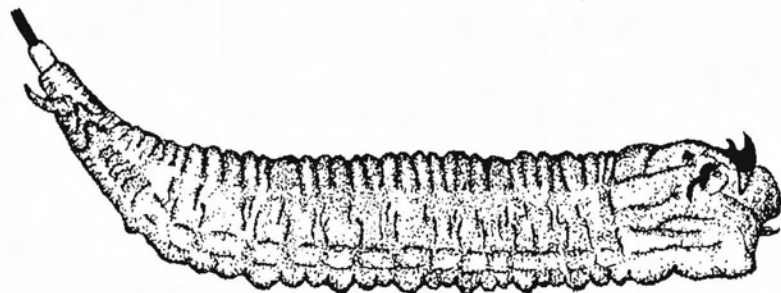


Colour Guide to **Hoverfly Larvae** (Diptera, Syrphidae)



Graham E. Rotheray
Dipterists Digest No.9

Colour Guide to Hoverfly Larvae
(Diptera, Syrphidae)
in
Britain and Europe



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Foreword

As naturalists we inevitably become interested in why our particular animals (or plants) seemingly thrive in some places yet are absent from others. Some species appear to be so rare that it is difficult to see how they survive at all. These matters of curiosity are indeed matters of survival, for our understanding of the needs of species is becoming crucial in the selection and management of places where a future can be offered.

Most dipterists develop their experience by searching for adult flies. This can tell us a great deal about the habits and habitats of species, though as experience grows one becomes very aware of the shortcomings of our knowledge. If we are ever to understand the ecology of hoverflies, we must not ignore the early stages. After all, the adult that we see is the product of weeks, months and sometimes years spent out of sight and out of mind, as befits a life cycle with distinct sexual and growing stages.

In *British Hoverflies* the opening paragraph of chapter 3 remarks that "the early stages require vigorous studies in their own right." With the publication of this special edition of *Dipterists Digest*, it is fair to say that the subject has indeed taken a vigorous stride forward.

The last decade has been a revolutionary one. Though Graham Rotheray would be the first to acknowledge the studies that went before, and the valued collaboration with others leading up to this present work, he has been in the forefront of widening our perspective on the life history of hoverflies. Those of us who have been privileged to take part in some of his outings, and heard his lectures, recognise the considerable breakthroughs he has made in field craft. Through his work, which has been a catalyst for others, there have been spectacular advances in the understanding of the ecology, status and conservation needs of some of our least known hoverflies.

Attention to taxonomic detail of larvae has also led to a revolution in the understanding of the evolutionary relationships between the genera of hoverflies, in collaboration with Francis Gilbert. The varied adaptations of hoverflies to varied life styles is in much better focus.

This publication, I believe, is an invitation to take part in this exciting phase in the study of hoverflies. Here is incentive to take up the challenge of developing the field craft that will lead, undoubtedly, to many more important advances. In some species we are already at the stage where it is easier to find and record the larvae than the adults. And even if you decide to confine your search to adults, the knowledge contained here provides an important perspective for anyone studying and recording our hoverfly fauna.

Alan Stubbs
Peterborough

Introduction

About 265 species of hoverfly occur in Britain. In Europe there are about 1,200 species. Altogether some 6,000 species exist worldwide occurring in every geographical region except the Antarctic. Hoverflies occupy all major habitats from coasts to mountains, from deserts to forests. They also occur in agricultural and urban situations. This assessment of the species richness and distribution of hoverflies, is based entirely on adults.

Like many insects, our knowledge of hoverflies relies heavily on adults. This is because they are easy to collect and study. With adults gaining most of the attention, a huge imbalance exists. In the USA for instance, the larvae of only about 7% of species are known (Thompson, 1990). In Europe the situation is little better with about 14% known and, in the best studied region of all, the British Isles, about 60% of species are known. Although reliance on adults is understandable, the imbalance is so striking that other stages must be investigated if knowledge is to advance.

In most insect families larvae usually exploit one particular kind of microhabitat. Hoverflies, however, are characterised by diverse, species-rich lineages occupying a range of microhabitats. There are phytophages mining and tunnelling in plants; mycophages in fungal fruiting bodies; predators attacking aphids, coccids, psyllids and larvae of beetles, moths, ants and wasps; and finally, saprophages occurring in media as diverse as dung, tree sap, nests of social insects, wet decaying wood and wet decaying vegetation (Appendix 1). Larvae are as variable in appearance as they are in feeding mode (Plates 1-16).

The magnitude of larval diversity raises the question whether syrphid evolution is governed more by innovations in larval rather than adult features. Analysis of evolutionary relationships suggests that larvae are important in this respect (Appendix 2).

Balancing knowledge of the different stages and understanding evolutionary relationships are not the only reasons for studying larvae. Detailed investigations of breeding sites are needed to conserve rare species. Some of these rank among Europe's most beautiful and endangered insects like the ancient woodland indicators, *Hammerschmidtia ferruginea* (Plate 10e) and *Caliprobola speciosa* (Plate 13b) (Speight, 1989).

Investigations of larval biology also provide essential data for managing the many common species that are economically useful and the few that are pests. The largest hoverfly group of all, comprising about a third of species, are predators of soft-bodied homoptera such as aphids, coccids and psyllids. These predators play, or can be made to play, important roles in controlling homopteran pests. Although the bulb flies, *Eumerus strigatus*, *Eumerus tuberculatus* (Plate 1a) and *Merodon equestris* (Plate 1b), are sometimes pests, other plant-breeding hoverflies can be beneficial. For example, *Cheilosia grossa* (= *corydon*) (Plate 2a,b) was recently imported to the USA to help control introduced European thistles threatening to take over pasture land (Rizza *et. al.*, 1988).

But for me, overlying all of this, is the simple fact that hoverfly larvae are wholly fascinating in their own right. Their behaviour, morphology and ecology is so varied and they have many special features. With so little known, there is much potential for discovering new information. There are larvae to find for the first time; larvae to describe and compare with

related species; morphology to analyse in relation to way of life; identification keys to write and behaviour and ecology to study. With a little willingness to pursue hoverflies beyond just catching and naming adults, a whole new subject invites exploration.

This guide will help by explaining how hoverfly larvae can be found, reared and preserved. It also provides keys, colour plates and diagnoses for identifying larvae and explains how their characteristic morphology can be studied. Finally, it provides an introduction to the whole subject of larval biology and to the literature against which new work should be planned.

