a relatively large braconid, has been recorded from noctuids, especially of the genus *Acronicta*, and from its size it would appear to be a solitary parasitoid although no details on its development have been published. The North American *S. bicolor* (Cresson), however, is much smaller, and is a gregarious parasitoid of *Acronicta* with brood sizes of up to 30. Cushman (1913) observed oviposition into very young larvae (though he failed to rear parasitoids from them) rather than eggs, and an external feeding phase on the cocooned prepupal host. The parasitoids make a close-packed array of cocoons in which the winter is passed. As single-sex broods appear to be common, it has been suggested (Clausen, 1940) that polyembryony may occur, but this speculation has not been properly investigated. Sigalphines have carried forward a reputation of being egg-larval parasitoids (cf. van Achterberg, 1984b) from their former association with chelonines (cf. Čapek, 1970) but, while this may indeed prove to be the case for some, no clear evidence has yet been advanced for it.

Identification. Given that *Acampsis alternipes* is the only species known to occur in Britain, it can be identified from the key to subfamilies. The front femur is black at the base, sharply changing to testaceous at the apex, an unusual leg colour pattern for a braconid. Marshall (1885) gave a description of *Sigalphus irrorator*.

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References

ACHTERBERG, C. van. 1974. A redescription of *Idiasta theodori* (van Vollenhoven, 1878) (Hymenoptera, Braconidae). *Zoologische Mededelingen* **48**: 23–27.

ACHTERBERG, C. van. 1975. A new species of *Chasmodon* Haliday (Hymenoptera, Braconidae, Alysiinae). *Zoologische Mededelingen* **49**: 73–79.

ACHTERBERG, C. van. 1976a. A new species of *Tanycarpa* Foerster from England (Hymenoptera, Braconidae, Alysiinae). *Entomologische Berichten* **36:** 12–15.

ACHTERBERG, C. van. 1976b. Revisionary notes on the genus *Coloneura* Foerster with description of a new subgenus, *Coloneurella*, from the Netherlands (Hym., Braconidae, Alysiinae). *Entomologische Berichten* **36:** 186–192.

ACHTERBERG, C. van. 1976c. A revision of the tribus Blacini (Hymenoptera, Braconidae, Helconinae). *Tijdschrift voor Entomologie* **118** (1975): 159–322.

ACHTERBERG, C. van. 1976d. A preliminary key to the subfamilies of the Braconidae (Hymenoptera). *Tijdschrift voor Entomologie* **119:** 33–78.

ACHTERBERG, C. van. 1977. The function of swarming in *Blacus* species (Hymenoptera, Braconidae, Helconinae). *Entomologische Berichten* **37:** 151–152.

ACHTERBERG, C. van. 1979a. A revision of the species of Amicrocentrinae, a new subfamily (Hymenoptera, Braconidae), with a description of the final larval instar of *Amicrocentrum curvinervis* by J. R. T. Short. *Tijdschrift voor Entomologie* **122:** 1–28.

ACHTERBERG, C. van. 1979b. A revision of the new subfamily Xyphozelinae (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* **122:** 29–46.

ACHTERBERG, C. van. 1979c. A revision of the subfamily Zelinae auct. (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* **122:** 241–479.

ACHTERBERG, C. van. 1983a. A revision of the new tribe Brulleiini (Hymenoptera: Braconidae). *Contributions of the American Entomological Institute* **20:** 281–306.

ACHTERBERG, C. van. 1983b. Revisionary notes on the genera *Dapsilarthra* auct. and *Mesocrina* Foerster (Hymenoptera, Braconidae, Alysiinae). *Tijdschrift voor Entomologie* **126:** 1–24.

ACHTERBERG, C. van. 1983c. Revisionary notes on the subfamily Gnaptodontinae, with description of eleven new species (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* **126:** 25–57.

ACHTERBERG, C. van. 1983d. Revisionary notes on the Palaearctic genera and species of the tribe Exothecini Foerster (Hymenoptera, Braconidae). *Zoologische Mededelingen* **57:** 339–355.

ACHTERBERG, C. van. 1984a. *Dapsilarthra* Foerster, 1862 (Insecta, Hymenoptera): proposed conservation under the plenary powers. Z.N.(S.) 2312. *Bulletin of Zoological Nomenclature* **41:** 53–55.

ACHTERBERG, C. van. 1984b. Essay on the phylogeny of Braconidae (Hymenoptera: Ichneumonoidea). *Entomologisk Tidskrift* **105:** 41–58.

ACHTERBERG, C. van. 1984c. Addition to the revision of the genus *Zele* Curtis (Hymenoptera: Braconidae). *Entomologische Berichten* **44:** 110–112.

ACHTERBERG, C. van. 1984d. Revision of the genera of Braconini with first and second metasomal tergites immovably joined (Hymenoptera, Braconidae, Braconinae). *Tijdschrift voor Entomologie* **127:** 137–164.

ACHTERBERG, C. van. 1984e. The preference of zoophagous Hymenoptera for certain types of plants as shown by the subfamily Gnaptodontinae (Braconidae). *In* Kaszab, K. (Ed.) *Verhandlungen X Internationalen Symposiums über Entomofaunistik Mitteleuropas (SIEEC)*: 97–98. Budapest.

ACHTERBERG, C. van. 1985a. Notes on Braconidae II. *Pigeria* gen. nov., a new Palaearctic genus of the Braconinae (Hymenoptera: Braconidae). *Zoologische Mededelingen* **59:** 168–174.

ACHTERBERG, C. van. 1985b. Notes on Braconidae V. The systematic position of the genera *Ecnomios* Mason and *Pselaphanus* Szépligeti (Hymenoptera: Braconidae). *Zoologische Mededelingen* **59:** 341–348.

ACHTERBERG, C. van. 1986. The holarctic genus *Anisocyrta* Foerster (Hymenoptera: Braconidae: Alysiinae). *Zoologische Mededelingen* **60:** 285–297.

ACHTERBERG, C. van. 1987a. Revision of the European Helconini (Hymenoptera: Braconidae: Helconinae). *Zoologische Mededelingen* **61:** 263–285.

ACHTERBERG, C. van. 1987b. Revisionary notes on the subfamily Orgilinae (Hymenoptera: Braconidae). *Zoologische Verhandelingen* **242:** 1–111.

ACHTERBERG, C. van. 1988a. The genera of the *Aspilota*-group and some descriptions of fungicolous Alysiini from the Netherlands (Hymenoptera: Braconidae: Alysiinae). *Zoologische Verhandelingen* **247:** 1–88.

ACHTERBERG, C. van. 1988b. Revision of the subfamily Blacinae Foerster (Hymenoptera, Braconidae). *Zoologische Verhandelingen* **249:** 1–324.

ACHTERBERG, C. van. 1988c. Parallelisms in the Braconidae (Hymenoptera) with special reference to the biology. *In* Gupta V. K. (Ed.) *Advances in parasitic Hymenoptera research*: 85–115. Leiden.

ACHTERBERG, C. van. 1989. Revision of the subtribe Monoctonina Mackauer sensu stricto (Hymenoptera: Braconidae: Aphidiinae). *Zoologische Mededelingen* **63:** 1–22.

ACHTERBERG, C. van. 1990a. Revision of the western Palaearctic Phanerotomini (Hymenoptera: Braconidae). *Zoologische Verhandelingen* **255:** 1–106.

ACHTERBERG, C. van. 1990b. Illustrated key to the subfamilies of the Holarctic Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Mededelingen* **64:** 1–20.

ACHTERBERG, C. van. 1990c. Revision of the genera *Foersteria* Szépligeti and *Polydegmon* Foerster (Hymenoptera: Braconidae), with the description of a new genus. *Zoologische Verhandelingen* **257:** 1–32.

ACHTERBERG, C. van & BIN, F. 1981. Notes on two species of *Dinotrema* Foerster (Hym., Braconidae, Alysiinae) with observations on the hymenopterous parasite-complex of *Spiniphora dorsalis* Becker (Dipt., Phoridae) in dead *Helix* spp. (Mollusca). *Entomologische Berichten* **41:** 104–112.

ACHTERBERG, C. van & HAESELBARTH, E. 1983. Revisionary notes on the European species of *Macrocentrus* Curtis sensu stricto (Hymenoptera: Braconidae). *Entomofauna* **4:** 37–59.

ACHTERBERG, C. van & O'CONNOR, J. P. 1990. Revision of the Palaearctic genus *Trachyusa* Ruthe (Hymenoptera: Braconidae). *Zoologische Mededelingen* **64:** 107–112.

ACHTERBERG, C. van & ORTEGA, G. 1983. A new species of *Orthostigma* Ratzeburg from Tenerife (Insecta: Hymenoptera, Braconidae). *Vieraea* **12:** 121–127.

ADAMS, C. H., CROSS, W. H. & MITCHELL, H. C. 1969. Biology of *Bracon mellitor*, a parasite of the boll weevil. *Journal of Economic Entomology* **62:** 889–895.

AHMAD, M. 1943. The morphology and biology of *Rhogas testaceus* (Spin.) a braconid internal parasite of spotted bollworms of cotton. *Indian Journal of Entomology* **5:** 189–205.

ALAUZET, C. 1987. Bioecologie de *Eubazus semirugosus*, *Coeloides abdominalis* et *C. sordidator* (Hym.: Braconidae) parasites de *Pissodes notatus* (Col.: Curculionidae) dans le sud de la France. *Entomophaga* **32:** 39–47.

ALFORD, D. V. 1968. The biology and immature stages of *Syntretus splendidus* (Marshall) (Hymenoptera: Braconidae, Euphorinae), a parasite of adult bumblebees. *Transactions of the Royal Entomological Society of London* **120:** 375–393.

ALLEN, A. A. 1982. Observations on the ectoparasitic stage of two *Homobbus* [sic] spp. (Hym: Braconidae). *Proceedings and Transactions of the British Entomological and Natural History Society* **15:** 11.

ALLEN, W. W. 1958. The biology of *Apanteles medicaginis* Muesebeck (Hymenoptera: Braconidae). *Hilgardia* **27:** 515–541.

ALPHEN, J. J. M. van & VET, L. E. M. 1986. An evolutionary approach to host finding and selection. *In* Waage, J. & Greathead, D. (Eds) *Insect parasitoids*: 23–61. London.

ALPHEN, J. J. M. van & VISSER, M. E. 1990. Superparasitism as an adaptive strategy for insect parasitoids. *Annual Review of Entomology* **35:** 59–79.

ARAKAWA, T. & KITANO, H. 1989. A possible reason for the decrease of the number of teratocytes in the body cavities of *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae) parasitized by *Apanteles glomeratus* L. (Hymenoptera: Braconidae). *Applied Entomology and Zoology* **24:** 229–231.

ARTHUR, A. P. 1981. Host acceptance by parasitoids. *In* Nordlund, D. A., Jones, R. L. & Lewis, W. J. (Eds) *Semiochemicals*: 97–120. New York.

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

ASKARI, A. & COPPEL, H. C. 1978. Observations on courtship and mating behavior of *Meteorus pulchricornis*, a gypsy moth parasitoid. *Annals of the Entomological Society of America* **71:** 364–366.

ASKARI, A., MERTINS, J. W. & COPPEL, H. C. 1977. Developmental biology and immature stages of *Meteorus pulchricornis* in the laboratory. *Annals of the Entomological Society of America* **70:** 655–659.

ASKEW, R. R. 1971. *Parasitic insects*. 316 pp. London.

ASKEW, R. R. & SHAW, M. R. 1986. Parasitoid communities: their size, structure and development. *In* Waage, J. & Greathead, D. (Eds) *Insect parasitoids*: 225–264. London.

AUBROOK, E. W. 1939. A contribution to the biology and distribution in Great Britain of *Boreus hyemalis* L. (Mecopt., Boreidae). *Journal of the Society for British Entomology* **2:** 13–21.

AUSTIN, A. D. 1989. Revision of the genus *Buluka* de Saeger (Hymenoptera: Braconidae: Microgastrinae). *Systematic Entomology* **14:** 149–163.

AUSTIN, A. D. 1990. Revision of the enigmatic Australasian genus *Miropotes* Nixon (Hymenoptera: Braconidae: Microgastrinae), with comments on the phylogenetic importance of the female ovipositor system. *Systematic Entomology* **15:** 43–68.

AVILLA, J. & ALBAJES, R. 1984. The influence of female age and host size on the sex ratio of the parasitoid *Opius concolor*. *Entomologia Experimentalis et Applicata* **35:** 43–47.

AYYAR, P. N. K. 1941. Investigations on *Spathius critolaus* Nixon, an important braconid parasite of the cotton-stem weevil, *Pempheres affinis* Fst. of south India. *Indian Journal of Agricultural Science* **10:** 879–900.

BALDUF, W. V. 1926. The bionomics of *Dinocampus coccinellae* Schrank. *Annals of the Entomological Society of America* **19:** 465–498.

BALDUF, W. V. 1966. Life of *Acrobasis rubrifasciella* (Lepidoptera: Phycitidae), its main parasite, *Agathis calcarata* (Hymenoptera: Braconidae), and three hyperparasites (Chalcidoidea). *Annals of the Entomological Society of America* **59:** 1038–1049.

BARLIN, M. R. & VINSON, S. B. 1981. The multiporous plate sensillum and its potential use in braconid systematics (Hymenoptera: Braconidae). *Canadian Entomologist* **113:** 931–938.

BARTLETT, B. R. 1964. Patterns in the host-feeding habit of adult parasitic Hymenoptera. *Annals of the Entomological Society of America* **57:** 344–350.

BASINGER, A. J. 1938. The orange tortrix, *Argyrotaenia citrana*. *Hilgardia* **11:** 635–669.

BEARD, R. L. 1972. Effectiveness of paralyzing venom and its relation to host discrimination by braconid wasps. *Annals of the Entomological Society of America* **65:** 90–93.

BEARD, R. L. 1978. Venoms of Braconidae. *In* Bettini S. (Ed.) *Arthropod venoms*: 773–800. Berlin.

BEAVER, R. A. 1965. Two braconids and a pteromalid (Hymenoptera) new to Britain. *Entomologist* **98:** 238–240.

BEAVER, R. A. 1967. Hymenoptera associated with elm bark beetles in Wytham Wood, Berks. *Transactions of the Society for British Entomology* **17:** 141–150.

BECKAGE, N. E. 1985. Endocrine interactions between endoparasitic insects and their hosts. *Annual Review of Entomology* **30:** 371–413.

BECKAGE, N. E., TEMPLETON, T. J., NIELSEN, B. D., COOK, D. I. & STOLTZ, D. B. 1987. Parasitism-induced hemolymph polypeptides in *Manduca sexta* (L.) larvae parasitized by the braconid wasp *Cotesia congregata* (Say). *Insect Biochemistry* **17:** 439–455.

BEESON, C. F. C. & CHATTERJEE, S. N. 1935. On the biology of the Braconidae (Hymenoptera). *Indian Forest Records* **1:** 105–138.

BEIRNE, B. P. 1941. A consideration of the cephalic structures and spiracles of the final instar larvae of the Ichneumonidae (Hym.). *Transactions of the Society for British Entomology* **7:** 123–190.

BEIRNE, B. P. 1942a. Observations on the life-history of *Praon volucre* Haliday (Hym.: Braconidae), a parasite of the mealy plum aphis (*Hyalopterus arundinis* Fab.). *Proceedings of the Royal Entomological Society of London* (A) **17:** 42–47.

BEIRNE, B. P. 1942b. Observations on the developmental stages of some Aphidiinae (Hym., Braconidae). *Entomologist's Monthly Magazine* **78:** 283–286.

BEIRNE, B. P. 1946. Notes on the biology of some hymenopterous parasites of the beech weevil (*Rhynchaenus fagi* L.) (Col.). *Proceedings of the Royal Entomological Society of London* (A) **21:** 7–11.

BELOKOBYLSKIJ, S. A. 1984. [On the division of the tribe Exothecini s.l. (Hymenoptera, Braconidae) in two with the description of a new genus and subgenus.] *Zoologicheskii Zhurnal* **63:** 1019–1026. (In Russian).

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

BERRY, P. A. 1947. *Anthonomus vestitus* and its natural enemies in Peru, and their importation into the United States. *Journal of Economic Entomology* **40:** 801–804.

BEYARSLAN, A. & FISCHER, M. 1990. Bestimmungsschlüssel zur Identifikation der paläarktischen *Bracon*-Arten des Subgenus *Glabrobracon* Tobias (Hymenoptera, Braconidae, Braconinae). *Annalen Naturhistorischen Museums Wien* **91**(B): 137–145.

BIGNELL, G. C. 1901. The Ichneumonidae (parasitic flies) of South Devon. Part II. Braconidae. *Transactions of the Devonshire Association for the Advancement of Science, Literature, and Art* **33:** 657–692.

BIGNELL, G. C. 1902. *Histeromerus mystacinus*, Wesm., in Devonshire. *Entomologist's Monthly Magazine* **28:** 288.

BLACKITH, R. R. & BLACKITH, R. 1986. *Pygostolus sticticus* Fab. (Hymenoptera: Braconidae) parasitic on *Otiorhynchus singularis* (L.) (Coleoptera: Curculionidae) in an Irish pine forest. *Irish Naturalists' Journal* **22:** 69–71.