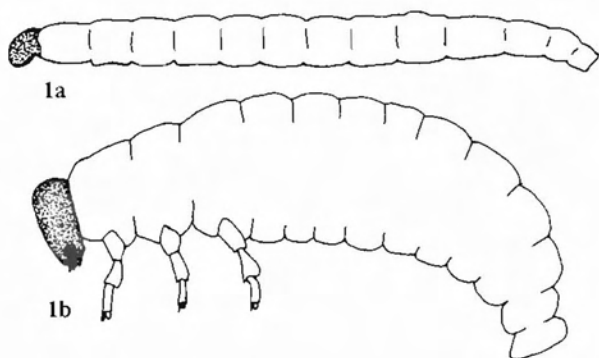


Fig. 1, (a) Larva of *Sciara* sp. (Diptera, Sciaridae), side view, showing head capsule; (b) Larva of *Chrysomela* sp. (Coleoptera, Chrysomelidae), side view, showing head capsule and thoracic legs.

1.1 How to recognise a hoverfly larva

Plates 1-16 show examples of hoverfly larvae from all the main groups. In recognising a hoverfly larva, remember that they do not possess segmented legs (Fig. 1) or a head capsule (Fig. 1). At first sight it might be difficult to see anything that could possibly work as a recognition feature i.e. a feature that they all uniquely possess, the presence of which identifies them as belonging to the family Syrphidae. Fortunately, however, there is just such a character - the posterior breathing tubes. In hoverflies these two tubes are fused at the point they emerge from the body into a single, elongate, brown or black structure (Fig. 2). The only exception to this general rule is a North American species, *Toxomerus polita*, in which the breathing tubes, although occurring on the same basal plate, have separated secondarily.

Except in one or two isolated cases, these tubes are separate in all other Diptera larvae. The most likely confusion is with certain drosophilids (Diptera, Drosophilidae) occurring in sap runs, which have the two tubes lying parallel to each other. But they are not fused, as can be tested with a pin.

Note, however, that the breathing tubes of first and second stages of all homopteran predators (the Syrphinae of Stubbs and Falk (1983), Plates 4b-10a) are separate, so be cautious in identifying all such larvae less than 6mm long. Rearing them will determine whether they develop to the third and final stage which has fused tubes and so belong to the Syrphidae.

Another important recognition feature is at the front end of the body. On the dorsal surface of the prothorax are 4-6 longitudinal impressions or grooves between which are rows of sensilla (Fig. 2). It is along these grooves that the prothorax folds when contracting: compare Plate 11f with 12a. No other Diptera larva possesses these features. In homopteran predators and *Microdon* larvae these grooves are very faint because the whole thorax is extremely narrow. Furthermore the prothorax and mesothorax are telescoped into the metathorax, which makes them difficult to see.

In brief, if the larva lacks a head capsule and segmented legs, and has a fused breathing tube projecting from the end of the body, it is probably a hoverfly. For confirmation, look for grooves on the prothorax and check the larva against the colour plates to see if the general appearance fits any of the pictures. For general help in identifying Diptera larvae see Smith (1989). In this guide, hoverfly larvae are further identified starting with Key I on page 46.

1.2 How to distinguish the third larval stage

Emerging from the egg, hoverfly larvae pass through three instars or stages before developing into pupae i.e. they shed their outer skin or integument, along with the mouthparts and respiratory organs, twice. Since the larva pupates inside its larval skin, the puparium is, in reality, the swollen integument of the third stage larva and so retains many of its features. The first two stages are relatively short, usually lasting a few days each. The third stage lasts from several days to many months, even years depending on species and situation. This guide is mostly about third stage larva. The keys will, however, work for the second stage larva of most species.

Distinguishing a third stage larva from the first two stages is easy for homopteran predators because only in that stage are the posterior breathing tubes fused into a single, elongate structure (Fig. 2). In other hoverfly larvae the tubes are fused from the first stage, and without detailed study it is sometimes difficult to decide if the third stage has been reached. When the larva has finished growing, however, third-stage larvae are not only large, but a pair of differentiated discs will appear on the dorsal surface of the first abdominal segment (Fig. 2). It is from these discs that the pupal spiracles will protrude. The appearance of these discs confirms that the third stage has been reached.

1.3 The main features of a hoverfly larva

Unlike adults the body regions and appendages of larvae are not as clear and without a microscope, larvae seem featureless. Nonetheless the basic body divisions of head, thorax and abdomen are present and it is important to recognise these and other structures. With a microscope a mass of detail will be revealed (Fig. 2).

Having prepared a larva for examination (page 26), view it first under low power and work out which are the head and rear ends and the dorsal and ventral surfaces. Recognise the rear end by the presence of the posterior breathing tubes or posterior respiratory process (prp) (Fig. 2). Look at the head end and check which are the dorsal and ventral surfaces. The dorsal surface usually has anterior spiracles protruding from it (Fig. 2). The ventral surface has the mouth, anal opening and locomotory organs (Fig. 2). Note the presence of any special features such as fleshy projections, hooks and spicules (Plate 12f; 13a,c-d). Turn the larva over to view the mouth and identify the various features according to Fig. 2. If the mouthparts, or any other feature is obscured for some reason, choose another specimen for examination. Where possible examine a series of specimens from each taxon rather than a single individual.

Next, try distinguishing the various segments with their characteristic arrangements of sensilla. Hoverfly larvae have three thoracic and eight abdominal segments. The head is very modified in common with other "higher" Diptera, and all that remains is the antenno-maxillary organs, the dorsal and ventral lips and the integument that connects them (Fig. 2). Bear in mind that the thorax of homopteran predators and *Microdon* larvae is extremely narrow and the prothorax and mesothorax are telescoped into the metathorax. This makes them impossible to see unless specially prepared (see page 30).

Segment boundaries are obscured by numerous folds and grooves. These grooves and folds result from muscles attached to the inner surface of the integument. They form various patterns and are of great phylogenetic importance. Despite the apparent "confusion" caused by grooves and folds, segment boundaries are present as indistinct, interrupted lines across the larva. To see them, turn the specimen sideways dorsal surface uppermost and using Fig. 2, identify the segments from prothorax to anal segment. Apart from the boundaries themselves, useful orientation features include the transverse rows of sensilla and the repeated pattern of grooves and folds along the lateral margins.

The sensilla are distributed in a regular pattern on each of the segments and are relatively uniform in number and position in all hoverfly larvae (Fig. 2). Count sensilla from pair 1 to pair 10/11 on each of the segments. There are different patterns of sensilla on the prothorax and the anal segment. Expect to encounter aberrations in sensilla. For instance, occasional sensilla will lack surrounding setae, some will appear to be "missing", and others divided into two.

Examine the locomotory organs, usually present on the mesothorax and the first six abdominal segments. They appear as pairs of oval-shaped structures projecting to varying degrees. Crochets may be present (Fig. 6).

The thorax sometimes bears conspicuous hooks and spicules (Plates 12f; 13a,c,d). The size and arrangement of hooks varies and tends to be specific for a particular genus providing useful characters for identification.