BOLDARUEV, V. O. 1958. *Rhogas dendrolimi* Mats. (Hymenoptera, Braconidae) an efficient parasite of *Dendrolimus sibiricus* Tshetv. (Lepidoptera, Lasiocampidae). *Entomologicheskoe Obozrenie* **36:** 829–835. (In Russian) [English translation in *Entomological Review, Washington* **37:** 716–720].

BOSCH, R. van den & HARAMOTO, F. H. 1951. *Opius oophilus* Fullaway, an egg-larval parasite of the oriental fruit fly discovered in Hawaii. *Proceedings of the Hawaiian Entomological Society* **14:** 251–255.

BOUCHARD, Y. & CLOUTIER, C. 1984. Honeydew as a source of host-searching kairomones for the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). *Canadian Journal of Zoology* **62:** 1513–1520.

BOYCE, H. R. 1936. Laboratory breeding of *Ascogaster carpocapsae* Vier. with notes on biology and larval morphology. *Canadian Entomologist* **68:** 241–246.

BRADLEY, W. G. & ARBUTHNOT, K. D. 1938. The relation of host physiology to development of the braconid parasite, *Chelonus annulipes* Wesmael. *Annals of the Entomological Society of America* **31:** 359–365.

BRIDWELL, J. C. 1918. Notes on the Bruchidae and their parasites in the Hawaiian islands. *Proceedings of the Hawaiian Entomological Society* **3:** 465–505.

BRINDLEY, M. D. 1939. Observations on the life-history of *Euphorus pallipes* (Curtis) (Braconidae), a parasite of Hemiptera-Heteroptera. *Proceedings of the Royal Entomological Society of London* (A) **14:** 51–56.

BRODEUR, J. & McNEIL, J. N. 1989. Seasonal microhabitat selection by an endoparasitoid through adaptive modification of host behaviour. *Science* **244:** 226–228.

BROODRYK, S. W. 1969a. The biology of *Chelonus (Microchelonus) curvimaculatus* Cameron (Hymenoptera: Braconidae). *Journal of the Entomological Society of Southern Africa* **32:** 169–189.

BROODRYK, S. W. 1969b. The biology of *Orgilus parcus* Turner (Hymenoptera: Braconidae). *Journal of the Entomological Society of Southern Africa* **32:** 243–257.

BRUES, C. T. 1923. *Termitobracon*, a termitophilous braconid from British Guiana. *Zoologica, New York* **3:** 427–432.

BRYDEN, J. W. & BISHOP, M. W. H. 1945. *Perilitus coccinellae* (Schrank) (Hym., Braconidae) in Cambridgeshire. *Entomologist's Monthly Magazine* **81:** 51–52.

BUCKINGHAM, G. R. & SHARKEY, M. J. 1988. Abdominal exocrine glands in Braconidae (Hymenoptera). *In* Gupta V. K. (Ed.) *Advances in parasitic Hymenoptera research*: 199–242. Leiden.

BÜHLER, A., HANZLIK, T. N. & HAMMOCK, B. D. 1985. Effects of parasitization of *Trichoplusia ni* by *Chelonus* sp. *Physiological Entomology* **10:** 383–394.

BURGESS, A. F. & CROSSMAN, S. S. 1929. Imported insect enemies of the gypsy moth and the brown-tail moth. *Technical Bulletin, United States Department of Agriculture* **86:** 1–147.

CALKINS, C. O. 1977. Notes on the cocoon construction behavior of *Apanteles militaris*. *Florida Entomologist* **60:** 65.

CAMERON, E. 1941. The biology and post-embryonic development of *Opius ilicis* n. sp., a parasite of the holly leaf-miner (*Phytomyza ilicis* Curt.). *Parasitology* **33:** 8–39.

ČAPEK, M. 1958. Revision der europäischen Arten der Gattung *Cosmophorus* Ratz. (Hym. Braconidae). *Acta Entomologica Musei Nationalis Pragae* **32**: 151–169.

ČAPEK, M. 1965. The classification of Braconidae (Hym.) in relation to host specificity. *Proceedings of the XII International Congress of Entomology*: 98–99.

ČAPEK, M. 1969. An attempt at a natural classification of the family Braconidae based on various unconventional characters (Hymenoptera). *Proceedings of the Entomological Society of Washington* **71:** 304–312.

ČAPEK, M. 1970. A new classification of the Braconidae (Hymenoptera) based on the cephalic structures of the final instar larva and biological evidence. *Canadian Entomologist* **102:** 846–875.

ČAPEK, M. 1971. The classification of Braconidae (Hymenoptera) from the viewpoint of their biology. *Proceedings of the XIII International Congress of Entomology* **1:** 120–121.

ČAPEK, M. 1973. Key to the final instar larvae of the Braconidae. *Acta Instituti Forestalis Zvolenensis* **4:** 259–268.

ČAPEK, M. 1975. Contribution to the knowledge of some remarkable species of Braconidae (Hymenoptera: Braconidae). *Biológia, Bratislava* **30:** 815–820.

ČAPEK, M. 1983. Relationships and taxonomic placement of the genus *Blacus* (Hymenoptera: Braconidae). *Contributions of the American Entomological Institute* **20:** 119–124.

ČAPEK, M. 1989. Lumčíkovité (Hym.: Braconidae) ako parazitoidy bzdôch (Het.). *Entomologické Problémy* **19:** 23–31.

ČAPEK, M. & CAPECKI, Z. 1979. A new genus and a new species of Euphorinae (Braconidae, Hymenoptera) from southern Poland. *Polskie Pismo Entomologiczne* **49:** 215–221.

ČAPEK, M. & DAVIDOVÁ-VILÍMOVÁ, J. 1978. On the life history of *Aridelus egregius* (Hymenoptera, Braconidae) a parasite of European *Coptosoma* (Heteroptera, Plataspidae). *Acta Entomologica Bohemoslovaca* **75:** 243–254.

ČAPEK, M., HLADIL, J. & ŠEDIVÝ, J. 1982. Zoznam blanokrídlych parasitov (Hymenoptera) dochovanych z hmysích hostitel'ov. časť VI. *Entomologické Problémy* **17:** 325–370.

ČAPEK, M. & ŠNOFLÁK, J. 1959. Beitrag zur Kenntnis der europäischen Arten der Gattung *Streblocera* Westwood (Hym., Braconidae). *Acta Societatis Entomologicae Čechosloveniae* **56:** 343–354.

CARLETON, M. 1939. The biology of *Pontania proxima* Lep., the bean gall sawfly of willows. *Journal of the Linnean Society* (Zoology) **40:** 575–624.

CHATTERJEE, P. N. 1943. Description of *Rhogas plecopterae* sp. nov. from India with notes on its biology and morphology. *Indian Journal of Entomology* **5:** 213–221.

CHERIAN, M. C. & ISRAEL, P. 1941. *Rhaconotus roslinensis* (Braconidae), a larval parasite of the sugarcane borer, *Scirpophaga rhodoproctalis*. *Indian Journal of Entomology* **3:** 173–176.

CHERNOGUZ, D. G. & REZNIK, S. Ya. 1987. Ethological and physiological components of host specificity of the braconid *Alysia manducator* Panz. (Hymenoptera, Braconidae). *Entomologicheskoe Obozrenie* **66:** 499–510. (In Russian) [English translation in *Entomological Review, Washington* **67** (2): 35–48].

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

CLAUSEN, C. P. 1940. *Entomophagous insects*. 688 pp. New York.

CLAUSEN, C. P. 1954. The egg-larval host relationship among the parasitic Hymenoptera. *Bollettino del Laboratorio di Zoologia Generale e Agraria della Facoltà Agraria in Portici* **33:** 119–133.

CLAUSEN, C. P. (Ed.) 1978. Introduced parasites and predators of arthropod pests and weeds: a world review. *Agricultural Handbook, United States Department of Agriculture* **480:** 1–545.

COLE, L. R. 1959. On a new species of *Syntretus* Förster (Hym., Braconidae) parasitic on an adult ichneumonid, with a description of the larva and notes on its life history and that of its host, *Phaeogenes invisor* (Thunberg). *Entomologist's Monthly Magazine* **95:** 18–21.

COX, J. A. 1932. *Ascogaster carpocapsae* Viereck, an important larval parasite of the codling moth and oriental fruit moth. *Technical Bulletin, New York State Agricultural Experiment Station* **188:** 1–26.

CRANHAM, J. E. & DANTHANARAYANA, W. 1966. Tea tortrix (*Homona coffearia* Nietner). *Advisory Phamphlet, Tea Research Institute Ceylon* **66** (5): 1–8.

CROZIER, R. H. 1975. Hymenoptera (Insecta 7). *In* John, B. (Ed.) *Animal cytogenetics* **3:** 1–95. Berlin.

CUSHMAN, R. A. 1913. Biological notes on a few rare or little known parasitic Hymenoptera. *Proceedings of the Entomological Society of Washington* **15:** 153–160.

CUSHMAN, R. A. 1923. A new subfamily of Braconidae (Hym.) from termite nests. *Proceedings of the Entomological Society of Washington* **25:** 54–56.

DANIEL, D. M. 1932. *Macrocentrus ancylivorus* Rohwer, a polyembryonic braconid parasite of the oriental fruit moth. *Technical Bulletin, New York State Agricultural Experiment Station* **187:** 1–101.

DE LEON, D. 1934. The morphology of *Coeloides dendroctoni* Cushman (Hymenoptera: Braconidae). *Journal of the New York Entomological Society* **42:** 297–317.

DE LEON, D. 1935. The biology of *Coeloides dendroctoni* Cushman (Hymenoptera-Braconidae) an important parasite of the mountain pine beetle (*Dendroctonus monticolae* Hopk.). *Annals of the Entomological Society of America* **28:** 411–424.

DE SAEGER, H. 1937. L'*Apanteles sagax* Wilkn. parasite de la pyrale du cotonnier. *Bulletin Agricole du Congo Belge* **28:** 147–150.

DEYRUP, M. 1981. A new species of *Cryptoxilos* (Hymenoptera: Braconidae) attacking adult *Lymantor decipiens* Leconte (Coleoptera: Scolytidae). *Entomological News* **92:** 177–180.

DITTRICK, L. E. & CHIANG, H. C. 1982. Developmental characteristics of *Macrocentrus grandii* as influenced by temperature and instar of its host, the European corn borer. *Journal of Insect Physiology* **28:** 47–52.

DIX, M. E. & FRANKLIN, R. T. 1983. Behavior of four braconid parasites and one pteromalid parasite of the southern pine beetle. *Journal of the Georgia Entomological Society* **18:** 125–138.

DONDALE, C. D. 1954. Biology of *Agathis laticinctus* (Cress.) (Hymenoptera: Braconidae), a parasite of the eye-spotted bud moth, in Nova Scotia. *Canadian Entomologist* **86:** 40–44.

DONISTHORPE, H. 1929. *Histeromerus mystacinus*, Wesmael; a coleopterous parasite. *Entomologist's Record and Journal of Variation* **41:** 125.

DONISTHORPE, H. 1940. *Xorides indicatorius* Latr. ? parasitic on *Leiopus nebulosus* L., and a list of other species of hymenopterous parasites of Coleoptera in Great Britain. *Entomologist* **73:** 14–20.

DOUTT, R. L. 1959. The biology of parasitic Hymenoptera. *Annual Review of Entomology* **4:** 161–182.

DOWDEN, P. B. 1938. *Rogas unicolor* (Wesm.), a braconid parasite of the satin moth. *Journal of Agricultural Research* **56:** 523–536.

DOWDEN, P. B. 1941. Parasites of the birch leaf-mining sawfly (*Phyllotoma nemorata*). *Technical Bulletin, United States Department of Agriculture* **757:** 1–55.

DOYEN, J. T. 1984. Systematics of *Eusattus* and *Conisattus* (Coleoptera; Tenebrionidae; Coniontini; Eusatti). *Occasional Papers of the California Academy of Sciences* **141:** 1–104.

DREA, J. J. 1968. Castration of male alfalfa weevils by *Microctonus* spp. *Journal of Economic Entomology* **61:** 1291–1295.

DREA, J. J., DYSART, R. J., COLES, L. W. & LOAN, C. C. 1972. *Microctonus stelleri* (Hymenoptera: Braconidae, Euphorinae), a new parasite of the alfalfa weevil introduced into the United States. *Canadian Entomologist* **104:** 1445–1456.

DUDARENKO, G. P. 1974. Formation of the abdominal carapace in braconids (Hymenoptera, Braconidae). *Entomologicheskoe Obozrenie* **53:** 114–129. (In Russian) [English translation in *Entomological Review, Washington* **53:** 80–90].

EADY, R. D. 1968. Some illustrations of microsculpture in the Hymenoptera. *Proceedings of the Royal Entomological Society of London* (A) **43:** 66–72.

EADY, R. D. 1974. The present state of nomenclature of wing venation in the Braconidae (Hymenoptera); its origins and comparison with related groups. *Journal of Entomology* (B) **43:** 63–72.

EADY, R. D. & CLARK, J. A. J. 1964. A revision of the genus *Macrocentrus* Curtis (Hym., Braconidae) in Europe, with descriptions of four new species. *Entomologist's Gazette* **15:** 97–127.

EDSON, K. M., BARLIN, M. R. & VINSON, S. B. 1982. Venom apparatus of braconid wasps: comparative ultrastructure of reservoirs and gland filaments. *Toxicon* **20:** 553–562.

EDSON, K. M. & VINSON, S. B. 1976. The function of the anal vesicle in respiration and excretion in the braconid wasp, *Microplitis croceipes*. *Journal of Insect Physiology* **22:** 1037–1043.

EDSON, K. M. & VINSON, S. B. 1977. Nutrient absorption by the anal vesicle of the braconid wasp, *Microplitis croceipes*. *Journal of Insect Physiology* **23:** 5–8.

EICHHORN, O. & PSCHORN-WALCHER, H. 1973. The parasites of the birch leaf-mining sawfly (*Fenusa pusilla* (Lep.), Hym.: Tenthredinidae) in central Europe. *Technical Bulletin, Commonwealth Institute of Biological Control* **16:** 79–104.

ELLER, F. J., TUMLINSON, J. H. & LEWIS, W. J. 1990. Intraspecific competition in *Microplitis croceipes* (Hymenoptera: Braconidae), a parasitoid of *Heliothis* species (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* **83:** 504–508.

ELLIOTT, E. A. & MORLEY, C. 1907. On the hymenopterous parasites of Coleoptera. *Transactions of the Entomological Society of London* **1907:** 7–75.

EVANS, A. C. 1933. Comparative observations on the morphology and biology of some hymenopterous parasites of carrion-infesting Diptera. *Bulletin of Entomological Research* **24:** 385–405.

EVENHUIS, H. H. 1969. Two *Ascogaster* species (Hymenoptera, Braconidae), parasites of leafrollers (Lepidoptera, Tortricidae) in apple orchards, with different host selection. *Entomologische Berichten* **29:** 159–160.

FALLIS, A. M. 1942. The life cycle of *Apanteles carpatus* (Say) (Hymenoptera: Braconidae), a parasite of the webbing clothes moth, *Tineola bisselliella* Hum. *Canadian Journal of Research* (D) **20:** 13–19.

FERRAN, A. & DAUMAL, J. 1973. Conséquences sur les larves d'*Anagasta kühniella* Zeller (Lep. Phycitidae) de l'élimination précoce par le froid de son endoparasite *Phanerotoma flavitestacea* Fischer (Hym. Braconidae). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris* (D) **277:** 869–872.

FINK, D. E. 1926. The biology of *Macrocentrus ancylivora* Rohwer, an important parasite of the strawberry leaf roller (*Ancylis comptana* Froehl.). *Journal of Agricultural Research* **32:** 1121–1134.

FINLAYSON, T. 1990. The systematics and taxonomy of final-instar larvae of the family Aphidiidae (Hymenoptera). *Memoirs of the Entomological Society of Canada* **152:** 1–74.

FINLAYSON, T. & HAGEN, K. S. 1979. Final-instar larvae of parasitic Hymenoptera. *Pest Management Papers, Simon Fraser University* **10:** 1–111.

FINNEY, G. L., FLANDERS, S. E. & SMITH, H. S. 1947. Mass culture of *Macrocentrus ancylivorus* and its host, the potato tuber moth. *Hilgardia* **17:** 437–483.

FISCHER, M. 1962. Das Genus *Synaldis* Förster (Hymenoptera, Braconidae). *Mitteilungen aus dem zoologischen Museum in Berlin* **38:** 1–21.

FISCHER, M. 1966. Über gezüchtete Braconiden aus Europa (Hymenoptera). *Zeitschrift für angewandte Entomologie* **58:** 323–339.

FISCHER, M. 1967. Revision der burgenländischen Arten der Gattungen *Synaldis*, *Aphaereta* und *Alysia* (Hymenoptera, Braconidae, Alysiinae). *Wissenschaftliche Arbeiten aus dem Burgenland* **38:** 92–135.

FISCHER, M. 1970. Zur Kenntnis der europäischen *Phaenocarpa* – Arten mit besonderer Berücksichtigung der Fauna Niederösterreichs (Hymenoptera, Braconidae, Alysiinae). *Zeitschrift für angewandte Zoologie* **57:** 409–498.

FISCHER, M. 1971a. Untersuchungen über die europäischen Alysiini mit besonderer Berücksichtigung der Fauna Niederösterreichs (Hymenoptera, Braconidae). *Polskie Pismo Entomologiczne* **41:** 19–160.

FISCHER, M. 1971b. Hym. Braconidae. World Opiinae. *Index of Entomophagous Insects.* 189 pp. Paris.