The anal segment has up to four pairs of fleshy projections, termed lappets. They are distinguished from other projections on the anal segment in bearing sensilla (Fig. 2). Lappets are modified into locomotory lobes in homopteran predators, and are inconspicuous in the long-tailed larvae of *Eristalis* and related genera (Plate 14).

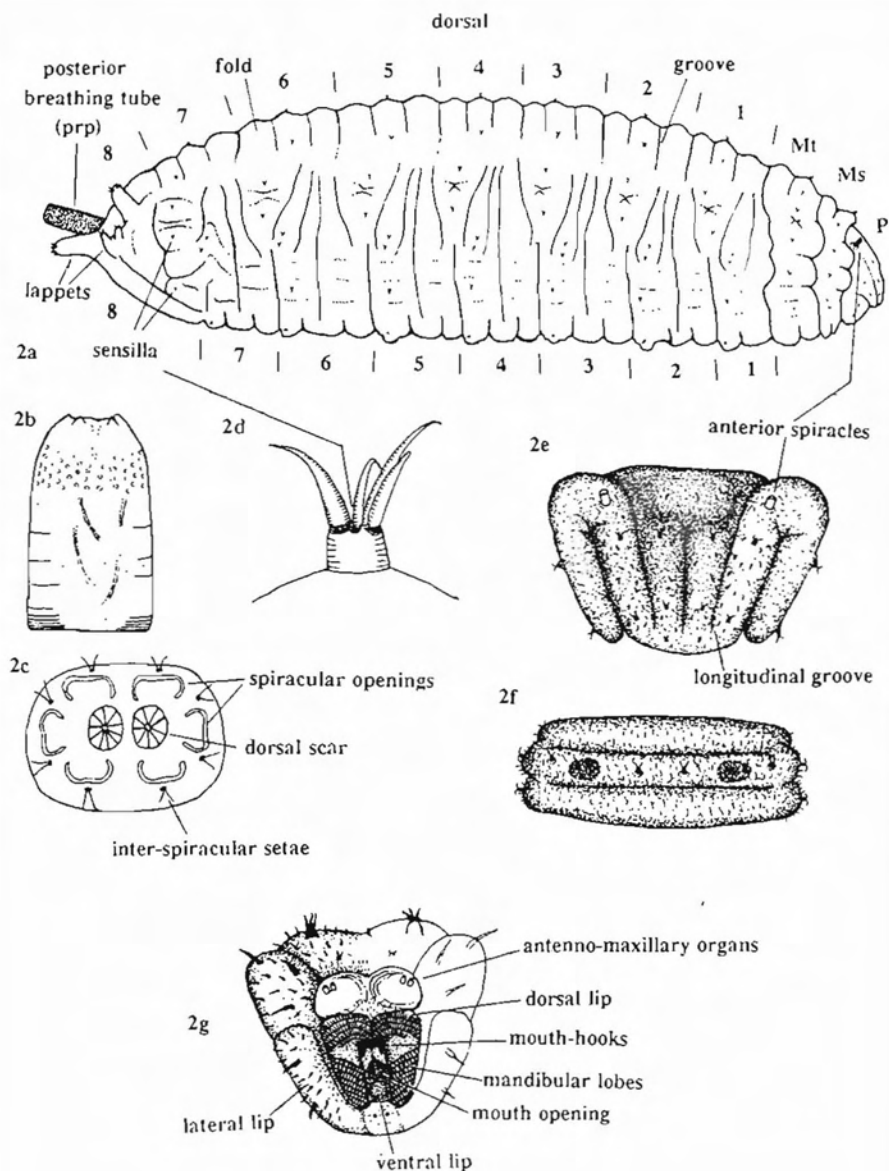


Fig. 2. *Eumerus tuberculatus*, third stage larva, (a) whole larva, side view showing main features and patterns of grooves and sensilla; (b) posterior respiratory process (prp), dorsal view; (c) tip of prp; (d) papilla surrounded by terminal setae, sensillum not shown, but lies at the tip of the papilla; (e) prothorax, dorsal view showing longitudinal grooves; (f) 1st abdominal segment, dorsal view showing pair of discs through which the pupal spiracles protrude; (g) prothorax, ventral view showing mouthparts.

2. Finding hoverfly larvae in the field

Larvae can be as easy to find as adults. In some cases easier. For over 80 years the supposedly endangered hoverfly, *Callicera rufa*, was known only from three localities. But by concentrating on larvae and puparia, rather than the elusive adult, we found this species at many sites in northern Scotland (Rotheray & MacGowan, 1990). Similarly, at a site in Cambridgeshire in 1990, Ivan Perry and myself found larvae of two Red Data Book species, *Mallota cimbiciformis* and *Pocota personata*. Despite a long history of entomological recording, *P. personata* was unknown from this site and *M. cimbiciformis* had not been seen for many decades (Rotheray, 1990; 1991).

As with rot-holes for *C. rufa*, once breeding sites are known they can be targeted for searching. Furthermore, larval stages are often present all year round, so sampling is not restricted to flight periods lasting a few weeks. The following section provides hints on finding larvae according to various feeding modes.

2.1 Phytophagous and mycophagous larvae

Eumerus, *Merodon*, *Portevinia*, *Cheilosia* (Plates 1-2)

Phytophagous and mycophagous hoverflies are very poorly known. Food-plants are in particular need of discovery. Even food-plants of such common species as *Cheilosia illustrata* are a mystery. Finding new food-plants is quite a detective act. It requires persistence, careful observation and luck! Much can be learnt from species whose larval food-plants are already known. As more larvae are discovered and knowledge increases, the task will become easier.

Experience helps: so learnt to find and rear larvae that are already known using the information in Table 1.

Watch females: as they spend much of their time on or near food-plants, particularly at night. I located the larva of *Cheilosia fraeterna* this way after finding females at night on rosettes of *Cirsium palustre* (Compositae). Watching females during daytime helps too. This was how Alan Stubbs and I made progress with *Cheilosia albitarsis*. From sitting on leaves of *Ranunculus repens* (Ranunculaceae) we saw females disappear into patches of plants only to reappear a few minutes later. Prompted by this behaviour, I searched the base of plants and found eggs. Further searching eventually revealed larvae tunnelling in rootstocks (Rotheray, 1991).