FISCHER, M. 1972a. Erste Gliederung der paläarktischen *Aspilota*-Arten (Hymenoptera, Braconidae, Alysiinae). *Polskie Pismo Entomologiczne* **42:** 323–459.

FISCHER, M. 1972b. Hymenoptera Braconidae (Opiinae I). *Das Tierreich* **91:** 1–620.

FISCHER, M. 1986. Neue Bestimmungsschlüssel für paläarktische Opiinae, neue Subgenera, Redeskriptionen und eine neue Art. (Hymenoptera, Braconidae). *Annalen Naturhistorischen Museums Wien* **88/89** (B): 607–662.

FISCHER, M. 1990. Westpaläarktische *Phaenocarpa*-Arten: Vorläufiger Bestimmungsschlüssel, Deskriptionen und Redeskriptionen (Hymenoptera, Braconidae, Alysiinae). *Annalen Naturhistorischen Museums Wien* **91**(B): 105–135.

FITTON, M. G., SHAW, M. R. & AUSTIN, A. D. 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society* **90:** 65–93.

FITTON, M. G., SHAW, M. R. & GAULD, I. D. 1988. Pimpline ichneumon-flies. Hymenoptera, Ichneumonidae (Pimplinae). *Handbooks for the Identification of British Insects* **7** (1): 1–110.

FLANDERS, R. V. & OATMAN, E. R. 1982. Laboratory studies on the biology of *Orgilus jenniae* (Hymenoptera: Braconidae), a parasitoid of the potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Hilgardia* **50** (8): 1–33.

FLANDERS, R. V. & OATMAN, E. R. 1987. Competitive interactions among endophagous parasitoids of potato tuberworm larvae in southern California. *Hilgardia* **55** (1): 1–34.

FLANDERS, S. E. 1942. Oösorption and ovulation in relation to oviposition in the parasitic Hymenoptera. *Annals of the Entomological Society of America* **35:** 251–266.

FLANDERS, S. E. 1973. Particularities of diverse egg deposition phenomena characterizing carnivoroid Hymenoptera (with morphological and physiological correlations). *Canadian Entomologist* **105:** 1175–1187.

FLEMING, J. G. W. & SUMMERS, M. D. 1986. *Campoletis sonorensis* endoparasitic wasps contain forms of *C. sonorensis* virus DNA suggestive of integrated and extrachromosomal polydnavirus DNAs. *Journal of Virology* **57:** 552–562.

FREEMAN, B. E. 1967. The biology of the white clover seed weevil *Apion dichroum* Bedel (Col. Curculionidae). *Journal of Applied Ecology* **4:** 535–552.

FRITZ, R. S. 1982. Selection for host modification by insect parasitoids. *Evolution* **36:** 283–288.

FÜHRER, E. 1968. Parasitäre Veränderungen am Wirt und ihre ökologische Bedeutung für den Parasiten. *Entomophaga* **13:** 241–250.

FÜHRER, E. & ELSUFTY, R. 1979. Produktion fungistatischer Metabolite durch Teratocyten von *Apanteles glomeratus* L. (Hym., Braconidae). *Zeitschrift für Parasitenkunde* **59:** 21–25.

GÄRDENFORS, U. 1986. Taxonomic and biological revision of Palaearctic *Ephedrus* Haliday (Hymenoptera: Braconidae, Aphidiinae). *Entomologica Scandinavica* Supplement **27:** 1–95.

GATENBY, J. B. 1919. Notes on the bionomics, embryology, and anatomy of certain Hymenoptera Parasitica, especially of *Microgaster connexus* (Nees). *Journal of the Linnean Society* (Zoology) **33:** 387–416.

GAULD, I. D. 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society* **35:** 351–377.

GAULD, I. [D.] & BOLTON, B. (Eds). 1988. *The Hymenoptera.* 332 pp. London.

GENIEYS, P. 1925. *Habrobracon brevicornis* Wesm. *Annals of the Entomological Society of America* **18:** 143–202.

GERDIN, S. & HEDQVIST, K.-J. 1985. *Perilitus areolaris* sp.n. (Hymenoptera: Braconidae), an imago-parasitoid of the large pine weevil, *Hylobius abietis* (Linnaeus), and its reproductive behaviour. *Entomologica Scandinavica* **15:** 363–369.

GERLING, D. 1971. Occurrence, abundance, and efficiency of some local parasitoids attacking *Spodoptera littoralis* (Lepidoptera: Noctuidae) in selected cotton fields in Israel. *Annals of the Entomological Society of America* **64:** 492–499.

GERLING, D. & ROTARY, N. 1973. Hypersensitivity, resulting from host-unsuitability, as exemplified by two parasite species attacking *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Entomophaga* **18:** 391–396.

GHOSH, S. M. & ABDURAHIMAN, U. C. 1984. Bioethology of *Meteoridea hutsoni* (Nixon) (Hymenoptera: Braconidae), a parasite of *Opisina arenosella* Walker, the black headed caterpillar pest of coconut. *Entomon, Trivandrum* **9:** 31–34.

GHOSH, S. M. & ABDURAHIMAN, U. C. 1986. Two new records of hyperparasites on *Opisina arenosella* Walker, the caterpillar pest of coconut. *Entomon, Trivandrum* **11:** 75–76.

GLAS, P. C. G. & VET, L. E. M. 1983. Host-habitat location and host location by *Diachasma alloeum* Muesebeck (Hym.; Braconidae), a parasitoid of *Rhagoletis pomonella* (Dipt.; Tephritidae). *Netherlands Journal of Zoology* **33:** 41–54.

GLEN, D. M. 1977. Ecology of the parasites of a predatory bug, *Blepharidopterus angulatus* (Fall.). *Ecological Entomology* **2:** 47–55.

GLOVER, P. M. 1934. The developmental stages of *Bracon tachardiae*, Cam. (Hym.). *Bulletin of Entomological Research* **25:** 521–539.

GLOVER, P. M. & CHATTERJEE, K. C. 1936. A preliminary note on the bionomics and economic importance of *Microbracon hebetor* Say, a braconid new to north India. *Proceedings of the Indian Academy of Sciences* **3:** 195–211.

GODFRAY, H. C. J. 1984. Intraspecific variation in the leaf-miner parasite *Exotela cyclogaster* Förster (Hymenoptera: Braconidae). *Proceedings and Transactions of the British Entomological and Natural History Society* **17:** 47–50.

GODFRAY, H. C. J. 1987. Subfamily Alysiinae. *In* Cock, M. J. W., Godfray, H. C. J. & Holloway, J. D. (Eds) *Slug and nettle caterpillars*: 164. Wallingford.

GODFRAY, H. C. J. & McGAVIN, G. C. 1985. *Colastes pubicornis* (Thomson) (Hym., Braconidae, Exothecini) new to Britain, with a first host record. *Entomologist's Monthly Magazine* **121:** 109–110.

GRAHAM-SMITH, G. S. 1919. Further observations on the habits and parasites of common flies. *Parasitology* **11:** 347–384.

GREANY, P. D., TUMLINSON, J. H., CHAMBERS. D. L. & BOUCH, G. M. 1977. Chemically mediated host finding by *Biosteres (Opius) longicaudatus*, a parasitoid of tephritid fruit fly larvae. *Journal of Chemical Ecology* **3:** 189–195.

GREATHEAD, D. J. (Ed.) 1976. A review of biological control in western and southern Europe. *Technical Communication, Commonwealth Institute of Biological Control* **7:** 1–182.

GREATHEAD, D. J. 1986. Parasitoids in classical biological control. *In* Waage, J. & Greathead, D. (Eds) *Insect parasitoids:* 289–318. London.

GRIFFITHS, D. C. 1960. The behaviour and specificity of *Monoctonus paludum* Marshall (Hym., Braconidae), a parasite of *Nasonovia ribis-nigri* (Mosley) on lettuce. *Bulletin of Entomological Research* **51:** 303–319.

GRIFFITHS, D. C. 1961. The development of *Monoctonus paludum* Marshall (Hym., Braconidae) in *Nasonovia ribis-nigri* on lettuce, and immunity reactions in other lettuce aphids. *Bulletin of Entomological Research* **52:** 147–163.

GRIFFITHS, G. C. D. 1964. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). I. General questions of taxonomy, biology and evolution. *Beiträge zur Entomologie* **14:** 823–914.

GRIFFITHS, G. C. D. 1966a. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). II. The parasites of *Agromyza* Fallén. *Beiträge zur Entomologie* **16:** 551–605.

GRIFFITHS, G. C. D. 1966b. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). III. The parasites of *Paraphytomyza* Enderlein, *Phytagromyza* Hendel and *Phytomyza* Fallén. *Beiträge zur Entomologie* **16:** 775–951.

GRIFFITHS, G. C. D. 1967. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). IV. The parasites of *Hexomyza* Enderlein, *Melanagromyza* Hendel, *Ophiomyia* Braschnikov and *Napomyza* Westwood. *Beiträge zur Entomologie* **17:** 653–696.

GRIFFITHS, G. C. D. 1968a. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). V. The parasites of *Liriomyza* Mik and certain small genera of Phytomyzinae. *Beiträge zur Entomologie* **18:** 5–62.

GRIFFITHS, G. C. D. 1968b. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). VI. The parasites of *Cerodontha* Rondani s. l. *Beiträge zur Entomologie* **18:** 63–152.

GRIFFITHS, G. C. D. 1984. The Alysiinae (Hym. Braconidae) parasites of the Agromyzidae (Diptera). VII. Supplement. *Beiträge zur Entomologie* **34:** 343–362.

GUPPY, J. C. & MELOCHE, F. 1987. Life history and description of the immature stages of *Dacnusa dryas* (Nixon) (Hymenoptera: Braconidae), a European parasite of the alfalfa blotch leafminer (Diptera: Agromyzidae) in eastern Canada. *Canadian Entomologist* **119:** 281–285.

HÅGVAR, E. B. 1988. Multiparasitism of the green peach aphid, *Myzus persicae*: competition in the egg stage between *Aphidius matricariae* and *Ephedrus cerasicola. Entomologia Experimentalis et Applicata* **47:** 275–282.

HAESELBARTH, E. 1962. Zur Biologie, Entwicklungsgeschichte und Ökologie von *Brachistes atricornis* Ratz. (Hym., Brac.) als eines Parasiten von *Pissodes piceae* (Ill.) (Col., Curc.). *Zeitschrift für angewandte Entomologie* **49:** 233–289.

HAESELBARTH, E. 1967. Zur Kenntnis der palaearktischen Arten der Gattung *Coeloides* Wesmael (Hymenoptera, Braconidae). *Mitteilungen der Münchner Entomologischen Gesellschaft* **57:** 20–53.

HAESELBARTH, E. 1971. Notizen zur Gattung *Pygostolus* Haliday (Hymenoptera, Braconidae). *Opuscula Zoologica* **112:** 1–8.

HAESELBARTH, E. 1973. Die *Blacus*-Arten Europas und Zentral-Asiens (Hymenoptera, Braconidae). *Veröffentlichungen der zoologischen Staatssammlung München* **16:** 69–170.

HAESELBARTH, E. 1979. Zur Parasitierung der Puppen von Forleule (*Panolis flammea* (Schiff.)), Kiefernspanner (*Bupalus piniarius* (L.)) und Heidelbeerspanner (*Boarmia bistortata* (Goeze)) in bayerischen Kiefernwäldern. *Zeitschrift für angewandte Entomologie* **87:** 186–202; 311–322.

HAESELBARTH, E. 1988. Zur Braconidengattung *Townesilitus* Haeselbarth & Loan, 1983. *Entomofauna* **9:** 429–460.

HAESELBARTH, E. & LOAN, C. 1983. *Townesilitus*, a new genus for a species group in *Microctonus* (Hymenoptera: Braconidae, Euphorinae). *Contributions of the American Entomological Institute* **20:** 384–387.

HAGEN, K. S. 1964. Developmental stages of parasites. *In* De Bach, P. (Ed.) *Biological control of insect pests and weeds*: 168–246. London.

HAGEN, K. S. & BOSCH, R. van den. 1968. Impact of pathogens, parasites, and predators on aphids. *Annual Review of Entomology* **13:** 325–384.

HAGSTRUM, D. W. & SMITTLE, B. J. 1977. Host-finding ability of *Bracon hebetor* and its influence upon adult parasite survival and fecundity. *Environmental Entomology* **6:** 437–439.

HAGSTRUM, D. W. & SMITTLE, B. J. 1978. Host utilization by *Bracon hebetor. Environmental Entomology* **7:** 596–600.

HANCOCK, G. L. R. 1925. Notes on the hibernation of Ichneumonidae and on some parasites of *Tortrix viridana* L. *Entomologist's Monthly Magazine* **61:** 23–28.

HANSON, H. S. 1937. Notes on the ecology and control of pine beetles in Great Britain. *Bulletin of Entomological Research* **28:** 185–242.

HARRIS, R. A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology, California Department of Food and Agriculture* **28:** 1–31.

HAVILAND, M. D. 1922. On the larval development of *Dacnusa areolaris* Nees (Braconidae), a parasite of Phytomyzinae (Diptera), with a note on certain chalcid parasites of phytomyzids. *Parasitology* **14:** 167–173.

HAWKINS, B. A., ASKEW, R. R. & SHAW, M. R. 1990. Influences of host feeding-niche and foodplant type on generalist and specialist parasitoids. *Ecological Entomology* **15:** 275–280.

HAWLITZKY, N. 1979. Devenir de l'oeuf et comportement de la larve de *Phanerotoma flavitestacea* (Hym.: Braconidae) lorsque la femelle pond dans des oeufs d'*Anagasta kuehniella* (Lep.: Pyralidae) ayant atteint des stades de devéloppement variés. *Entomophaga* **24:** 237–245.

HEDQVIST, K.-J. 1976. New species of *Spathius* Nees, 1818 and a key to the species of Europe and Canary Islands (Hym. Ichneumonoidea, Braconidae). *Eos* **51** (1975): 51–63.

HEGAZI, E. M. & FÜHRER, E. 1985. Instars of *Microplitis rufiventris* (Hym.: Braconidae) and their relative developmental speed under different photoperiods. *Entomophaga* **30:** 231–243.

HEGAZI, E. M., SCHOPF, A., FÜHRER, E., & FOUAD, S. H. 1988. Developmental synchrony between *Spodoptera littoralis* (Boisd.) and its parasite *Microplitis rufiventris* Kok. *Journal of Insect Physiology* **34:** 773–778.

HELLÉN, W. 1958. Zur Kenntnis der Braconiden (Hym.) Finnlands. II. Subfamilie Helconinae (part.). *Fauna Fennica* **4:** 3–37.

HILL, C. C. & SMITH, H. D. 1931. *Heterospilus cephi* Rohwer, a parasite of the European wheat sawfly, *Cephus pygmaeus* (L.). *Journal of Agricultural Research* **43:** 597–609.

HINCKS, W. D. 1944. On the 'shirt-button' cocoon of *Dyscritulus planiceps* (Marshall) (Hym. Aphidiidae). *Naturalist, Hull* **1944:** 93–96.

HINCKS, W. D. 1952. *Hysteromerus* [sic] *mystacinus* Wesmael in the New Forest (Hym., Braconidae). *Journal of the Society for British Entomology* **4:** 115.

HINTON, H. E. 1954. Insect blood. *Science Progress* **168:** 684–696.

HODSON, A. C. 1939. *Sarcophaga aldrichi* Parker as a parasite of *Malacosoma disstria* Hbn. *Journal of Economic Entomology* **32:** 396–401.

HUDDLESTON, T. 1976. A revision of *Elasmosoma* Ruthe (Hymenoptera, Braconidae) with two new species from Mongolia. *Annales Historico-Naturales Musei Nationalis Hungarici* **68:** 215–225.

HUDDLESTON, T. 1978. Braconidae [and] Aphidiidae. *In* Kloet, G. S. & Hincks, W. D. *A check list of British insects*. (2nd edn) Part 4: Hymenoptera. *Handbooks for the Identification of British Insects* **11** (4): 46–62.

HUDDLESTON, T. 1980. A revision of the western Palaearctic species of the genus *Meteorus* (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) **41:** 1–58.

HUDDLESTON, T. 1984. The Palaearctic species of *Ascogaster* (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) **49:** 341–392.

HUDDLESTON, T. & GAULD, I. 1988. Parasitic wasps (Ichneumonoidea) in British light-traps. *Entomologist* **107:** 134–154.

HUDDLESTON, T. & WALKER, A. K. 1988. *Cardiochiles* (Hymenoptera: Braconidae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. *Bulletin of Entomological Research* **78:** 435–461.

INGRAM, W. R. 1981. The parasitoids of *Spodoptera littoralis* (Lep.: Noctuidae) and their role in population control in Cyprus. *Entomophaga* **26:** 23–37.

IPERTI, G. 1964. Les parasites des coccinelles aphidiphages dans les Alpes-Maritimes et les Basses-Alpes. *Entomophaga* **9:** 153–180.

IVANOVA-KASAS, O. M. 1972. Polyembryony in insects. *In* Counce, S. J. and Waddington, C. H. (Eds) *Developmental systems: insects* **1:** 243–271. London.

IWATA, K. 1959. The comparative anatomy of the ovary in Hymenoptera. Part III. Braconidae (including Aphidiidae) with descriptions of ovarian eggs. *Kontyû* **27:** 231–238.