Table 1 Food-plants and fungi for phytophagous and mycophagous hoverfly larvae

Species	Plant/fungus	Site	Reference
<i>Eumerus strigatus</i>	<i>Narcissus, Iris tulip, onion</i>	bulb	Hodson (1927; 1932)
<i>E. tuberculatus</i>	<i>Narcissus, Iris Parsnip</i>	bulb	Hodson (1927; 1932)
<i>Merodon equestris</i>	<i>Narcissus</i> etc see page 79	bulb	Hodson (1932a)
<i>Portevinia maculata</i>	<i>Allium ursinum</i>	bulb	Speight (1986); Rotheray (1991)
<i>Cheilosia alpibila</i>	<i>Cirsium palustre</i>	stem	Andrewes (1944) Rotheray (1988a)
<i>C. albitarsis</i>	<i>Ranunculus</i>	rootstock	Rotheray (1991)
<i>C. antiqua</i>	<i>Primula</i>	rootstock	Carpenter (1913) Rotheray (1991)
<i>C. bergenstammi</i>	<i>Senecio jacobaea</i>	stem/ root	Smith (1979)
<i>C. caerulescens*</i>	<i>Sempevirum</i> spp.; <i>Solidago vigaurea</i> ; <i>Tussilago forfara</i> ; <i>Geum montanum</i>	rhizome	D'Águilar and Coutin (1988)
<i>C. canicularis*</i>	<i>Petasites</i> spp.	rhizome	Dušek (1962); Rotheray (1990a)
<i>C. chloris*</i>	<i>Petasites</i> sp.	root	Kaltenbach (1874)
<i>C. cynocephala</i>	<i>Carduus nutans</i>	stem	Frauenfeld (1866); Kaltenbach (1874); Dušek and Láška (1962)
<i>C. fasciata*</i>	<i>Allium ursinum</i>	leaf mine	Beling (1888); Dušek and Láška (1962); Nielsen (1979); Hövmeyer (1987); Rotheray (1990a)

<i>C. fraterna</i>	<i>Cirsium palustre</i>	stem/ rosette	Stubbs (1980) Rotheray(1988a)
<i>C. grossa</i> (= <i>corydon</i>)	<i>Cirsium</i> spp. <i>Carduus</i> spp.	stem/ root	Nurse (1910); Dušek and Láska (1962); Rizza <i>et. al.</i> , (1988) Rotheray (1988a)
<i>C. hercyniae</i> *	<i>Amanita muscaria</i>	fungal fruiting body	Vimmer (1925)
<i>C. longula</i>	spp. of <i>Boletus</i> ; <i>Suillus</i> ; <i>Leccinum</i>	fungal fruiting body	Buxton (1955); Hackman and Meinander (1979); Rotheray (1990a)
<i>C. morio</i> *	<i>Picea</i>	cambium	Trägårdh (1923); Hellrigl (1992)
<i>C. mutabilis</i>	<i>Carduus acanthoides</i>	root	Rossi (1848)
<i>C. nitidula</i> *	<i>Matricaria Chamomilla</i>	stem	Kaltenbach (1874)
<i>C. omissa</i> *	<i>Senecio nemorensis</i>	stem/ root	Dušek (1962)
<i>C. pagana</i>	<i>Anthriscus sylvestris</i>	decaying roots	Stubbs (1980); Rotheray (1990a)
<i>C. praecox</i>	<i>Hieracium pilosella</i>	?rosette	Claussen (1980)
<i>C. proxima</i>	<i>Cirsium</i> spp.	rosette	Rotheray (1988a)
<i>C. scutellata</i>	spp. of <i>Boletus</i> ; <i>Polyporus</i> etc	fungal fruiting body	Dufour (1840); Frauenfeld (1868);Brindle (1965); Rotheray (1990a)

<i>C. semifasciata</i>	<i>Umbilicus rupestris</i> ; <i>Sedum telephium</i>	leaf mine	Hering (1957); Rotheray (1988)
<i>C. variabilis</i>	<i>Scrophularia nodosa</i>	root	Fryer (1915); Dušek (1962); Rotheray (1990a)
<i>C. velutina</i>	<i>Scrophularia nodosa</i>	root	Brischke (1880)
<i>C. vernalis</i>	? <i>Achillea</i> ; ? <i>Matricaria</i> ; ? <i>Sonchus</i>	stem	Kaltenbach (1874); Hardy (1872)
<i>C. vulpina</i>	<i>Cynara scolymus</i>	root	Brunel and Cadou (1990)

* species not in Britain

Search plants thoroughly for signs of attack: phytophagous hoverflies oviposit on, not into, plants. Consequently eggs can be found on plant surfaces. Also larvae have to tunnel into the food-plant and signs of this are usually left behind. For example, small holes on the underside of leaves of rosettes of *C. palustre* betray the presence of *C. fraterna*; small amounts of dry, brown frass in the centre of *Primula vulgaris* plants (Primulaceae) indicate the presence of *Cheilosia antiqua* (Plate 1f) and, on the ground in pinewoods, liquified *Boletus* toadstools (Boletaceae) almost always mean *Cheilosia longula* or *Cheilosia scuellata* (Plate 2 c,d). Plants with distorted shapes are also worth searching. For example multi-stemmed *Cirsium* (Compositae) are usually a sign of infestation by *Cheilosia grossa* (Plate 2b).

Having discovered eggs, entry holes or some other sign and subject to any legal protection which the plant has eg under the Wildlife and Countryside Act 1981, the plant should be carefully dissected to find larvae. This can be done either in the field or, better still, at home. Small larvae are inconspicuous and careful, methodical searching is necessary to find them. Look for movement which often gives them away and the prp (posterior respiratory process) is sometimes conspicuous. When dissecting plants follow feeding tracks, although many will be insects other than hoverflies. Some species graze the outside of roots and plants need to be carefully dug up with a core of soil. The soil should be carefully washed off the roots and searched before the plant is dissected.

Examine plants during autumn and winter for late-developing larvae: a long-standing enigma of some phytophagous hoverflies is that despite the abundance of adults, larvae are rarely found. One possible explanation is provided in the case of *Portevinia maculata*. In this species eggs are laid in June and July close to the bulbs of the food-plant, *Allium ursinum* (Liliaceae), but the larvae remain small and inconspicuous until November/December. Only then do they really start to grow and develop and become easy to spot.

The larva of *C. albitarsis* is also a late developer. It remains small until September and leaves the food-plant as a full grown larva in late autumn to overwinter as a pupa in the soil.

Late-developing larvae adapt these hoverflies to the life cycles of their food-plants. *Allium ursinum* bulbs start to develop during November and the larva of *P. maculata* is probably taking advantage of the period when food reserves are mobilised. The larva of *C. albitarsis* delays its development until the rootstock is large. Other phytophagous larvae may be similar explaining the difficulty of finding them during the summer.

Despite the possibility of late-developers, it is still worth looking for larvae throughout the season. Most of the species reared to date are not late-developers but leave the food-plant or fungus to pupate in the soil during the autumn: sieving or careful searches of soil cores close to the plant, are the best ways to find them.