JACKSON, D. J. 1928. The biology of *Dinocampus (Perilitus) rutilus* Nees, a braconid parasite of *Sitona lineata* L. – Part 1. *Proceedings of the Zoological Society of London* **1928:** 597–630.

JERVIS, M. A. & KIDD, N. A. C. 1986. Host-feeding strategies in hymenopteran parasitoids. *Biological Reviews of the Cambridge Philosophical Society* **61:** 395–434.

JOHANSSON, A. S. 1951. Studies on the relation between *Apanteles glomeratus* L. (Hym., Braconidae) and *Pieris brassicae* L. (Lepid., Pieridae). *Norsk Entomologisk Tidsskrift* **8:** 145–186.

JOHNSON, B. 1959. Effect of parasitization by *Aphidius platensis* Brèthes on the developmental physiology of its host, *Aphis craccivora* Koch. *Entomologia Experimentalis et Applicata* **2:** 82–99.

JOHNSON, B. 1965. Premature breakdown of prothoracic glands in parasitized aphids. *Nature, London* **206:** 958–959.

JOHNSON, S. J. & SMITH, J. W. 1980. Biology of *Orgilus elasmopalpi* (Hym.: Braconidae) with *Elasmopalpus lignosellus* (Lep.: Pyralidae) as host. *Annals of the Entomological Society of America* **73:** 572–575.

JONES, D. 1985. Endocrine interaction between host (Lepidoptera) and parasite (Cheloninae: Hymenoptera): is the host or the parasite in control? *Annals of the Entomological Society of America* **78:** 141–148.

JONES, D. 1987. Material from adult female *Chelonus* sp. directs expression of altered developmental programme of host Lepidoptera. *Journal of Insect Physiology* **33:** 129–134.

JONES, R. E. 1987. Ants, parasitoids, and the cabbage butterfly *Pieris rapae*. *Journal of Animal Ecology* **56:** 739–749.

JONES, W. T. 1982. Sex ratio and host size in a parasitoid wasp. *Behavioral Ecology and Sociobiology* **10:** 207–210.

JUILLET, J. A. 1960. Immature stages, life histories, and behaviour of two hymenopterous parasites of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *Canadian Entomologist* **92:** 342–346.

JUILLET, J. A. 1964. Influence of weather on flight activity of parasitic Hymenoptera. *Canadian Journal of Zoology* **42:** 1133–1141.

KAINOH, Y., HIYORI, T. & TAMAKI, Y. 1982. Kairomone of the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* **17:** 102–110.

KAINOH, Y. & TAMAKI, Y. 1982. Searching behavior and oviposition of the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* **17:** 194–206.

KARIYA, M. 1932. [Observations on a braconid species parasitic on ants.] *Konchu Sekai* **36:** 298–301 (In Japanese).

KAWAKAMI, T. 1985. Development of the immature stages of *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae), an egg-larval parasitoid of the smaller tea tortrix moth, *Adoxophyes* sp. (Lepidoptera: Tortricidae). *Applied Entomology and Zoology* **20:** 380–386.

KAWAKAMI, T. & KAINOH, Y. 1985. Host discrimination and competition in the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae). *Applied Entomology and Zoology* **20:** 362–364.

KAWAKAMI, T. & KAINOH, Y. 1986. Host specificity of the egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hymenoptera: Braconidae) among five tortricid and one noctuid species. *Applied Entomology and Zoology* **21:** 8–14.

KEILIN, D. & PICADO, C. 1913. Évolution et formes larvaires du *Diachasma crawfordi* n. sp. braconide parasite d'une mouche des fruits. *Bulletin Scientifique de la France et de la Belgique* **47:** 203–214.

KERR, W. E. 1962. Genetics of sex determination. *Annual Review of Entomology* **7:** 157–176.

KING, B. H. 1989. Host-size-dependent sex ratios among parasitoid wasps: does host growth matter? *Oecologia* **78:** 420–426.

KING, L. A. L. 1933. Some insects of the Clyde area and their parasites. *Glasgow Naturalist* **11:** 3–8.

KING, P. E., RATCLIFFE, N. A. & COPLAND, M. J. W. 1969. The structure of the egg membranes in *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae). *Proceedings of the Royal Entomological Society of London* (A) **44:** 137–142.

KITANO, H. 1976. Studies on the courtship behavior of *Apanteles glomeratus* L. 3. On the behavior of males and females after their emergence from cocoons. *Physiology and Ecology, Japan* **17:** 383–393.

KITANO, H. 1982. Effect of the venom of the gregarious parasitoid *Apanteles glomeratus* on its hemocytic encapsulation by host, *Pieris*. *Journal of Invertebrate Pathology* **40:** 61–67.

KITANO, H. 1986. The role of *Apanteles glomeratus* venom in the defensive response of its host, *Pieris rapae crucivora*. *Journal of Insect Physiology* **32:** 369–375.

KLOET, G. S. & HINCKS, W. D. 1945. *A check list of British insects*. 483 pp. Stockport.

KÖNIG, R. 1967. Ein Beitrag zur Kenntnis einiger Braconidenarten in Schleswig-Holstein (Hymenoptera: Braconidae, Blacinae). *Faunistisch-Ökologische Mitteilungen* **3:** 112–121.

KÖNIGSMANN, E. 1960. Revision der paläarktischen Arten der Gattung *Idiasta*. *Beiträge zur Entomologie* **10:** 624–654.

KÖNIGSMANN, E. 1969. Beitrag zur Revision der Gattung *Orthostigma* (Hymenoptera, Braconidae). *Deutsche Entomologische Zeitschrift* **16:** 1–53.

KOLAIB, M. O. 1987. Biology of *Zele chlorophthalma* Nees. *Indian Journal of Agricultural Sciences* **57:** 491–493.

KOPELKE, J. P. 1983. Die gallenbildenden *Pontania*-Arten – ihre Sonderstellung unter den Blattwespen. Teil II: Konkurrenz und Koexistenz, Parasitismus. *Natur und Museum* **113:** 11–23.

KRING, T. J. & KRING, J. B. 1988. Aphid fecundity, reproductive longevity, and parasite development in the *Schizaphis graminum* (Rondani) (Homoptera: Aphididae) – *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) system. *Canadian Entomologist* **120:** 1079–1083.

LAING, D. R. & CALTAGIRONE, L. E. 1969. Biology of *Habrobracon lineatellae* (Hymenoptera: Braconidae). *Canadian Entomologist* **101:** 135–142.

LAING, J. E. & LEVIN, D. B. 1982. A review of the biology and a bibliography of *Apanteles glomeratus* (L.) (Hymenoptera: Braconidae). *Biocontrol News and Information* **3:** 7–23.

LATHROP, F. H. & NEWTON, R. C. 1933. The biology of *Opius melleus* Gahan, a parasite of the blueberry maggot. *Journal of Agricultural Research* **46:** 143–160.

LAWRENCE, P. O. 1982. *Biosteres longicaudatus*: developmental dependence on host (*Anastrepha suspensa*) physiology. *Experimental Parasitology* **5:** 396–405.

LAWRENCE, P. O. 1986. Host-parasite hormonal interactions: an overview. *Journal of Insect Physiology* **32:** 295–298.

LAWRENCE, P. O. 1988. Intraspecific competition among first instars of the parasitic wasp *Biosteres longicaudatus*. *Oecologia* **74:** 607–611.

LEJEUNE, R. R. & SILVER, G. T. 1961. Parasites and hyperparasites of the satin moth, *Stilpnotia salicis* Linnaeus, (Lymantriidae) in British Columbia. *Canadian Entomologist* **93:** 456–467.

LELUK, J. & JONES, D. 1989. *Chelonus* sp. near *curvimaculatus* venom proteins: analysis of their potential role and processing during development of host *Trichoplusia ni*. *Archives of Insect Biochemistry and Physiology* **10:** 1–12.

LENTEREN, J. C. van. 1981. Host discrimination by parasitoids. *In* Nordlund, D. A., Jones, R. L. & Lewis, W. J. (Eds) *Semiochemicals*: 153–179. New York.

LENTZ, G. L. & PEDIGO, L. P. 1974. Life history phenomena of *Rogas nolophanae* and *Winthemia sinuata*, parasites of the green cloverworm. *Annals of the Entomological Society of America* **67:** 678–680.

LEONARDI, G. 1926. Elenco delle specie di insetti dannosi e loro parassiti ricordati in Italia fino all'anno 1911. Parte II, fascicolo III. Ord. Coleoptera. *Annali del Regio Instituto Superiore Agrario di Portici* (Serie Terza) **1:** 148–295.

LESTON, D. 1961. Observations on the mirid (Hem.) hosts of Braconidae (Hym.) in Britain. *Entomologist's Monthly Magazine* **97:** 65–71.

LEWIS, W. J. 1970. Life history and anatomy of *Microplitis croceipes* (Hymenoptera:

Braconidae) a parasite of *Heliothis* spp. (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* **63:** 67–70.

LIPKOW, E. 1965. Braconiden als Schmarotzer von Staphyliniden. *Entomophaga* **10:** 377–381.

LIU, S.-s. & CARVER, M. 1982. The effect of temperature on the adult integumental colouration of *Aphidius smithi*. *Entomologia Experimentalis et Applicata* **32:** 54–60.

LIU, S.-s. & CARVER, M. 1985. Studies on the biology of *Aphidius sonchi* Marshall (Hymenoptera: Aphidiidae), a parasite of the sowthistle aphid, *Hyperomyzus latucae* (L.) (Hemiptera: Aphididae). *Bulletin of Entomological Research* **75:** 199–208.

LOAN, C. C. 1963a. The bionomics of *Sitona scissifrons* (Coleoptera: Curculionidae) and its parasite *Microctonus sitonae* (Hymenoptera: Braconidae). *Annals of the Entomological Society of America* **56:** 600–612.

LOAN, C. C. 1963b. Parasitism of the dogwood flea-beetle, *Altica corni*, in Ontario. *Journal of Economic Entomology* **56:** 537–538.

LOAN, C. C. 1964. Observations on the biology of *Centistes excrucians* Haliday (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Ontario* **94** (1963): 56–61.

LOAN, C. C. 1965. Life cycle and development of *Leiophron pallipes* Curtis (Hymenoptera: Braconidae, Euphorinae) in five mirid hosts in the Belleville district. *Proceedings of the Entomological Society of Ontario* **95** (1964): 115–121.

LOAN, C. C. 1967. Studies on the taxonomy and biology of the Euphorinae (Hymenoptera: Braconidae). II. Host relations of six *Microctonus* species. *Annals of the Entomological Society of America* **60:** 236–240.

LOAN, C. C. 1972. Parasitism of adult *Notoxus anchora* Henz. (Coleoptera: Anthicidae) by *Syrrhizus agilis* (Cress.) (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Ontario* **103:** 76.

LOAN, C. C. 1974a. *Microctonus apiophaga*, new species, (Hymenoptera: Braconidae, Euphorinae) a parasite of adult *Apion* weevils in Britain (Coleoptera: Curculionidae). *Proceedings of the Entomological Society of Washington* **76:** 186–189.

LOAN, C. C. 1974b. The European species of *Leiophron* Nees and *Peristenus* Foerster (Hymenoptera: Braconidae, Euphorinae). *Transactions of the Royal Entomological Society of London* **126:** 207–238.

LOAN, C. C. 1980. *Leiophron maculipennis* (Hymenoptera: Braconidae, Euphorinae) a parasite of *Diaphnocoris chlorionis* (Heteroptera: Miridae) in eastern Ontario. *Naturaliste Canadien* **107:** 49–50.

LOAN, C. 1983. Host and generic relations of the Euphorini (Hymenoptera: Braconidae). *Contributions of the American Entomological Institute* **20:** 388–397.

LOAN, C. C., GERBER, G. H. & REID, D. G. 1971. Biosystematics of the tingid parasite *Holdawayella* in Ontario (Hymenoptera: Braconidae, Euphorinae). *Canadian Entomologist* **103:** 1273–1284.

LOAN, C. & HOLDAWAY, F. G. 1961a. *Pygostolus falcatus* (Nees) (Hymenoptera, Braconidae), a parasite of *Sitona* species (Coleoptera, Curculionidae). *Bulletin of Entomological Research* **52:** 473–488.

LOAN, C. & HOLDAWAY, F. G. 1961b. *Microctonus aethiops* (Nees) auctt. and *Perilitus rutilus* (Nees) (Hymenoptera: Braconidae), European parasites of *Sitona* weevils (Coleoptera: Curculionidae). *Canadian Entomologist* **93:** 1057–1079.

LOAN, C. C. & HOLLIDAY, N. J. 1979. Euphorinae parasitic on ground beetles with descriptions of three new species of *Microctonus* Wesmael (Hymenoptera: Braconidae, and Coleoptera: Carabidae). *Naturaliste Canadien* **106:** 393–397.

LOAN, C. C., KLEIN, M. G. & COPPEL, H. C. 1969. *Microctonus glyptosceli* n. sp., a parasite of *Glyptoscelis pubescens* (F.) in Wisconsin (Hymenoptera: Braconidae: Euphorinae & Coleoptera: Chrysomelidae). *Proceedings of the Entomological Society of Washington* **71:** 230–233.

LOAN, C. C. & MATTHEWS, R. 1973. *Cosmophorus capeki* n. sp., from New York (Hymenoptera: Braconidae: Euphorinae). *Proceedings of the Entomological Society of Washington* **75:** 205–208.

LUFF, M. L. 1976. The biology of *Microctonus caudatus* (Thomson), a braconid parasite of the ground beetle *Harpalus rufipes* (Degeer). *Ecological Entomology* **1:** 111–116.

LUFF, M. L. 1977. *Centistes nasutus* (Wesm.) (Hym., Braconidae) parasitizing *Amara apricaria* Payk. (Col., Carabidae). *Entomologist's Monthly Magazine* **112:** 40.

LYLE, G. T. 1914. Contributions to our knowledge of the British Braconidae. No 1. Meteoridae. *Entomologist* **47:** 73–77; 119–125.

LYLE, G. T. 1923. Contributions to our knowledge of the British Braconidae. No 7. Chelonidae. [Partim] *Entomologist* **56:** 147–149.

LYNGNES, R. 1955. Zur Kenntnis der Biologie von *Spathius exarator* L. (Hym. Bracon.). *Zeitschrift für angewandte Entomologie* **38:** 73–81.

LYNGNES, R. 1960. Shape and function of the ovipositor in the three hymenopterous species: *Ephialtes extensor* Thom. (Ichneumonidae), *Spathius exarator* L. (Braconidae), and *Plutothrix coelius* Walk. (Chalcididae). *Norsk Entomologisk Tidsskrift* **11:** 122–134.

McALLISTER, M. K. & ROITBERG, B. D. 1987. Adaptive suicidal behaviour in pea aphids. *Nature, London* **328:** 797–799.

McALLISTER, M. K. & ROITBERG, B. D. 1988. Assumptions about suicidal behaviour of aphids. *Nature, London* **332:** 494–495.

McCOLLOCH, J. W. 1918. Notes on false wireworms with especial reference to *Eleodes tricostata* Say. *Journal of Economic Entomology* **11:** 212–224.

MACEDO, M. V. de & MONTEIRO, R. F. 1989. Seed predation by a braconid wasp, *Allorhogas* sp. (Hymenoptera). *Journal of the New York Entomological Society* **97:** 358–363.

MacGILL, E. I. 1923. The life-history of *Aphidius avenae* (Hal.), a braconid parasitic on the nettle aphis (*Macrosiphum urticae*). *Proceedings of the Royal Society of Edinburgh* **43:** 51–71.

MACKAUER, M. 1959. Die europäischen Arten der Gattungen *Praon* und *Areopraon* (Hymenoptera: Braconidae, Aphidiinae). *Beiträge zur Entomologie* **9:** 810–865.

MACKAUER, M. 1968. Aphidiidae. *Hymenopterorum Catalogus* (nova editio) **3:** 1–103.

MACKAUER, M. & STARÝ, P. 1967. Hym. Ichneumonoidea. World Aphidiidae. *Index of Entomophagous Insects.* 195 pp. Paris.

MADEL, G. 1963. Beiträge zur Morphologie und Biologie von *Meteorus fragilis* Wesm. (Hym. Brac.) – ein Endoparasit des Mondvogels *Phalera bucephala* L. (Lep., Notodontidae). *Zeitschrift für angewandte Entomologie* **53:** 1–47.

MAETÔ, K. 1983. A systematic study on the genus *Polemochartus* Schulz (Hymenoptera, Braconidae), parasitic on the genus *Lipara* Meigen (Diptera, Chloropidae). *Kontyû* **51:** 412–425.

MAETÔ, K. 1987. A comparative morphology of the male internal reproductive organs of the family Braconidae (Hymenoptera, Ichneumonoidea). *Kontyû* **55:** 32–42.

MAETÔ, K. 1990. Phylogenetic relationships and host associations of the subfamily Meteorinae Cresson (Hymenoptera, Braconidae). *Japanese Journal of Entomology* **58:** 383–396.

MARSH, P. M. 1965. The Nearctic Doryctinae. I. A review of the subfamily with a taxonomic revision of the tribe Hecabolini (Hymenoptera: Braconidae). *Annals of the Entomological Society of America* **58:** 668–699.

MARSH, P. M. 1970. The Nearctic Doryctinae, VIII. The genera *Liobracon* and *Pedinotus*, with notes on the definition of the subfamily (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **72:** 313–317.