Finally, do not waste time looking for wilted plants as a sign of infestation: the exception is *Cheilosia semifasciata*, the larva of which mines the leaves of *Umbilicus rupestris* and *Sedum telephium* (Crassulaceae) (Plate 2e,f). Leaves mined by this species tend to collapse, and looking for plants with wilted leaves is a good way to find the larva. Usually, however, phytophagous larvae do not cause their foodplants to wilt.

Phytophagous and mycophagous hoverfly larvae are truly fascinating. When examined in detail, numerous features are revealed that adapt them to various feeding modes such as tunnelling, leaf-mining, mycophagy and sap-feeding (Rotheray, 1990a; 1991). Unique specializations further adapt them to particular situations. For example, the leaf-mining larva of *C. semifasciata* mines several leaves during its development and uses a remarkable grasping organ on its anal segment to move about (Rotheray, 1988). The existence of groups adapted to tunnelling, mining etc suggest that the large genus *Cheilosia* is unnatural, and needs revision. This happened to another formally large hoverfly genus, *Syrphus* sensu Coe, (1953): many genera are now recognised from within Coe's concept of *Syrphus*, verified both on adult and larval characters (Dušek & Láška, 1967; Vockeroth, 1969; Rotheray & Gilbert, 1989). As more phytophagous and mycophagous larvae are found, they will play a key role in evaluating the status of the genus *Cheilosia*.

2.2 Predacious larvae

Pipizella - *Eupeodes*, *Microdon*, *Volucella*, (Plates 3c-10a)

Three groups of predatory hoverfly larvae exist. The largest group, comprising about a third of all hoverfly species, are mostly predators of soft-bodied homoptera such as aphids, coccids and psyllids (Plate 8a), although a few specialise on other types of prey (Plate 4b, Table 2). These predators are accorded subfamily rank (Syrphinae) in recent classification schemes (Stubbs & Falk, 1983; Vockeroth & Thompson 1987). A second group is *Microdon* which feed on ant larvae and pupae and finally, there is *Volucella*, some species of which feed on the larvae and pupae of bees and wasps.

To find homopteran predators, search among infestations of coccids, psyllids and particularly aphids. Homopterans occur on a wide range of plants from grasses to trees and are easily found by hand-searching plants. Rotheray (1989) gives details on finding and identifying

aphids on a range of common plants and Blackman (1974) provides a general introduction to aphids, including a foodplant list.

Having found an aphid colony, hand search it bearing in mind that homopteran predators are cryptically coloured (camouflaged) and merge into the background (Rotheray, 1986). On many plants larvae hide during the day next to raised leaf veins, on bark and in leaf curls often well apart from the aphids. They are active mostly at dawn and dusk, which are good times to watch them hunting.

Hand-searching aphid colonies is only one method. Trees and shrubs can be beaten with a beating tray. Much better, however, is to remove infested parts of plants into clear plastic bags and keep them in cool, shaded conditions (to reduce condensation). Within a day or so, larvae will be seen on the sides of the bag. At the end of the season, or before if aphids migrate, search the leaf litter under previously infested plants for overwintering larvae. Among pines, wood ants (*Formica*) can sometimes be seen carrying hoverfly larvae back to the nest (A.E. Stubbs *pers. comm.*)

Hoverfly predators of gall-inducing aphids such as adelgids on conifers (see Carter, 1971) and *Pemphigus* species on poplars do not necessarily spend all their time inside the galls. For example Kurir (1963) sampled thousands of *Pemphigus* galls but found very few larvae. Many galls are not only small in relation to the size of a third stage hoverfly larva but the aphids physically resist predation (Foster, 1990). The hoverfly predators of these aphids include some rare pipizines. The larvae of these species probably rest on bark during daytime where, pipizine larvae at least, would be well camouflaged with their mottled brown and black appearance (Plate 5c).

Microdon is another genus with predatory larvae. *Microdon* larvae are obligatory inhabitants of ant nests and were thought to be specialised saprophages (Donisthorpe, 1927). But several American species are now known to feed on ant pupae (Duffield, 1981; Garnett et al., 1985) as does, *Microdon mutabilis* in Britain (B. Barr, *pers. comm.*). Predation is probably the rule in this group.

Microdon eggeri larvae can be found under bark of well-decayed, ant-infested pine or birch logs or stumps. Boyd Barr (*pers. comm.*) found *Microdon mutabilis* larvae and puparia under rocks covering ant nests. *Microdon devius* larvae have been found in nest mounds of *Lasius flavus* (Rotheray, 1991). Several ant nests may need searching before finding *Microdon* larvae and careful hand searching is required. A good method is to work through the ant nest on a white sheet. The contents of the nest should be replaced immediately after searching. Minimise destruction to ant nests by dividing them down the middle and searching one half only. Searching is easier on cool days when ants are inactive.

The third group of predators belong to the genus *Volucella* which, with the exception of *Volucella inflata*, are obligatory inhabitants of bee and wasp nests. Again conflicting reports exist about larval diets and recent evidence suggests a range of strategies (Rupp, 1989). *Volucella pellucens* (Plate 3f) appears to be both a predator and scavenger eating live and dead wasp larvae. *Volucella inanis* (Plate 4a), however, is an ectoparasitoid of wasp larvae and pupae. *Volucella inflata* occurs in sap runs (S.R. Miles, *pers. comm.*). The diet of *V.*

inflata is unknown: it might be a predator within sap runs or may feed on the 'sap itself.

Volucella larvae are best collected in the autumn when the wasps/bees have left the nest. The nest should be broken apart and thoroughly searched. Expect to find small and large individuals.

Table 2 Known and suspected(?) prey of hoverfly predators other than homoptera

Species	Prey species	Reference
<i>Platycheirus</i> (in part)	?generalised predators in leaf litter	see p.85
<i>Xanthandrus</i> <i>comtus</i>	gregarious microlepidopteran caterpillars	Chapman (1906); Lyons (1968); Shaw & Rotheray (1990); Rotheray & Bland (1992)
<i>Chrysotoxum</i>	?ant broods	Rotheray & Gilbert (1989)
<i>Dasysyrphus</i> <i>iricinctus</i>	tenthredinid & noctuid larvae	Gäbler (1939); Friederichs <i>et. al.</i> , (1940)
<i>Doros conopseus</i>	?ant broods in wood	Lundbeck (1916)
<i>Parasyrphus</i> <i>nigritarsis</i>	chrysomelid beetle larvae on <i>Alnus</i> & <i>Salix</i>	Schneider (1953)
<i>Xanthogramma</i>	fed by worker ants in <i>Lasius</i> nests	Hölldobler (1929)

2.3 Saprophagous larvae

Saprophagy is the most frequent larval feeding mode (Appendix 1). The mouthparts of saprophagous hoverflies are adapted to gathering and concentrating micro-organisms suspended in a fluid medium. Consequently, they occur only in wet or moist circumstances. Suggestions for finding saprophagous larvae within their most important microhabitats are dealt with below.