MARSH, P. M. 1978. The braconid parasites (Hymenoptera) of *Heliothis* species (Lepidoptera: Noctuidae). *Proceedings of the Entomological Society of Washington* **80:** 15–36.

MARSH, P. M. 1979. Family Braconidae. *In* Krombein, K. V., Hurd, P. D., Smith, D. R. & Burks. B. D. (Eds) *Catalog of Hymenoptera in America north of Mexico* **1:** 144–313. Washington.

MARSH, P. M. 1982. Two new species of *Heterospilus* (Hymenoptera: Braconidae) from Mexico being introduced against the cotton boll weevil, *Anthonomus grandis* (Coleoptera: Curculionidae). *Proceedings of the Entomological Society of Washington* **84:** 849–854.

MARSH, P. M., SHAW, S. R. & WHARTON, R. A. 1987. An identification manual for the North American genera of the family Braconidae. *Memoirs of the Entomological Society of Washington* **13:** 1–98.

MARSHALL, T. A. 1885–1899. Monograph of British Braconidae. *Transactions of the Entomological Society of London* **1885:** 1–280; **1887:** 51–131; **1889:** 149–211; **1891:** 7–61; **1894:** 497–534; **1895:** 363–398; **1897:** 1–31; **1899:** 1–79.

MARSHALL, T. A. 1888–1900. Les Braconides. *In* André, E. (Ed.) *Species des Hyménoptères d'Europe et d'Algérie* **4:** 1–603; **5:** 1–635; **5** (ii): 1–373; 1*–82*. Paris.

MARTIN, A. 1947. *An introduction to the genetics of Habrobracon juglandis Ashmead.* 205 pp. New York.

MASON, H. C. 1948. *Chremylus rubiginosus* (Nees), a braconid parasite of the casemaking clothes moth. *Annals of the Entomological Society of America* **41:** 28–40.

MASON, W. R. M. 1973. Recognition of *Zemiotes* (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **75:** 213–215.

MASON, W. R. M. 1974. A generic synopsis of Brachistini (Hymenoptera: Braconidae) and recognition of the name *Charmon* Haliday. *Proceedings of the Entomological Society of Washington* **76:** 235–246.

MASON, W. R. M. 1976. A revision of *Dyscoletes* Haliday (Hymenoptera: Braconidae). *Canadian Entomologist* **108:** 855–858.

MASON, W. R. M. 1978. A synopsis of the Nearctic Braconini, with revisions of Nearctic species of *Coeloides* and *Myosoma*. *Canadian Entomologist* **110:** 721–768.

MASON, W. R. M. 1979. A new *Rogas* (Hymenoptera: Braconidae) parasite of tent caterpillars (*Malacosoma* spp. Lepidoptera: Lasiocampidae) in Canada. *Canadian Entomologist* **111:** 783–786.

MASON, W. R. M. 1981. The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): a phylogeny and reclassification of Microgastrinae. *Memoirs of the Entomological Society of Canada* **115:** 1–147.

MASON, W. R. M. 1985. The correct spelling for *Adelius* Haliday (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **87:** 896.

MASON, W. R. M. 1986. Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. *Proceedings of the Entomological Society of Washington* **88:** 1–7.

MASURIER, A. D. le. 1987. A comparative study of the relationship between host size and brood size in *Apanteles* spp. (Hymenoptera: Braconidae). *Ecological Entomology* **12:** 383–393.

MATHUR, R. N. 1959. Breeding technique and utilisation of *Cedria paradoxa* Wilk. (Hym., Braconidae) for biological control of teak defoliator. *Entomologist's Monthly Magazine* **95:** 248–250.

MATTHEWS, R. W. 1969. The behaviour of three wasp parasites of a Costa Rican bark beetle, with description of a new species of *Ecphylus* (Hymenoptera, Braconidae). *Journal of the Georgia Entomological Society* **4:** 111–118.

MATTHEWS, R. W. 1974. Biology of Braconidae. *Annual Review of Entomology* **19:** 15–32.

MATTHEWS, R. W. 1975. Courtship in parasitic wasps. *In* Price, P. W. (Ed.) *Evolutionary strategies of parasitic insects and mites*: 66–86. New York.

MELTON, C. W. & BROWNING, H. W. 1986. Life history and reproductive biology of *Allorhogas pyralophagus* (Hymenoptera: Braconidae), a parasite imported for release against *Eoreuma loftini* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* **79:** 402–406.

MENDEL, Z. 1986. Hymenopterous parasitoids of bark beetles (Scolytidae) in Israel: relationships between host and parasitoid size, and sex ratio. *Entomophaga* **31**: 127–137.

MOOK, J. H. 1961. Observations on the oviposition behaviour of *Polemon liparae* Gir. (Hym., Braconidae). *Archives Néerlandaises de Zoologie* **14:** 423–430.

MORLEY, C. 1909a. Notes on Braconidae – VIII.: On a part of Marshall's collection. *Entomologist* **42:** 61–62.

MORLEY, C. 1909b. Notes on Braconidae, X: on the Pachylommatinae, with descriptions of new species. *Entomologist's Monthly Magazine* **45:** 209–214.

MORLEY, C. 1935. A beech-tree's insects and their parasites. *Entomologist's Monthly Magazine* **71:** 90–91.

MORLEY, C. 1937. The Hymenoptera of Suffolk. Portio tertio et ultimo. *Transactions of the Suffolk Naturalists' Society* **3:** 223–248.

MUESEBECK, C. F. W. 1918. Two important introduced parasites of the brown-tail moth. *Journal of Agricultural Research* **14:** 191–206.

MUESEBECK, C. F. W. 1927. A revision of the parasitic wasps of the subfamily Braconinae occurring in America north of Mexico. *Proceedings of the United States National Museum* **69** (16): 1–73.

MUESEBECK, C. F. W. 1936a. The genera of parasitic wasps of the braconid subfamily Euphorinae, with a review of the Nearctic species. *Miscellaneous Publications, United States Department of Agriculture* **241:** 1–38.

MUESEBECK, C. F. W. 1936b. On two little known genera of Braconidae (Hymenoptera). *Proceedings of the Entomological Society of Washington* **37:** 173–177.

MUESEBECK, C. F. W. 1937. A new West Indian species of *Mirax* Haliday parasitic on the coffee leaf-miner (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **39:** 139–141.

MUESEBECK, C. F. W. 1963. Host relationships of the Euphorini (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* **65:** 306.

MUNRO, J. W. 1917. The structure and life-history of *Bracon* sp.: a study of parasitism. *Proceedings of the Royal Society of Edinburgh* **36** (1915–1916): 313–333.

MYERS, J. G. 1927. The habits of *Alysia manducator* (Hym., Braconidae). *Bulletin of Entomological Research* **17:** 219–229.

NÄGELI, W. 1936. Die kleine Fichtenblattwespe. (*Lygaeonematus pini* Retz. = *Nematus abietinus* Christ). *Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen* **19:** 213–381.

NARAYANAN, E. S., SUBBA RAO, B. R. & THAKERE, K. R. 1961. The biology and some aspects of morphology of the immature stages of *Chelonus narayani* Subba Rao (Braconidae: Hymenoptera). *Proceedings of the National Institute of Sciences of India* (B) **27:** 68–82.

NEALIS, V. & RÉGNIÈRE, J. 1987. The influence of parasitism by *Apanteles fumiferanae* Vier. (Hymenoptera: Braconidae) on spring dispersal and changes in the distribution of larvae of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist* **119:** 141–146.

NELSON, W. A. & FARSTAD, C. W. 1953. Biology of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae), an important native parasite of the wheat stem sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae), in western Canada. *Canadian Entomologist* **85:** 103–107.

NEW, T. R. 1970. The life histories of two species of *Leiophron* Nees (Hymenoptera, Braconidae) parasitic on Psocoptera in southern England. *Entomologist's Gazette* **21:** 39–48.

NICKELS, C. B., PIERCE, W. C. & PINKNEY, C. C. 1950. Parasites of the pecan nut casebearer in Texas. *Technical Bulletin, United States Department of Agriculture* **1011:** 1–21.

NIXON, G. E. J. 1934. On the synonymy of *Elasmosoma berolinensis* Ruthe, as known in England. *Entomologist's Monthly Magazine* **70:** 182–183.

NIXON, G. E. J. 1938. Notes on the taxonomy and synonymy of *Zele*, Curtis, and *Macrocentrus*, Curtis (Hym., Braconidae). *Bulletin of Entomological Research* **29:** 415–424.

NIXON, G. E. J. 1943–1954. A revision of the European Dacnusini (Hym., Braconidae). *Entomologist's Monthly Magazine* **79:** 20–34; 159–168; **80:** 88–108; 140–151; 193–200; 249–255; **81:** 189–204; 217–229; **82:** 279–300; **84:** 207–224; **85:** 289–298; **90:** 257–290.

NIXON, G. E. J. 1965. A reclassification of the tribe Microgasterini (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) Supplement **2:** 1–284.

NIXON, G. E. J. 1968. A revision of the genus *Microgaster* Latreille (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) **22:** 33–72.

NIXON, G. E. J. 1970. A revision of the N.W. European species of *Microplitis* Förster (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) **25:** 1–30.

NIXON, G. E. J. 1972. A revision of the north-western European species of the *laevigatus*-group of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* **61:** 701–743.

NIXON, G. E. J. 1973. A revision of the north-western European species of the *vitripennis*, *pallipes*, *octonarius*, *triangulator*, *fraternus*, *formosus*, *parasitellae*, *metacarpalis* and *circumscriptus*-groups of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* **63:** 169–230.

NIXON, G. E. J. 1974. A revision of the north-western European species of the *glomeratus*-group of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* **64:** 453–524.

NIXON, G. E. J. 1976. A revision of the north-western European species of the *merula*, *lacteus*, *vipio*, *ultor*, *ater*, *butalidis*, *popularis*, *carbonarius* and *validus*-groups of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* **65:** 687–732.

NIXON, G. E. J. 1986. A revision of the European Agathidinae (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History)* (Entomology) **52:** 183–243.

OATMAN, E. R., PLATNER, G. R. & GREANY, P. D. 1969. The biology of *Orgilus lepidus* (Hymenoptera: Braconidae), a primary parasite of the potato tuberworm. *Annals of the Entomological Society of America* **62:** 1407–1414.

OBRTEL, R. 1960. Premature stages of *Triaspis caudatus* (Nees) (Hym.: Braconidae). *Folia Zoologica* **9:** 35–38.

OBRYCKI, J. J., TAUBER, M. J. & TAUBER, C. A. 1985. *Perilitus coccinellae* (Hymenoptera: Braconidae): parasitization and development in relation to host-stage attacked. *Annals of the Entomological Society of America* **78:** 852–854.

ODEBIYI, J. A. & OATMAN, E. R. 1972. Biology of *Agathis gibbosa* (Hymenoptera: Braconidae), a primary parasite of the potato tuberworm. *Annals of the Entomological Society of America* **65:** 1104–1114.

ODEBIYI, J. A. & OATMAN, E. R. 1977. Biology of *Agathis unicolor* (Schrottky) and *Agathis gibbosa* (Say) (Hymenoptera: Braconidae), primary parasites of the potato tuberworm. *Hilgardia* **45:** 123–151.

O'DONNELL, D. J. 1987a. Larval development and the determination of the number of instars in aphid parasitoids (Hymenoptera: Aphidiidae). *International Journal of Insect Morphology and Embryology* **16:** 3–15.

O'DONNELL, D. J. 1987b. A comparison of techniques used to study the morphology of final instar larvae of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae). *Systematic Entomology* **12:** 231–238.

O'DONNELL, D. J. 1989. A morphological and taxonomic study of first instar larvae of Aphidiinae (Hymenoptera: Braconidae). *Systematic Entomology* **14:** 197–219.

OGLOBLIN, A. A. 1913. [Contribution to the biology of Coccinellidae.] *Entomologicheskoe Obozrenie* **13:** 24–43. (In Russian).

OGLOBLIN, A. A. 1924. Le rôle du blastoderme extraembryonnaire du *Dinocampus terminatus* Nees pendant l'état larvaire. *Mémoires de la Société Royale des Sciences de Bohème* **3:** 1–27.

OLIVIER, E. 1893. [No title.] *Annales de la Société Entomologique de France* **1893:** 71.

OPINION 162. 1945. Suspension of the rules for *Bracon* Fabricius [1804–1805] (Class Insecta, Order Hymenoptera). *Opinions of the International Commission on Zoological Nomenclature* **2:** 321–330.

OPINION 1424. 1987. *Gnamptodon* Haliday, 1833 (Insecta, Hymenoptera): *Bracon pumilio* Nees, 1834 designated as type species. *Bulletin of Zoological Nomenclature* **44:** 55–56.

OPINION 1510. 1988. *Microgaster* Latreille, 1804 (Insecta, Hymenoptera): *Microgaster australis* Thomson, 1895 designated as the type species. *Bulletin of Zoological Nomenclature* **45:** 239–240.

OSBORNE, P. 1960. Observations on the natural enemies of *Meligethes aeneus* (F.) and *M. viridescens* (F.) (Coleoptera: Nitidulidae). *Parasitology* **50:** 91–110.

OSMAN, S. E., RAWASH, I. A. & EL-GAYAR, F. 1985. The effect of the larval endoparasite *Microplitis rufiventris* Kok. (Hym., Braconidae) on the blood picture and cuticle formation of *Spodoptera littoralis* (Boisd.) larvae. *Bulletin of the Entomological Society of Egypt* **13** (1982–1983): 183–189.

PAILLOT, A. 1937. Sur le développement polyembryonnaire d'*Amicroplus collaris* Spin. parasite des chenilles d'*Euxoa segetum* Schiff. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris* **204:** 810–812.

PAPP, J. 1968. A survey of the *Phaenocarpa* Förster species of the Carpathian Basin, central Europe (Hymenoptera, Braconidae: Alysiinae). *Beiträge zur Entomologie* **18:** 569–603.

PAPP, J. 1975. Three new European species of *Colastes* Hal. with taxonomic remarks (Hymenoptera: Braconidae, Exothecinae). *Acta Zoologica Academiae Scientiarum Hungaricae* **21:** 411–423.

PAPP, J. 1976a. Key to the European *Microgaster* Latr. species, with a new species and taxonomical remarks (Hymenoptera: Braconidae, Microgasterinae). *Acta Zoologica Academiae Scientiarum Hungaricae* **22:** 97–117.

PAPP, J. 1976b. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgasterinae). I. The species-groups. *Annales Historico-Naturales Musei Nationalis Hungarici* **68:** 251–274.

PAPP, J. 1978. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgasterinae) II. The *laevigatus*-group, 1. *Annales Historico-Naturales Musei Nationalis Hungarici* **70:** 265–301.

PAPP, J. 1979. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgasterinae) III. The *laevigatus*-group, 2. *Annales Historico-Naturales Musei Nationalis Hungarici* **71:** 235–250.

PAPP, J. 1980. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgasterinae). IV. The *lineipes*-, *obscurus*- and *ater*-group. *Annales Historico-Naturales Musei Nationalis Hungarici* **72:** 241–272.

PAPP, J. 1981. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae). V. The *lacteus-*, *longipalpis-*, *ultor-*, *butalidis-* and *vipio-*group. *Annales Historico-Naturales Musei Nationalis Hungarici* **73:** 263–291.

PAPP, J. 1982. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae), VI. The *laspeyresiella-*, *merula-*, *falcatus-*, and *validus-*group. *Annales Historico-Naturales Musei Nationalis Hungarici* **74:** 225–267.

PAPP, J. 1983. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae), VII. The *carbonarius-*, *circumscriptus-*, *fraternus-*, *pallipes-*, *parasitellae-*, *vitripennis-*, *liparidis-*, *octonarius-* and *thompsoni-*group. *Annales Historico-Naturales Musei Nationalis Hungarici* **75:** 247–283.

PAPP, J. 1984a. Two new species of *Mirax* Haliday in the Palaearctic Region (Hymenoptera: Braconidae, Adeliinae). *Folia Entomologica Hungarica* **45:** 167–171.

PAPP, J. 1984b. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae), VIII. The *metacarpalis-*, *formosus-*, *popularis-* and *suevus-*group. *Annales Historico-Naturales Musei Nationalis Hungarici* **76:** 265–295.

PAPP, J. 1984c. Palaearctic species of *Microgaster* Latreille (=*Microplitis* Förster) with description of seven new species (Hymenoptera, Braconidae, Microgastrinae). *Entomologische Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden* **47:** 95–140.

PAPP, J. 1986. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae). IX. The *glomeratus-*group, 1. *Annales Historico-Naturales Musei Nationalis Hungarici* **78:** 225–247.

PAPP, J. 1987. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae). X. The *glomeratus-*group 2 and the *cultellatus-*group. *Annales Historico-Naturales Musei Nationalis Hungarici* **79:** 207–258.

PAPP, J. 1988. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae). XI. "Homologization" of the species-groups of *Apanteles* s.l. with Mason's generic taxa. Checklist of genera. Parasitoid/host list 1. *Annales Historico-Naturales Musei Nationalis Hungarici* **80:** 145–175.

PAPP, J. 1989. *Mirax heinrichi* sp. n. from the U.S.A. and taxonomic bionomic data of two European *Mirax* species (Hymenoptera: Braconidae, Adeliinae). *Folia Entomologica Hungarica* **50:** 105–110.