2.3.1 Sap runs

Ferdinandea, *Volucella inflata*, *Brachyopa*, *Hammerschmidtia*, *Sphegina*, *Xylota*, *Ceriana*, *Myathropa* (Plates 3a, 10b-e, 11d&f, 12b, 14f)

Sap often exudes from trees (Plate 15a,b). Exudations of sap, or sap runs, are a natural part of the woodland ecosystem and, sometimes, an individual tree will have several of them. They vary in size from meagre trickles to huge deluges and can endure for several years. They may dry up and start again. They occur on almost any size or age of tree, although they are most frequent on larger trees. Although sap runs occur on most tree species some, such as *Aesculus*, *Ulmus* and *Taxus*, seem more prone to them than others.

Tree sap is under pressure and it will flow like oil when the vessels carrying it are fractured. Sap vessels fracture in various ways: storms and high winds bending and twisting trees; close-growing branches rubbing against each other; when branches are cut or broken; when the sapwood is injured. The tree may attempt to repair the damage but micro-organisms can interfere. For example, if damaged sapwood is invaded by bacteria belonging to the genus *Erwinia*, associated fermentation creates pressure inside the tree forcing out sap and dissolved gases. This may result in a more or less continuous extrusion of sap. The wood-boring larvae of certain insects also create sap runs, such as the Goat Moth, *Cossus cossus* in broad-leaved trees and the weevil, *Hylobius abietus* in conifers. As far as hoverfly larvae are concerned, whatever the cause, it is micro-organisms within the sap that are the source of food.

Sap runs may be looked for at any time but are most active from April-July. The easiest sap runs to find are those in which streaks of wet sap run down the bark (Plate 15 a-b). But look for smaller sap runs and search them thoroughly because large amounts of sap are sometimes hidden between the bark and the sapwood. Look particularly at the base of trees for sap runs in splits and cracks and other crevices. A knife or chisel is a useful tool for probing into cracks but care is needed not to cause damage. Where sap runs reach the ground, sap-soaked soil should also be searched.

Sap runs caused by *C. cossus* caterpillars are usually hidden from view. A good clue, apart from their reputation of smelling like goats, are triangular-shaped areas at the base of trees which have no bark. *Cossus cossus* caterpillars are found by probing under the bark at the apex of such areas. *Hylobius abietus* sap runs are also hidden from view but are easily found by peeling bark from 1-3 year old conifer stumps, particularly in plantations after the trees have been felled.

Having located a sap run check its margins for puparia. Larvae themselves are usually found

within the sap. A wide range of hoverfly larvae are found in sap runs (Table 3). *Brachyopa* are easily the most abundant and dozens of larvae can be present. Adult sap-breeding hoverflies are found on or about sap runs. When collecting larvae they are sometimes so abundant as to be a bit of a nuisance!

Although sap runs are sometimes numerous, be conservation-minded when working with them: minimise damage to the sap run; remove only small amounts of sap; take only a few larvae.

Table 3 Hoverfly larvae from sap runs

Species	Tree species	Reference
<i>Psilota</i>	<i>Quercus</i> ; <i>Ficus</i>	Kassebeer*
<i>Ferdinandea</i>	<i>Acer</i> ; <i>Aesculus</i> <i>Malus</i> **; <i>Populus</i> <i>Quercus</i> **; <i>Salix</i> **	Lundbeck (1916) Rotheray (1990) Dušek and Láška (1988)
<i>Volucella inflata</i>	<i>Quercus</i>	Miles*
<i>Brachyopa bicolor</i>	<i>Fagus</i> ; <i>Quercus</i>	Rotheray (1991)
<i>B. insensilis</i>	<i>Aesculus</i> ; <i>Quercus</i> ** <i>Ulmus</i>	Lundbeck (1916) Rotheray (1991)
<i>B. pilosa</i>	<i>Fagus</i> ; <i>Populus</i> ; <i>Quercus</i>	Rotheray (1991)
<i>B. scutellaris</i>	<i>Fraxinus</i> ; <i>Taxus</i> ; <i>Ulmus</i>	Malloch Society*
<i>Hammerschmidtia ferruginea</i>	<i>Populus tremula</i>	Rotheray (1991)
<i>Sphegina</i>	<i>Fagus</i> ; <i>Populus</i> <i>Ulmus</i>	Hartley (1961)
<i>Xylota coeruleiventris</i>	<i>Abies</i> ***	Watt, Robertson and Rotheray*
<i>X. segnis</i>	<i>Abies</i> ***	Watt, Robertson & Rotheray*
<i>X. tarda</i>	<i>Populus tremula</i>	Malloch Society*

<i>Ceriana</i> (not British)	<i>Populus; Ulmus</i>	Lundbeck (1916)
<i>Spixomorpha</i> (not British)	deciduous trees	Kassebeer*
<i>Myathropa florea</i>	<i>Aesculus; Fagus</i>	Rotheray (1990)

* unpublished records from the individuals stated, see acknowledgements for Malloch Society; ** including *Cossus cossus* sap runs; *** from *Hylobius abietus* sap runs

2.3.2 Under bark

Brachyopa, Hammerschmidtia, Sphegina, Chalcosyrphus, Brachypalpus, Lejota, Myathropa, Microdon (Plates 3a, 10b-e, 11d&f)

When a tree or branch falls (Plate 15e-f) the sap under the bark decays and sometimes forms a thick, wet, pungent-smelling layer which is rich in food for hoverfly larvae (Table 4). This layer is temporary because the bark cracks eventually and breaks away from the sapwood. This lets in air killing micro-organisms and drying the sap. The speed of this process is determined chiefly by species of tree, size of branch and its physical circumstances. In moist, shady conditions with a 30cm diameter branch, the process is slow and may last up to four years. The larger the tree or branch the thicker the layer. However, not all trees are equally prone to forming layers of decaying sap. For example, *Pinus, Populus* and *Ulmus* trees are particularly good, *Betula* and *Fagus* less so.

When investigating fallen trees or branches, concentrate on the underside first where the heaviest concentrations of sap are likely to be. Cut ends of branches are also good. Do not be put off by trees and branches partially immersed in water. They are just as suitable. The formation of a wet layer of decaying sap and its eventual drying out is uneven and wet sap can be patchy in distribution. Lever up bark at various points to find the best areas. As before, caution is needed not to remove or loosen too much bark lest the microhabitat be destroyed.