PARKER, D. L. 1935. *Apanteles solitarius* (Ratzeburg), an introduced braconid parasite of the satin moth. *Technical Bulletin, United States Department of Agriculture* **477:** 1–17.

PARKER, H. L. 1931a. *Macrocentrus gifuensis* Ashmead, a polyembryonic braconid parasite in the European corn borer. *Technical Bulletin, United States Department of Agriculture* **230:** 1–62.

PARKER, H. L. 1931b. Notes on *Meteorus* (*Zemiotes*) *nigricollis* Thomson, an occasional parasite of the European corn borer. *Proceedings of the Entomological Society of Washington* **33:** 93–103.

PARNELL, J. R. 1964. The parasite complex of the two seed beetles *Bruchidius ater* (Marsham) (Coleoptera: Bruchidae) and *Apion fuscirostre* Fabricius (Coleoptera: Curculionidae). *Transactions of the Royal Entomological Society of London* **116:** 73–88.

PARROTT, P. J. & GLASGOW, H. 1916. The leaf-weevil (*Polydrusus impressifrons* Gyll.). *Technical Bulletin, New York State Agricultural Experiment Station* **56:** 1–22.

PAUL, A. V. N., PARSHAD, B. & KUMAR, P. 1980. Age and density effect of the laboratory host, *Corcyra cephalonica* Stainton (Lep., Pyral.), on the egg-larval parasitoid *Chelonus blackburni* Cameron (Hym., Braconidae). *Zeitschrift für angewandte Entomologie* **90:** 391–395.

PEMBERTON, C. E. & WILLARD, H. F. 1918a. Interrelations of fruit-fly parasites in Hawaii. *Journal of Agricultural Research* **12:** 285–295.

PEMBERTON, C. E. & WILLARD, H. F. 1918b. A contribution to the biology of fruit-fly parasites in Hawaii. *Journal of Agricultural Research* **15:** 419–466.

PIEK, T. (Ed.) 1986. *Venoms of the Hymenoptera. Biochemical, pharmacological and behavioural aspects.* 570 pp. London.

PIERCE, W. D. & HOLLOWAY, T. E. 1912. Notes on the biology of *Chelonus texanus* Cress. *Journal of Economic Entomology* **5:** 425–428.

PIERRE, A. 1893. Un parasite des fourmis *Elasmosoma berolinense* Ruth. *Revue Scientifique du Bourbonnais et du Centre de la France* **6:** 112–114.

POLASZEK, A. 1986. The effects of two species of hymenopterous parasitoid on the reproductive system of the pea aphid, *Acyrthosiphon pisum. Entomologia Experimentalis et Applicata* **40:** 285–292.

PORTER, K. 1983. Multivoltinism in *Apanteles bignellii* and the influence of weather on synchronisation with its host *Euphydryas aurinia. Entomologia Experimentalis et Applicata* **34:** 155–162.

POWELL, W. 1980. *Toxares deltiger* (Haliday) (Hymenoptera: Aphidiidae) parasitising the cereal aphid, *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae), in southern England: a new host-parasitoid record. *Bulletin of Entomological Research* **70:** 407–409.

POWELL, W. 1982. The identification of hymenopterous parasitoids attacking cereal aphids in Britain. *Systematic Entomology* **7:** 465–473.

POWERS, N. R. & OATMAN, E. R. 1984. Biology and temperature responses of *Chelonus kellieae* and *Chelonus phthorimaeae* (Hymenoptera: Braconidae) and their host, the potato tuberworm, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Hilgardia* **52** (9): 1–32.

PRINCE, G. J. 1976. Laboratory biology of *Phaenocarpa persimilis* Papp (Braconidae: Alysiinae), a parasitoid of *Drosophila. Australian Journal of Zoology* **24:** 249–264.

PRINCIPI, M. M., MEMMI, M. & SGOBBA, D. 1979. Reperti su *Chrysopophthorus chrysopimaginis* Goidanich, parassita solitario delle immagini di neurotteri crisopidi. *Bollettino dell'Istituto di Entomologia della Universita degli Studi di Bologna* **34:** 247–273.

PROKOPY, R. J. & WEBSTER, R. P. 1978. Oviposition-deterring pheromone of *Rhagoletis pomonella* a kairomone for its parasitoid *Opius lectus. Journal of Chemical Ecology* **4:** 481–494.

PROPER, A. B. 1934. Hyperparasitism in the case of some introduced lepidopterous tree defoliators. *Journal of Agricultural Research* **48:** 359–376.

PSCHORN-WALCHER, H. & KRIEGL, M. 1965. Zur Kenntnis der Parasiten der Bürsthorn-Blattwespen der Gattung *Arge* Schrank (Hymenoptera: Argidae). *Zeitschrift für angewandte Entomologie* **56:** 263–275.

PUNGERL, N. B. 1983. Variability in characters commonly used to distinguish *Aphidius* species (Hymenoptera: Aphidiidae). *Systematic Entomology* **8:** 425–430.

PUNGERL, N. B. 1984. Host preferences of *Aphidius* (Hymenoptera: Aphidiidae) populations parasitising pea and cereal aphids (Hemiptera: Aphididae). *Bulletin of Entomological Research* **74:** 153–161.

PUNGERL, N. B. 1986. Morphometric and electrophoretic study of *Aphidius* species (Hymenoptera: Aphidiidae) reared from a variety of aphid hosts. *Systematic Entomology* **11:** 327–354.

PUTERKA, G. J., SLOSSER, J. E., PRICE, J. R. & MEINKE, L. J. 1986a. Host/plant relationships used by the boll weevil (Coleoptera: Curculionidae) parasite *Bracon mellitor* (Hymenoptera: Braconidae) in the Texas rolling plains. *Environmental Entomology* **15:** 880–883.

PUTERKA, G. J., SLOSSER, J. E., PRICE, J. R. & MEINKE, L. J. 1986b. *Bracon* spp. and their host insects and plants in the Texas rolling plains. *Southwestern Entomologist* **11:** 249–254.

PUTMAN, W. L. 1963. The strawberry leaf roller, *Ancylis comptana fragariae* (Walsh and Riley) (Lepidoptera: Tortricidae), as a source of overwintered *Macrocentrus ancylivorus* Rohwer (Hymenoptera: Braconidae) in Ontario. *Canadian Entomologist* **95:** 1022–1023.

PUTTLER, B. & THEWKE, S. E. 1970. Biology of *Microplitis feltiae* (Hymenoptera: Braconidae), a parasite of black cutworm *Agrotis ipsilon. Annals of the Entomological Society of America* **63:** 645–648.

QUEDNAU, F. W. 1970. Notes on life-history, fecundity, longevity and attack pattern of *Agathis pumila* (Hymenoptera: Braconidae), a parasite of the larch casebearer. *Canadian Entomologist* **102:** 736–745.

QUICKE, D. L. J. 1987a. First host record for the genus *Hyboteles* van Achterberg (Hymenoptera, Braconidae). *Proceedings and Transactions of the British Entomological and Natural History Society* **20:** 122.

QUICKE, D. L. J. 1987b. The Old World genera of braconine wasps (Hymenoptera: Braconidae). *Journal of Natural History* **21:** 43–157.

QUICKE, D. L. J. 1987c. A new subfamily of Braconidae, the Vaepellinae, based on a new genus and species from Ghana (Insecta, Hymenoptera). *Zoologica Scripta* **16:** 73–77.

QUICKE, D. L. J. 1988. Higher classification, biogeography and biology of the Braconinae (Hymenoptera: Braconidae). *In* Gupta, V. K. (Ed.) *Advances in parasitic Hymenoptera research*: 117–138. Leiden.

QUICKE, D. L. J. 1989. Further new host records for genera and species of Braconinae (Hym., Braconidae). *Entomologist's Monthly Magazine* **125:** 199–205.

QUICKE, D. L. J. & ACHTERBERG, C. van. 1990. Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandelingen* **258:** 1–95.

QUICKE, D. L. J. & HUDDLESTON, T. 1989. The Australian braconid wasp subfamily Mesostoinae (Hymenoptera: Braconidae) with the description of a new species of *Mesostoa*. *Journal of Natural History* **23:** 1309–1317.

QUICKE, D. L. J. & SHARKEY, M. J. 1989. A key to and notes on the genera of Braconinae (Hymenoptera: Braconidae) from America north of Mexico with descriptions of two new genera and three new species. *Canadian Entomologist* **121:** 337–361.

RASNITSYN, A. P. 1980. The origin and evolution of Hymenoptera. *Trudy̆ Paleontologicheskogo Instituta Akademiya Nauk SSSR* **174:** 1–191. (In Russian) [English translation by Agriculture Canada, 1984. Ottawa].

RASNITSYN, A. P. 1988. An outline of evolution of the hymenopterous insects (order Vespida). *Oriental Insects* **22:** 115–145.

RECHAV, Y. 1978. Biological and ecological studies of the parasitoid *Chelonus inanitus* (Hym.: Braconidae) in Israel. IV. Oviposition, host preferences and sex ratio. *Entomophaga* **23:** 95–102.

RECHAV, Y. & ORION, T. 1975. The development of the immature stages of *Chelonus inanitus*. *Annals of the Entomological Society of America* **68:** 457–462.

REED-LARSEN, D. A. & BROWN, J. J. 1990. Embryonic castration of the codling moth, *Cydia pomonella* by an endoparasitoid, *Ascogaster quadridentata*. *Journal of Insect Physiology* **36:** 111–118.

RICHARDS, O. W. 1957. A note on the genus *Mirax* Hal. (Hym., Braconidae, Microgasterinae). *Entomologist* **90:** 120–122.

RICHARDS, O. W. 1960. On some British species of *Perilitus* Nees (Hymenoptera: Braconidae). *Proceedings of the Royal Entomological Society of London* (B) **29:** 140–144.

RICHARDS, O. W. 1977. Hymenoptera, introduction and key to families. *Handbooks for the Identification of British Insects* **6** (1): 1–100.

RICHERSON, J. V. & BORDEN, J. H. 1972. Host finding by heat perception in *Coeloides brunneri* (Hymenoptera: Braconidae). *Canadian Entomologist* **104:** 1877–1881.

RICHERSON, J. V., BORDEN, J. H. & HOLLINGDALE, J. 1972. Morphology of a unique sensillum placodeum on the antennae of *Coeloides brunneri* (Hymenoptera: Braconidae). *Canadian Journal of Zoology* **50:** 909–913.

ROBERT, A. 1961. Les hyménoptères parasites des charançons de l'orme et leur influence sur leurs hôtes dans le Québec. *Annales de la Société Entomologique du Québec* **6:** 121–143.

ROHWER, S. A. 1914. Synopsis of the North American species of the genus *Capitonius* Brullé. *Canadian Entomologist* **46:** 316–322.

ROSENBERG, H. T. 1934. The biology and distribution in France of the larval parasites of *Cydia pomonella* L. *Bulletin of Entomological Research* **25:** 201–256.

ROTHERAM, S. M. 1967. Immune surface of eggs of a parasitic insect. *Nature, London* **214:** 700.

ROTHERAY, G. E. 1981. Host searching and oviposition behaviour of some parasitoids of aphidophagous Syrphidae. *Ecological Entomology* **6:** 79–87.

ROTHERAY, G. E. 1988. Larval morphology and feeding patterns of four *Cheilosia* species (Diptera: Syrphidae) associated with *Cirsium palustre* L. Scopoli (Compositae) in Scotland. *Journal of Natural History* **22:** 17–25.

RUSSO, G. 1938. VI contributo alla conoscenza dei coleotteri scolitidi. Fleotribo: *Phloeotribus scarabaeoides* (Bern.) Fauv. Parte seconda. Biografia, simbionti, danni e lotta. *Bollettino del Regio Laboratorio di Entomologia Agraria di Portici* **2:** 3–420.

RYAN, R. B. 1962. Durations of the immature stadia of *Coeloides brunneri* (Hymenoptera: Braconidae) at various constant temperatures, with descriptions of the five larval instars. *Annals of the Entomological Society of America* **55:** 403–409.

RYAN, R. B. 1985. A hypothesis for decreasing parasitization of larch casebearer (Lepidoptera: Coleophoridae) on larch foliage by *Agathis pumila*. *Canadian Entomologist* **117:** 1573–1574.

RYAN, R. B. & RUDINSKY, J. A. 1962. Biology and habits of the Douglas-fir beetle parasite, *Coeloides brunneri* Viereck (Hymenoptera: Braconidae), in western Oregon. *Canadian Entomologist* **94:** 748–763.

SAFFER, B. 1982. A systematic revision of the genus *Cenocoelius* (Hymenoptera; Braconidae) in North America including Mexico. *Polskie Pismo Entomologiczne* **52:** 73–167.

SALKELD, E. H. 1967. Histochemistry of the excretory system of the endoparasitoid *Aphaereta pallipes* (Say) (Hymenoptera: Braconidae). *Canadian Journal of Zoology* **45:** 967–973.

SALT, G. 1931. Parasites of the wheat-stem sawfly, *Cephus pygmaeus*, Linnaeus, in England. *Bulletin of Entomological Research* **22:** 479–545.

SALT, G. 1961. Competition among insect parasitoids. *Symposia of the Society for Experimental Biology* **15:** 96–119.

SALT, G. 1968. The resistance of insect parasitoids to the defence reactions of their hosts. *Biological Reviews of the Cambridge Philosophical Society* **43:** 200–232.

SALT, G. 1970. *The cellular defence reactions of insects.* 118 pp. Cambridge.

SATO, Y. 1980. Experimental studies on parasitization by *Apanteles glomeratus* V. Relationships between growth rate of parasitoid and host age at the time of oviposition. *Entomophaga* **25:** 123–128.

SATO, Y., TANAKA, T., IMAFUKU, M. & HIDAKA, T. 1983. How does diurnal *Apanteles kariyai* parasitize and egress from a nocturnal host larva? *Kontyû* **51:** 128–139.

SCHLINGER, E. I. & HALL, J. C. 1960. The biology, behavior and morphology of *Praon palitans* Muesebeck, an internal parasite of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton) (Hymenoptera: Braconidae, Aphidiinae). *Annals of the Entomological Society of America* **53:** 144–160.

SCHLINGER, E. I. & HALL, J. C. 1961. The biology, behavior, and morphology of *Trioxys utilis*, an internal parasite of the spotted alfalfa aphid, *Therioaphis maculata* (Hymenoptera: Braconidae, Aphidiinae). *Annals of the Entomological Society of America* **54:** 34–45.

SCHRÖDER, D. 1974. A study of the interactions between the internal larval parasites of *Rhyacionia buoliana* (Lepidoptera: Olethreutidae). *Entomophaga* **19:** 145–171.

SEITNER, M. & NÖTZL, P. 1925. *Pityophthorus henscheli* Seitner und sein Parasit *Cosmophorus henscheli* Ruschka. *Zeitschrift für angewandte Entomologie* **11:** 187–196.

SÉMÉRIA, Y. 1976. Un braconide, *Chrysopophthorus chrysopimaginis* Goidanich (Hymenoptera, Braconidae) parasite des imagos de Chrysopinae (Planipennia, Chrysopidae). *Bulletin Mensuel de la Société Linnéenne de Lyon* **45:** 102–106; 127.

SHARKEY, M. J. 1985. Notes on the genera *Bassus* Fabricius and *Agathis* Latreille, with a description of *Bassus arthurellus* n. sp. (Hymenoptera: Braconidae). *Canadian Entomologist* **117:** 1497–1502.

SHARMA, V. 1984. A new subfamily Excultinae with description of type genus, from Jammu (India) (Hymenoptera, Braconidae). *Reichenbachia* **22:** 75–77.

SHAW, M. R. 1981a. Delayed inhibition of host development by the nonparalyzing venoms of parasitic wasps. *Journal of Invertebrate Pathology* **37:** 215–221.

SHAW, M. R. 1981b. Some parasites (Hymenoptera) of *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in Cornwall. *Entomologist's Gazette* **32:** 36–38.

SHAW, M. R. 1983a. *Aphaereta pallipes* (Say) (Hym: Braconidae) new to Britain and the Palaearctic Region, with remarks on other parasites of Diptera. *Entomologist's Monthly Magazine* **119:** 73–74.

SHAW, M. R. 1983b. On[e] evolution of endoparasitism: the biology of some genera of Rogadinae (Braconidae). *Contributions of the American Entomological Institute* **20:** 307–328.

SHAW, M. R. 1988a. *Spathius curvicaudis* Ratzeburg (Hym.: Braconidae) new to Britain and parasitising *Agrilus pannonicus* (Piller and Mitterpacher) (Col.: Buprestidae). *Entomologist's Record and Journal of Variation* **100:** 215–216.

SHAW, M. R. 1988b. *Meteorus brevicauda* Thomson (Hymenoptera: Braconidae) reared from larvae of *Zeugophora subspinosa* (Fabricius) (Coleoptera: Chrysomelidae). *Entomologist's Gazette* **39:** 205–206.

SHAW, M. R. 1989. *Cosmophorus cembrae* Ruschka new to Britain (Hymenoptera: Braconidae: Euphorinae). *Entomologist's Gazette* **40:** 241–243.

SHAW, M. R. 1990. Parasitoids of European butterflies and their study. *In* Kudrna, O. (Ed.) *Butterflies of Europe* **2:** 449–479. Wiesbaden.

SHAW, M. R. & ASKEW, R. R. 1976a. Ichneumonoidea (Hymenoptera) parasitic upon leaf-mining insects of the orders Lepidoptera, Hymenoptera and Coleoptera. *Ecological Entomology* **1:** 127–133.