Table 4 Hoverfly larvae under bark of fallen trees and branches

Species	Tree species	Reference
<i>Brachyopa pilosa</i>	<i>Fagus</i> <i>Quercus</i> *	McLean and Stubbs (1990) Rotheray (1991)
<i>Hammerschmidtia ferruginea</i>	<i>Populus tremula</i>	Rotheray (1991)

<i>Sphegina</i>	various deciduous trees in wet conditions <i>Betula</i> ; <i>Populus</i> ; <i>Quercus</i>	Hartley (1961); Rotheray (1990)
<i>Chalcosyrphus nemorum</i>	various deciduous trees	Hartley (1961)
<i>Brachypalpus</i> (in part)	fallen log	Heiss (1938)
<i>Lejota</i> (not British)	fallen log	Metcalf (1913)
<i>Myathropa florea</i>	<i>Populus tremula</i>	Perry**
<i>Microdon eggeri</i>	with ants in <i>Pinus</i> and <i>Betula</i> stumps and logs	Syms (1935); Malloch Society**

* under bark of recently created stump; ** records from the individuals stated, see acknowledgements for members of the Malloch Society

2.3.3 Rot-holes

Brachyopa, *Xylota*, *Brachypalpus*, *Brachypalpoides*, *Criorhina*, *Spilomyia*, *Milesia*, *Callicera*, *Pocota*, *Blera*, *Myolepta*, *Mallota*, *Myathropa* (Plates 12-14)

Rot-holes (Plate 15c-d) are a natural part of the woodland ecosystem and can be numerous. They range from a few centimetres to more than a metre deep. Large ones will occupy the entire interior of a tree or branch. Rot-holes full of liquid or wet, decaying wood are best for hoverflies.

Rot-holes are generally more frequent in the lower half of older trees. Rot-holes in dead or fallen timber are just as productive as those in live, upright trees. They occur in almost all tree species with those in *Fagus*, *Fraxinus*, *Ulmus*, *Aesculus* and *Quercus* being particularly productive. Individual rot-holes may last for many years and are used by successive generations of hoverflies.

Three basic types exist. First, bark-lined rot-holes are often formed where two or more branches grow from the same point (Plate 15c). The natural cavity so created tends to trap water, leaves, twigs and other vegetation. The resulting decay creates a favourable habitat for a limited fauna, particularly *Myathropa florea* in broad-leaved trees or *Callicera rufa* in pines. Rot-holes of this type are particularly common on *Fagus* and in deeply fissured bark of fallen trees and branches.

A second very important type of rot-hole involves decay of the heartwood. Heartwood is the

dead material at the centre of a tree or branch. The agents responsible for its decay are bracket fungi (Polyporaceae) and species such as the honey fungus, *Armillaria mellea* (Basidiomycetes) (Peace, 1962). These fungi enter the tree through roots, cut or broken branches and damaged bark. Without showing any external sign, they live within the tree for many years gradually growing through the heartwood causing it to become soft. This softened heartwood eventually falls away and a hollow tree is formed. If a branch is cut or broken before this happens then wind and rain will erode the softened, exposed heartwood and a hole will be formed.

Moisture often accumulates in these holes and secondary decay by micro-organisms invariably follows creating a source of food for hoverfly larvae. Rot-holes of this type are very productive and many of the rare, dead wood or "saproxylic" species breed in them (Table 5).

A third type of rot-hole is formed when trees twist and bend in storms and high winds causing the bark to split and separate from the sapwood. The space so formed may fill with water and sap which subsequently decays to form a medium for larvae. Sometimes the split is little more than a hairline crack and these rot-holes are completely hidden from view.

The best way to locate rot-holes is simply to walk round trees looking for holes and tapping the trunk for a hollow sound indicating a hidden cavity. Having located a rot-hole there is a preferred way to proceed.

First, using a torch if necessary and before disturbing the contents, look inside and round the margins for larvae and puparia. Puparia are often stuck down and it is best to remove them on surrounding pieces of wood.

Second, collect the contents of the rot-hole into plastic bags. If the rot-hole is too small to reach into, larvae may be dislodged to the surface by stirring up the contents with a stick or long-handled spoon. If the rot-hole appears dry, do not be put off. Remove dry, upper layers into plastic bags and see if moist conditions start to appear. Pay particular attention to the bottom of the rot-hole where larvae often aggregate. If the bottom cannot be reached or if the rot-hole starts to fill with seemingly endless quantities of liquid, dislodge larvae to the surface by stirring up the contents.

Search the contents of plastic bags on the ground. Finally, be conservation-minded and collect only a few larvae of each type. Only remove small amounts of rot-hole material and return the rest making sure that dry upper layers, if any, are replaced last.

Table 5 Hoverfly larvae from rot-holes

Species	Tree species	Reference
<i>Brachyopa</i>	<i>Acer</i> (sap soaked)	Speight (1974) Rotheray*
<i>Xylota sylvarum</i>	? <i>Fagus</i>	Stubbs*

<i>X. xanthocnema</i>	<i>Taxus</i> <i>Quercus</i>	Hartley (1961) Rotheray (1990)
<i>Brachypalpus laphriformis</i>	<i>Quercus</i>	Rotheray (1991)
<i>Brachypalpoides lenta</i>	<i>Fagus</i>	Malloch Society*
<i>Criorhina floccosa</i>	<i>Ulmus</i>	Hartley*
<i>Spilomyia</i> (not British)	<i>Quercus</i>	Maier* USA
<i>Milesia</i> (not British)	water-filled cavities in stumps	Snow (1958); Maier (1982) both USA
<i>Callicera aurata</i> (= <i>aenea</i>)	<i>Fagus</i>	Rotheray (1991)
<i>C. rufa</i>	<i>Pinus</i> <i>Larix decidua</i>	Coe (1938); Rotheray and MacGowan (1990) MacGowan*
<i>C. spinolae</i>	<i>Populus</i> ("Turanga") <i>Fagus</i>	Zimina (1986) Perry, Stubbs and Rotheray*
<i>Pocota personata</i>	<i>Fraxinus</i> <i>Fagus</i>	Donisthorpe (1928) Shillito (1947) Hartley* Rotheray (1991)
<i>Blera</i>	<i>Quercus</i>	Schuhmacher (1968)
<i>Myolepra luteola</i>	<i>Fagus</i> ; <i>Aesculus</i> <i>Quercus</i>	Hartley (1961) Rotheray (1990)
<i>Mallota cimbiciformis</i>	<i>Acer</i> ; <i>Aesculus</i> <i>Fagus</i> ; <i>Ulmus</i>	Britten (1916); Lundbeck (1916); Coe (1953a); Maibach & Goeldlin (1989); Rotheray (1990)
<i>Myathropa florea</i>	<i>Acer</i> ; <i>Aesculus</i> <i>Fagus</i> ; <i>Populus</i>	Hartley (1961) Rotheray (1990)

* unpublished records from the individuals stated

2.3.4 Decaying tree roots

Xylota, *Brachypalpoides*, *Criorhina*, *Caliprobola*, *?Blera*, *Myathropa* (Plates 12a,c&d, 13b, 14f)

For decades observers have reported seeing adult hoverflies on or about stumps and old trees (Lundbeck, 1916; Stubbs & Falk, 1983). However, little attempt has been made to explain why hoverflies find them attractive.