SHAW, M. R. & ASKEW, R. R. 1976b. Parasites. *In* Heath, J. (Ed.) *The moths and butterflies of Great Britain and Ireland* **1:** 24–56. Oxford.

SHAW, M. R. & ASKEW, R. R. 1979. Hymenopterous parasites of Diptera (Hymenoptera Parasitica). *In* Stubbs, A. & Chandler, P. (Eds) *A dipterist's handbook*: 164–171. Hanworth.

SHAW, S. R. 1983. A taxonomic study of Nearctic *Ascogaster* and a description of a new genus *Leptodrepana* (Hymenoptera: Braconidae). *Entomography* **2:** 1–54.

SHAW, S. R. 1985. A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). *Entomography* **3:** 277–370.

SHAW, S. R. 1988. Euphorine phylogeny: the evolution of diversity in host-utilization by parasitoid wasps (Hymenoptera: Braconidae). *Ecological Entomology* **13:** 323–335.

SHAW, S. R. & EDGERLY, J. S. 1985. A new braconid genus (Hymenoptera) parasitizing webspinners (Embiidina) in Trinidad. *Psyche, Cambridge* **92:** 505–512.

SHENEFELT, R. D. 1960. *Ropalophorus* Haliday – a genus new to North America (Hymenoptera: Braconidae: Euphorinae). *Annals of the Entomological Society of America* **53:** 542–546.

SHENEFELT, R. D. 1965. A contribution towards knowledge of the world literature regarding Braconidae (Hymenoptera: Braconidae). *Beiträge zur Entomologie* **15:** 243–500.

SHENEFELT, R. D. 1969. Braconidae 1. Hybrizoninae, Euphorinae, Cosmophorinae, Neoneurinae, Macrocentrinae. *Hymenopterorum Catalogus* (nova editio) **4:** 1–176.

SHENEFELT, R. D. 1970a. Braconidae 2. Helconinae, Calyptinae, Mimagathidinae, Triaspinae. *Hymenopterorum Catalogus* (nova editio) **5:** 177–306.

SHENEFELT, R. D. 1970b. Braconidae 3. Agathidinae. *Hymenopterorum Catalogus* (nova editio) **6:** 307–428.

SHENEFELT, R. D. 1972. Braconidae 4. Microgasterinae: *Apanteles*. *Hymenopterorum Catalogus* (nova editio) **7:** 429–668.

SHENEFELT, R. D. 1973a. Braconidae 5. Microgasterinae & Ichneutinae. *Hymenopterorum Catalogus* (nova editio) **9:** 669–812.

SHENEFELT, R. D. 1973b. Braconidae 6. Cheloninae. *Hymenopterorum Catalogus* (nova editio) **10:** 813–936.

SHENEFELT, R. D. 1974. Braconidae 7. Alysiinae. *Hymenopterorum Catalogus* (nova editio) **11:** 937–1113.

SHENEFELT, R. D. 1975. Braconidae 8. Exothecinae, Rogadinae. *Hymenopterorum Catalogus* (nova editio) **12:** 1115–1262.

SHENEFELT, R. D. 1978. Braconidae 10. Braconinae, Gnathobraconinae, Mesostoinae, Pseudodicrogeniinae, Telengainae, Ypsistocerinae plus Braconidae in genera, major groups, unplaced genera and species. *Hymenopterorum Catalogus* (nova editio) **15:** 1425–1872.

SHENEFELT, R. D. 1980. Braconidae 11. Introduction, guide to host names, index to braconid names. *Hymenopterorum Catalogus* (nova editio) **16:** 1–384.

SHENEFELT, R. D. & MARSH, P. M. 1976. Braconidae 9. Doryctinae. *Hymenopterorum Catalogus* (nova editio) **13:** 1263–1424.

SHORT, J. R. T. 1952. The morphology of the head of larval Hymenoptera with special reference to the head of the Ichneumonoidea, including a classification of the final instar larvae of the Braconidae. *Transactions of the Royal Entomological Society of London* **103:** 27–84.

SIGWALT, B. 1977. La nomenclature alaire de Comstock-Needham dans l'étude des braconides: distinction des genres *Phanerotoma* et *Phanerotomella* (Hym., Braconidae, Cheloninae). *Annales de la Société Entomologique de France* (Nouvelle Serie) **13:** 525–534.

SIMMONDS, F. J. 1947a. The biology of the parasites of *Loxostege sticticalis*, L., in North America – *Bracon vulgaris* (Cress.) (Braconidae, Agathinae). *Bulletin of Entomological Research* **38:** 145–155.

SIMMONDS, F. J. 1947b. The biology of the parasites of *Loxostege sticticalis*, L., in North America – *Meteorus loxostegei*, Vier. (Braconidae, Meteorinae). *Bulletin of Entomological Research* **38:** 373–379.

SINGH, R. & SRIVASTAVA, M. 1987. Bionomics of *Trioxys indicus* Subba Rao and Sharma, an aphidiid parasitoid of *Aphis craccivora* Koch. 25. The role of host haemolymph in the host stage preference by the parasitoid. *Giornale Italiano di Entomologia* 3 (17): 409–412.

SIVINSKI, J. & WEBB, J. C. 1989. Acoustic signals produced during courtship in *Diachasmimorpha* (=*Biosteres*) *longicaudata* (Hymenoptera: Braconidae) and other Braconidae. *Annals of the Entomological Society of America* **82:** 116–120.

SLANSKY, F. 1986. Nutritional ecology of endoparasitic insects and their hosts: an overview. *Journal of Insect Physiology* **32:** 255–261.

SLUSS, R. 1968. Behavioral and anatomical responses of the convergent lady beetle to parasitism by *Perilitus coccinellae* (Schrank). *Journal of Invertebrate Pathology* **10:** 9–27.

SLUSS, R. R. & LEUTENEGGER, R. 1968. The fine structure of the trophic cells of *Perilitus coccinellae. Journal of Ultrastructure Research* **25:** 441–451.

SMITH, O. J. 1953. Species, distribution, and host records of the braconid genera *Microctonus* and *Perilitus* (Hymenoptera: Braconidae). *Ohio Journal of Science* **53:** 173–178.

SMITH, O. J., DIBOLL, A. G. & ROSENBERGER, J. H. 1955. Laboratory studies of *Pelecystoma harrisinae* (Ashmead), an adventive braconid parasite of the western grape leaf skeletonizer. *Annals of the Entomological Society of America* **38:** 232–237.

ŠNOFLÁK, J. 1952. La monographie de *Triaspis* Hal. (*Sigalphus* Latr.) (Hym. Bracon.) de la Tchécoslovaquie. *Acta Entomologica Musei Nationalis Pragae* **28** (1950): 285–395.

SOMMERMAN, K. M. 1956. Parasitization of nymphal and adult psocids (Psocoptera). *Proceedings of the Entomological Society of Washington* **58:** 149–152.

SOMSEN, H. W. & LUGINBILL, P. 1956. *Bracon lissogaster* Mues., a parasite of the wheat stem sawfly. *Technical Bulletin, United States Department of Agriculture* **1153:** 1–7.

SOTERES, K. M., BERBERET, R. C. & McNEW; R. W. 1984. Parasitic insects associated with lepidopterous herbivores on alfalfa, *Medicago sativa*, in Oklahoma, USA. *Environmental Entomology* **13:** 787–793.

SOUTHWOOD, T. R. E. 1957. Observations on swarming in Braconidae (Hymenoptera) and Coniopterygidae (Neuroptera). *Proceedings of the Royal Entomological Society of London* (A) **32:** 80–82.

SPENCER, H. 1926. Biology of the parasites and hyperparasites of aphids. *Annals of the Entomological Society of America* **19:** 119–157.

STAMP, N. E. 1981. Behavior of parasitized aposematic caterpillars: advantageous to the parasitoid or the host? *American Naturalist* **118:** 715–725.

STARÝ, P. 1957. Notes on the Braconidae (Hym.) of Czechoslovakia IV. (Part I). *Acta Societatis Entomologicae Čechosloveniae* **54:** 277–292.

STARÝ, P. 1966. *Aphid parasites of Czechoslovakia.* 242 pp. The Hague.

STARÝ, P. 1970. Biology of aphid parasites (Hymenoptera: Aphidiidae) with respect to integrated control. *Series Entomologica* **6:** 1–643.

STARÝ, P. 1973. A review of *Aphidius*-species (Hymenoptera, Aphidiidae) of Europe. *Annotationes Zoologicae et Botanicae* **84:** 1–85.

STARÝ, P. 1987. Subject bibliography of aphid parasitoids (Hymenoptera: Aphidiidae) of the world, 1758–1982. *Monographs to Applied Entomology* **25:** 1–101.

STARÝ, P. & REJMÁNEK, M. 1981. Number of parasitoids per host in different systematic groups of aphids: the implications for introduction strategy in biological control (Homoptera: Aphidoidea; Hymenoptera: Aphidiidae). *Entomologica Scandinavica* Supplement **15:** 341–351.

STEARNS, L. A. 1928. The larval parasites of the oriental peach moth (*Laspeyresia molesta* Busck) with special reference to the biology of *Macrocentrus ancylivora* Rohwer. *Bulletin of the New Jersey Agricultural Experiment Station* **460:** 1–24.

STOLTZ, D. B. 1986. Interactions between parasitoid-derived products and host insects: an overview. *Journal of Insect Physiology* **32:** 347–350.

STOLTZ, D. B. & FAULKNER, G. 1978. Apparent replication of an unusual virus-like particle in both a parasitoid wasp and its host. *Canadian Journal of Microbiology* **24:** 1509–1514.

STOLTZ, D. B., GUZO, D., BELLAND, E. R., LUCAROTTI, C. J. & MACKINNON, E. A. 1988. Venom promotes uncoating in vitro and persistence in vivo of DNA from a braconid polydnavirus. *Journal of General Virology* **69:** 903–907.

STOLTZ, D. B., GUZO, D. & COOK, D. 1986. Studies on polydnavirus transmission. *Virology* **155:** 120–131.

STOLTZ, D. B., KRELL, P., COOK, D., MACKINNON, E. A. & LUCAROTTI, C. J. 1988. An unusual virus from the parasitic wasp *Cotesia melanoscela. Virology* **162:** 311–320.

STOLTZ, D. B., KRELL, P., SUMMERS, M. D. & VINSON, S. B. 1984. Polydnaviridae – a proposed family of insect viruses with segmented, double-stranded, circular DNA genomes. *Intervirology* **21:** 1–4.

STOLTZ, D. B. & VINSON, S. B. 1979. Viruses and parasitism in insects. *Advances in Virus Research* **24:** 125–171.

STRAND, M. R., JOHNSON, J. A. & CULIN, J. D. 1988. Developmental interactions between the parasitoid *Microplitis demolitor* (Hymenoptera: Braconidae) and its host *Heliothis virescens* (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* **81:** 822–830.

STRICKLAND, E. H. 1923. Biological notes on parasites of prairie cutworms. *Bulletin of the Department of Agriculture, Canada, Entomological Branch* **26:** 1–40.

STYER, E. L., HAMM, J. J. & NORDLUND, D. A. 1987. A new virus associated with the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae): replication in noctuid host larvae. *Journal of Invertebrate Pathology* **50:** 302–309.

SUDHEENDRAKUMAR, V. V., MOHAMED, U. V. K., NARENDRAN, T. C. & ABDURAHIMAN, U. C. 1982. Biology and morphology of immature stages of *Bracon brevicornis* (Hymenoptera: Braconidae) an important biological control agent of the black-headed caterpillar pest of coconut. *Journal of the Bombay Natural History Society* **79:** 254–260.

SULLIVAN, D. J. 1987. Insect hyperparasitism. *Annual Review of Entomology* **32:** 49–70.

SYME, P. D. & GREEN, G. W. 1972. The effect of *Orgilus obscurator* (Hymenoptera: Braconidae) on the development of the European pine shoot moth (Lepidoptera: Olethreutidae). *Canadian Entomologist* **104:** 523–530.

TADIĆ, M. D. 1958. *Apanteles hyphantriae* Riley, an egg parasite of the fall webworm. *Proceedings of the X International Congress of Entomology* **4:** 859–861.

TAEGER, A. 1989. *Die Orgilus-Arten der Palaarktis (Hymenoptera, Braconidae)*. 260 pp. Berlin.

TAGAWA, J. 1987. Post-mating changes in the oviposition tactics of the parasitic wasp *Apanteles glomeratus* L. (Hymenoptera: Braconidae). *Applied Entomology and Zoology* **22:** 537–542.

TANAKA, T. 1987a. Calyx and venom fluids of *Apanteles kariyai* (Hymenoptera: Braconidae) as factors that prolong larval period of the host, *Pseudaletia separata* (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* **80:** 530–533.

TANAKA, T. 1987b. Effect of the venom of the endoparasitoid, *Apanteles kariyai* Watanabe, on the cellular defence reaction of the host, *Pseudaletia separata* Walker. *Journal of Insect Physiology* **33:** 413–420.

TEMERAK, S. A. 1984. Suitability of five lepidopteran host insects to the ectolarval parasitoid *Bracon brevicornis* Wesmael. *Zeitschrift für angewandte Entomologie* **97:** 210–213.

THORPE, W. H. 1933. Notes on the natural control of *Coleophora laricella*, the larch case-bearer. *Bulletin of Entomological Research* **24:** 271–291.

TIMBERLAKE, P. H. 1916. Note on an interesting case of two generations of a parasite reared from the same individual host. *Canadian Entomologist* **48:** 89–91.

TOBIAS, V. I. 1966. Generic groupings and evolution of parasitic Hymenoptera of the subfamily Euphorinae (Hymenoptera, Braconidae). II. *Entomologischeskoe Obozrenie* **45:** 612–633. (In Russian) [English translation in *Entomological Review, Washington* **45:** 348–358].

TOBIAS, V. I. 1967. A review of the classification, phylogeny and evolution of the family Braconidae (Hymenoptera). *Entomologicheskoe Obozrenie* **46:** 645–669. (In Russian) [English translation in *Entomological Review, Washington* **46:** 387–399].

TOBIAS, V. I. 1971. A review of the Braconidae (Hymenoptera) of the USSR. *Trudy̆ Vsesoyuznogo Entomologicheskogo Obshchestva* **54:** 156–268. (In Russian) [English translation by Amerind, 1975. New Delhi].

TOBIAS, V. I. 1983. [On the study of the genus *Acrisis* Förster, 1862, and the tribe Acrisidini Hellén, 1957 (Hymenoptera, Braconidae, Doryctinae).] *Trudy̆ Vsesoyuznogo Entomologicheskogo Obshchestva* **65:** 155–168. (In Russian).

TOBIAS, V. I. 1986. Subfamily Microgasterinae. *Handbook to the Insects of the European part of the USSR* 3. Hymenoptera. Part 4: 344–459. Leningrad. (In Russian).

TOWER, D. G. 1915. Biology of *Apanteles militaris*. *Journal of Agricultural Research* **5:** 495–507.

TOWNES, H. 1958. Some biological characteristics of the Ichneumonidae (Hymenoptera) in relation to biological control. *Journal of Economic Entomology* **51:** 650–652.

TOWNES, H. 1969. The genera of Ichneumonidae, part 1. *Memoirs of the American Entomological Institute* **11:** 1–300.

TREMBLAY, E. 1978. Stadi dell'evoluzione morfologica e parassitaria di alcuni generi di

Aphidiinae (Hymenoptera Braconidae). *Atti XI Congresso Nazionale Italiano di Entomologia*: 311–316.

TREMBLAY, E. 1981. Le armature genitali maschili degli Aphidiinae (Hymenoptera Braconidae). II. *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri' Portici* **38:** 251–263.

ULLYETT, G. C. 1945. Distribution of progeny by *Microbracon hebetor* Say. *Journal of the Entomological Society of Southern Africa* **8:** 123–131.

ULLYETT, G. C. 1949. Distribution of progeny by *Chelonus texanus* Cress. (Hymenoptera: Braconidae). *Canadian Entomologist* **81:** 25–44.

VANCE, A. M. 1931. *Apanteles thompsoni* Lyle, a braconid parasite of the European corn borer. *Technical Bulletin, United States Department of Agriculture* **233:** 1–28.

VANCE, A. M. 1932a. The biology and morphology of the braconid *Chelonus annulipes* Wesm., a parasite of the European corn borer. *Technical Bulletin, United States Department of Agriculture* **294:** 1–48.

VANCE, A. M. 1932b. *Microgaster tibialis* Nees as a hymenopterous parasite of *Pyrausta nubilalis* Hubn. [sic] in Europe. *Annals of the Entomological Society of America* **25:** 121–134.

VARLEY, G. C. & BUTLER, C. G. 1933. The acceleration of development of insects by parasitism. *Parasitology* **25:** 263–268.

VET, L. E. M. & ALPHEN, J. J. M. van. 1985. A comparative functional approach to the host detection behaviour of parasitic wasps. I. A qualitative study on Eucoilidae and Alysiinae. *Oikos* **44:** 478–486.

VET, L. E. M. & JANSE, C. J. 1984. Fitness of two sibling species of *Asobara* (Braconidae: Alysiinae), larval parasitoids of Drosophilidae in different microhabitats. *Ecological Entomology* **9:** 345–354.

VET, L. E. M., JANSE, C. [J.], ACHTERBERG, C. van & ALPHEN, J. J. M. van. 1984. Microhabitat location and niche segregation in two sibling species of drosophilid parasitoids: *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae). *Oecologia* **61:** 182–188.

VET, L. E. M., MEYER, M., BAKKER, K. & ALPHEN, J. J. M. van. 1984. Intra- and interspecific host discrimination in *Asobara* (Hymenoptera) larval endo-parasitoids of Drosophilidae: comparison between closely related and less closely related species. *Animal Behaviour* **32:** 871–874.

VET, L. E. M. & OPZEELAND, K. van. 1984. The influence of conditioning on olfactory microhabitat and host location in *Asobara tabida* (Nees) and *A. rufescens* (Foerster) (Braconidae: Alysiinae) larval parasitoids of Drosophilidae. *Oecologia* **63:** 171–177.

VEVAI, E. J. 1942. On the bionomics of *Aphidius matricariae* Hal., a braconid parasite of *Myzus persicae* Sulz. *Parasitology* **34:** 141–151.

VIGGIANI, G. 1962. Contributi alla conoscenza degli insetti fitofagi minatori e loro simbionti. II. Studio morfo-biologico del *Colastes braconius* Hal. (Hym. Braconidae) e nota su altri entomoparassiti della *Napomyza lonicerella* Hend. (Dipt. Agromyzidae). *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri' Portici* **20:** 185–244.

VINSON, S. B. 1975a. Source of material in the tobacco budworm which initiates host-searching by the egg-larval parasitoid, *Chelonus texanus*. *Annals of the Entomological Society of America* **68:** 381–384.

VINSON, S. B. 1975b. Biochemical coevolution between parasitoids and their hosts. *In* Price, P. W. (Ed.) *Evolutionary strategies of parasitic insects and mites*: 14–48. New York.

VINSON, S. B. 1976. Host selection by insect parasitoids. *Annual Review of Entomology* **21:** 109–133.

VINSON, S. B. 1981. Habitat location. *In* Nordlund, D. A., Jones, R. L. & Lewis, W. J. (Eds) *Semiochemicals*: 51–77. New York.

VINSON, S. B. 1984a. How parasitoids locate their hosts: a case of insect espionage. *In* Lewis, T. (Ed.) *Insect communication*: 325–348. London.

VINSON, S. B. 1984b. Parasitoid-host relationship. *In* Bell. W. J. & Cardé, R. T. (Eds) *Chemical ecology of insects*: 205–233. London.

VINSON, S. B. 1988. Comparison of host characteristics that elicit host recognition behaviour of parasitoid Hymenoptera. *In* Gupta, V. K. (Ed.) *Advances in parasitic Hymenoptera research*: 285–291. Leiden.

VINSON, S. B. & BARBOSA, P. 1987. Interrelationships of nutritional ecology and parasitoids. *In* Slansky, F. & Rodriguez, J. G. (Eds) *Nutritional ecology of insects, mites, spiders, and related invertebrates*: 673–695. New York.

VINSON, S. B. & IWANTSCH, G. F. 1980a. Host suitability for insect parasitoids. *Annual Review of Entomology* **25:** 397–419.

VINSON, S. B. & IWANTSCH, G. F. 1980b. Host regulation by insect parasitoids. *Quarterly Review of Biology* **55:** 143–165.

WAAGE, J. & GREATHEAD, D. (Eds). 1986. *Insect parasitoids.* 389 pp. London.

WADE, J. S. & ST GEORGE, R. A. 1923. Biology of the false wireworm *Eleodes suturalis* Say. *Journal of Agricultural Research* **26:** 547–566.

WALKER, A. K., JOSHI, N. K. & VERMA, S. K. 1990. The biosystematics of *Syntretomorpha szaboi* Papp (Hymenoptera: Braconidae: Euphorinae) attacking the oriental honey bee, *Apis cerana* Fabricius. (Hymenoptera: Apidae), with a review of braconid parasitoids attacking bees. *Bulletin of Entomological Research* **80:** 79–83.

WALKER, A. K., KITCHING, I. J. & AUSTIN, A. D. 1990. A reassessment of the phylogenetic relationships within the Microgastrinae (Hymenoptera: Braconidae). *Cladistics* **6:** 291–306.

WALKER, M. F. 1962. Some observations on the biology of the ladybird parasite *Perilitus coccinellae* (Schrank) (Hym., Braconidae) with special reference to host selection and recognition. *Entomologist's Monthly Magazine* **97:** 240–244.

WALLEY, G. S. 1941. A new species of *Mirax* parasitic on *Coptodisca arbutiella* Bsk. (Hymenoptera, Braconidae). *Canadian Entomologist* **73:** 83–84.

WALOFF, N. 1961. Observations on the biology of *Perilitus dubius* (Wesmael) (Hymenoptera: Braconidae), a parasite of the chrysomelid beetle *Phytodecta olivacea* (Förster). *Proceedings of the Royal Entomological Society of London* (A) **36:** 96–102.

WALOFF, N. 1967. Biology of three species of *Leiophron* (Hymenoptera: Braconidae, Euphorinae) parasitic on Miridae on broom. *Transactions of the Royal Entomological Society of London* **119:** 187–213.

WASMANN, E. 1897. *In* Marshall, T. A. *in* André, E. (Ed.) *Species des Hyménoptères d'Europe et d'Algérie* **5:** 188–189. Paris.

WATANABE, C. 1942. A supplementary note on the genus *Streblocera* Westwood (Hymenoptera: Braconidae). *Insecta Matsumurana* **16:** 158.

WATANABE, C. 1961. Notes on five braconid parasites of some wood-boring beetles (Hymenoptera, Braconidae). *Publications, Entomological Laboratory, University of Osaka Prefecture* **6:** 111–114.

WATANABE, C. 1962. Occurrence of *Pelecystoma tricolor* Wesmael in Japan (Hymenoptera: Braconidae). *Insecta Matsumurana* **25:** 41–43.

WEISS, M. J., WILLIAMS, R. N. & LOAN, C. C. 1978. Euphorine parasitism of *Stelidota geminata* (Say) (Coleoptera: Nitidulide) with description of a new species of *Microctonus* Wesmael (Hymenoptera: Braconidae). *Naturaliste Canadien* **105:** 323–326.

WELLINGS, P. W., MORTON, R. & HART, P. J. 1986. Primary sex-ratio and differential progeny survivorship in solitary haplo-diploid parasitoids. *Ecological Entomology* **11:** 341–348.

WESELOH, R. M. 1981. Host location by parasitoids. *In* Nordlund, D. A., Jones, R. L. & Lewis, W. J. (Eds) *Semiochemicals*: 79–95. New York.

WHARTON, R. A. 1977. New World *Aphaereta* species (Hymenoptera: Braconidae: Alysiinae), with a discussion of terminology used in the tribe Alysiini. *Annals of the Entomological Society of America* **70:** 782–803.

WHARTON, R. 1980. Review of the Nearctic Alysiini (Hymenoptera, Braconidae) with discussion of generic relationships within the tribe. *University of California Publications in Entomology* **88:** 1–112.

WHARTON, R. A. 1984. Biology of the Alysiini (Hymenoptera: Braconidae), parasitoids of cyclorrhaphous Diptera. *Technical Monograph, Texas Agricultural Experiment Station* **11:** 1–39.

WHARTON, R. A. 1985. Characterization of the genus *Aspilota* (Hymenoptera: Braconidae). *Systematic Entomology* **10:** 227–237.

WHARTON, R. A. 1986. The braconid genus *Alysia* (Hymenoptera): a description of the subgenera and a revision of the subgenus *Alysia*. *Systematic Entomology* **11:** 453–504.

WHARTON, R. A. 1987. Changes in nomenclature and classification of some opiine Braconidae (Hymenoptera). *Proceedings of the Entomological Society of Washington* **89:** 61–73.

WHARTON, R. A. 1988a. The braconid genus *Alysia* (Hymenoptera): a revision of the subgenus *Anarcha*. *Contributions of the American Entomological Institute* **25** (2): 1–69.

WHARTON, R. A. 1988b. Classification of the braconid subfamily Opiinae (Hymenoptera). *Canadian Entomologist* **120:** 333–360.

WHARTON, R. A. & MARSH, P. M. 1978. New World Opiinae (Hymenoptera: Braconidae) parasitic on Tephritidae (Diptera). *Journal of the Washington Academy of Sciences* **68:** 147–167.

WHEELER, A. G. & LOAN, C. C. 1984. *Peristenus henryi* (Hymenoptera: Braconidae, Euphorinae), a new species parasitic on the honeylocust plant bug, *Diaphnocoris chlorionis* (Hemiptera: Miridae). *Proceedings of the Entomological Society of Washington* **86:** 669–672.

WHITE, M. J. D. 1973. *Animal cytology and evolution.* 961 pp. Cambridge.

WHITFIELD, J. B. 1987. Male swarming by a microgastrine braconid, *Apanteles coniferae* (Haliday) (Hymenoptera). *Proceedings and Transactions of the British Entomological and Natural History Society* **20:** 133–135.

WHITFIELD, J. B. 1988. Revision of the Nearctic species of the genus *Stiropius* Cameron (=*Bucculatriplex* Auct.) with the description of a new related genus (Hymenoptera: Braconidae). *Systematic Entomology* **13:** 373–385.

WHITFIELD, J. B. & WAGNER, D. L. In press. Annotated key to the genera of Braconidae (Hymenoptera) attacking leafmining Lepidoptera in the Holarctic Region. *Journal of Natural History* **25**.

WILBERT, H. 1960. *Apanteles pieridis* (Bouché) (Hym., Braconidae), ein parasit von *Aporia crataegi* (L.) (Lep., Pieridae). *Entomophaga* **5:** 183–211.

WILKINSON, D. S. 1936. On two braconids (Hym.) bred from economic hosts. *Bulletin of Entomological Research* **27:** 385–388.

WILLARD, H. F. 1920. *Opius fletcheri* as a parasite of the melon fly in Hawaii. *Journal of Agricultural Research* **20:** 423–438.

WISHART, G. 1946. Laboratory rearing of *Macrocentrus gifuensis* Ashm., a parasite of the European corn borer. *Canadian Entomologist* **78:** 78–82.

WISHART, G. & STEENBURGH, W. E. van. 1934. Contribution to the technique of propagation of *Chelonus annulipes* Wesm.; an imported parasite of the European corn borer. *Canadian Entomologist* **66:** 121–125.

WITTER, J. A. & KULMAN, H. M. 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8:** 723–731.

WRIGHT, D. W., GEERING, Q. A. & ASHBY, D. G. 1947. The insect parasites of the carrot fly, *Psila rosae*, Fab. *Bulletin of Entomological Research* **37:** 507–529.

WYLIE, H. G. 1982. An effect of parasitism by *Microctonus vittatae* (Hymenoptera: Braconidae) on emergence of *Phyllotreta cruciferae* and *Phyllotreta striolata* (Coleoptera: Chrysomelidae) from overwintering sites. *Canadian Entomologist* **114:** 727–732.

WYLIE, H. G. 1984. Oviposition and survival of three Nearctic euphorine braconids in crucifer-infesting flea beetles (Coleoptera: Chrysomelidae). *Canadian Entomologist* **116:** 1–4.

WYLIE, H. G. 1985. Posterior dispersal of eggs and larvae of *Microctonus vittatae* (Hymenoptera: Braconidae) in crucifer-infesting flea beetles (Coleoptera: Chrysomelidae). *Canadian Entomologist* **117:** 541–545.

WYLIE, H. G. & LOAN, C. 1984. Five Nearctic and one introduced euphorine species (Hymenoptera: Braconidae) that parasitize adults of crucifer-infesting flea beetles (Coleoptera: Chrysomelidae). *Canadian Entomologist* **116:** 235–246.

YAO, A.-I. 1987. Ring-like structure: a mortality factor due to *Opius concolor* (Hym.: Braconidae) besides parasitism on *Anastrepha suspensa* (Diptera: Tephritidae). *In* Economopoulos A. P. (Ed.) *Fruit flies*: 511–514. New York.

YEARGAN, K. V. & BRAMAN, S. K. 1986. Life history of the parasite *Diolcogaster facetosa* (Weed) (Hymenoptera: Braconidae) and its behavioural adaptation to the defensive response of a lepidopteran host. *Annals of the Entomological Society of America* **79:** 1029–1033.

ZAYKOV, A. 1982. The European species of *Symphya* Förster (Hymenoptera: Braconidae). *Acta Zoologica Academiae Scientiarum Hungaricae* **28:** 171–179.

ZHANG, D. & DAHLMAN, D. L. 1989. *Microplitis croceipes* teratocytes cause developmental arrest of *Heliothis virescens* larvae. *Archives of Insect Biochemistry and Physiology* **12:** 51–61.

ZINNERT, K.-D. 1969. Vergleichende Untersuchungen zur Morphologie und Biologie der Larvenparasiten (Hymenoptera: Ichneumonidae und Braconidae) mitteleuropäischer Blattwespen aus der Subfamilie Nematinae (Hymenoptera: Tenthredinidae). *Zeitschrift für angewandte Entomologie* **64:** 180–217; 277–306.

ZORIN, P. V. 1930. [The biology of *Microgaster marginatus* Nees (Hymenoptera).] *Entomologicheskoe Obozrenie* **24:** 220–224. (In Russian).

Glossary

Alecithal (eggs): Without yolk. Such eggs are usually very small and absorb nutrients from the host's haemolymph. They are found only in endoparasitoids.

Anal vesicle: An evagination of the proctodeum, forming a more or less spherical external vesicle; found in early-instar larvae of many endoparasitic Braconidae.

Apneustic (respiration): Not involving air. Apneustic respiration takes place without the involvement of spiracles, which are either absent or closed in the early instars of most endoparasitic braconids.

Caudate (larva): A larval form in which a long, tapering, fleshy appendage arises from the last abdominal segment. The first-instar larva is caudate in the majority of endoparasitic braconid subfamilies, but the structure is lost in later instars.

Cyclostome: The condition in which a characteristic semicircular opening (properly called the hypoclypeal depression) is formed between the concave apical border of the clypeus and the mandibles (leaving exposed the labrum, which is usually concave and shining) (figs 18, 19, 27, 32, 38). The condition occurs in several related braconid subfamilies (Histeromerinae, Doryctinae, Braconinae and Rogadinae in Britain) that are commonly referred to as the cyclostome group.

Ectoparasitoid: A parasitoid species whose larvae feed on the host from an external position.

Endoparasitoid: A parasitoid species whose larvae feed on the host from a position within its body.

Exodont (mandibles): Mandibles that are rather spatulate and outcurved (figs 17, 44, 45) and do not meet at the tips when closed. They occur throughout the subfamily Alysiinae, but not in other Braconidae.

Gregarious (parasitoid): A parasitoid species whose larvae develop in groups of two or more in or on one host individual.

Haemocytic (defence): A non-specific defence mechanism of insects in which cells in the haemolymph coagulate around foreign bodies such as parasitoid eggs or larvae and so isolate them; a process often called encapsulation.

Hyperparasitoid: A secondary parasitoid that develops on or in a primary parasitoid.

Idiobiont: A parasitoid species that does not permit the host any further significant activity after it has been attacked. (Contrast koinobiont).

Koinobiont: A parasitoid species whose host continues significant development, feeding or other activity after it has been attacked. (Contrast idiobiont).

Meconium: The voided waste products that had been retained as gut contents during an earlier period of development. Most Braconidae first void meconium as final-instar larvae just before their moult to the pupal stage, but in some (Opiinae and Alysiinae) the whole meconium is retained until the adult stage is reached.

Morula: Embryo during the process of cleavage, before the blastula stage.

Multiparasitism: The harbouring of more than one parasitoid species by a single host individual.

Parasitoid: An insect in which the adult is free-living but the larval stage obligatorily feeds on a single host individual that is killed as a direct result of the association. The term is used partly to avoid confusion with the familiar meaning of 'parasite', which does not imply the death of the host, but most derivative terms appropriate to parasitoids are formed from the stem 'parasite' rather than the more cumbersome 'parasitoid'.

Pensile: Hanging by a thread.

Polyembryony: The repeated division of a single egg resulting in the development of several larvae.

Proovigenic (species): Species in which the adult female has its entire complement of eggs fully mature at or soon after eclosion. (Contrast synovigenic).

Pseudohyperparasitoid: A secondary parasitoid that attacks a primary parasitoid only after the primary parasitoid has completed its feeding association with the primary host.

Superparasitism: The deposition of a clutch of eggs (which may be several or a single egg) on or in a host that has already been parasitised by a member of the same species. A clutch of eggs is defined as the egg or eggs laid during a single oviposition bout. If the second clutch is laid by a second female conspecific superparasitism results; if a female revisits a host to lay a second clutch self superparasitism occurs.

Synovigenic (species): Species in which eggs continue to mature throughout the life of the adult. (Contrast proovigenic).

Teratocytes: Discrete cells, originating from an endoparasitoid, that float in the host's haemolymph absorbing nutrients and becoming greatly enlarged. In Braconidae they originate from the trophamnion, which disintegrates when the larva hatches from the egg.

Thelytoky or **thelytokous parthenogenesis:** The process whereby diploid females are produced from unfertilised eggs.

Trophamnion: A layer of cells surrounding the developing embryo of some koinobiont parasitoids which takes in nutrients from the host haemolymph to nourish the developing parasitoid.

Vesiculate (larva): A larva possessing an anal vesicle (q.v.).

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