Stumps (Plate 16a) and old trees (Plate 16c) have often been invaded by heart-rot fungi. These fungi penetrate deep into the roots. Here secondary decay by micro-organisms invariably follows and, contained by the bark, wet decay builds up and forms "underground rot-holes". It is quite remarkable how large amounts of wet decaying wood exist in the roots of old trees and stumps when all above is completely dry (Plate 16b). Such pockets of wet decay may persist for many years and are used over and over again by successive generations of hoverflies.

Female hoverflies are probably attracted by odours emanating from the secondary decay. *Criorhina berberina* females have been observed ovipositing up to 3m away from the nearest stump. On digging a short way underground, decaying roots were always encountered.

Apart from watching where adult females lay eggs, the best method of finding larvae in decaying roots is to locate an old, crumbling *Fagus* stump (Plate 16a). Other species of tree are also suitable except possibly *Quercus* whose stumps are often too dry. A mere fragment will do because, like icebergs, a greater mass often exists below ground. For protection wear rubber gloves and probe round the margins looking for a soft, wet seam of decaying wood and follow it down into the roots. Scoop up handfuls of wet material and carefully search it for larvae (Plate 16b). As with rot-holes, larvae are sometimes far away from the surface and considerable persistence is needed to find them. Several stumps may need examining before finding a wet seam. When ready to pupate, larvae move up to drier areas and puparia can be found behind loose pieces of bark or in the upper soil layers round the stump.

Sometimes the entire underground mass of the stump is decayed. In the few such stumps that I have seen, many hundreds of larvae were present. Such stumps are clearly major breeding sites (Table 6).

Upturned trees can also be good places to try although they dry out after a year or so. Search for wet decaying wood at the upturned end. The roots left in the ground are also worthwhile examining. As before, when searching stumps and hollow trees be conservation minded. Do not destroy the stump or tree. Put decayed wood back. Take only a few larvae.

Table 6 Hoverfly larvae from decaying tree roots

Species	Tree species	Reference
<i>Xylota sylvarum</i>	<i>Fagus</i> <i>Abies</i>	Rotheray (1990) Watt & Rotheray*
<i>Brachypalpoides lenta</i>	<i>Fagus</i>	Malloch Society*
<i>Criorhina berberina</i>	<i>Betula</i> <i>Fagus</i> <i>Fraxinus</i>	Hartley (1961) Rotheray (1991) Malloch Society*
<i>C. floccosa</i>	<i>Fagus</i>	Rotheray (1991)
<i>C. ranunculi</i>	<i>Fagus</i>	Oates* see Rotheray (1991)
<i>Caliprobola speciosa</i>	<i>Fagus</i>	Rotheray (1991)
<i>Blera</i>	<i>Pinus</i>	Rotheray* (to be confirmed)
<i>Myathropa florea</i>	<i>Fagus</i>	Rotheray (1990)

* unpublished records from individuals stated, see acknowledgements for members of the Malloch Society

2.3.5 Decaying vegetation

Rhingia, *Chrysogaster*, *Syritta*, *Neoascia*, *Xylota segnis*, *Tropidia*, *Sericomyia*, *Eristalis*, *Helophilus*, *Lejops* (Plate 3a, 10f, 11, 14)

Larvae breeding in decaying vegetation exploit many sites, from dung to peat (Table 7). As with decaying wood, their diet appears to be micro-organisms associated with the decay.

The general methods of searching decaying vegetation are hand-searching and sieving. For example, search with a trowel exposed areas at the margins of ditches, ponds, bogs and marshes (Plate 16e), particularly where mud and dead vegetation accumulates, or among the roots of aquatic vegetation (Plate 16f). Many *Parhelophilus* and *Eoseristalis* species are associated with False Bulrush, *Typha latifolia* (Typhaceae) and the larva of *Chrysogaster hirtella* is usually found under clumps of Marsh Marigold, *Caltha palustris* (Ranunculaceae).

Table 7 Hoverfly larvae from decaying vegetation, mud and dung

Species	Habitat	Reference
<i>Rhingia campestris</i>	cow dung	Coe (1942)
<i>Chrysogaster hirtella</i>	among roots of emergent vegetation in ponds & ditches, under clumps of <i>Caltha palustris</i>	Hartley (1961) Maibach*
<i>C. solstitialis</i>	mud & decaying plants at margins of woodland ponds & ditches	Hartley (1961)
<i>Orthonevra</i>	mud & decaying plants at margins of ponds & ditches	Hartley (1961)
<i>Lejogaster splendida</i>	decaying vegetation in stands of <i>Typha</i>	Hartley (1961)
<i>Syritta pipiens</i>	decaying <i>Narcissus</i> bulbs; wet manure, compost & silage	Hodson (1931) Hartley (1961)
<i>Neoscia podagrica</i>	wet manure	Hartley (1961)
<i>Neoscia</i> spp.	decaying vegetation at margins of ponds and ditches	Hartley (1961)
<i>Xylota segnis</i>	decaying potatoes	Blackith & Blackith (1989)
<i>Tropidia scita</i>	decaying vegetation at margins of ponds and ditches	Decler and Rotheray (1990)
<i>Sericomyia</i>	edges of moorland pools; peat cuttings etc	Bloomfield (1897) Hartley (1961)
<i>Anasimyia Parhelophilus Helophilus hybridus</i>	mud & decaying plants, especially <i>Typha</i> , in ponds and ditches	Hartley (1961)

<i>H. pendulus</i>	farmyard drains, wet manure, silage, wet sawdust	Hartley (1961)
<i>Eristalinus aeneus</i>	pools with decaying seaweed on the seashore	Hartley (1961)
<i>E. sepulchralis</i>	mud & decaying plants in ponds, estuarine marsh pools; farmyard drains	Hartley (1961)
<i>Eristalis abusivus</i>	mud at edge of moorland pool	Hartley (1961)
<i>Eristalis</i> spp.	wet manure, mud and decaying plants in ponds	Hartley (1961)
<i>Lejops vittata</i>	mud & decaying <i>Typha</i> in ponds & ditches	Waitzbauer (1976)

On land, search wet compost, dung and manure (Plate 16d). Larvae are often well concealed and persistence is needed to locate them. On the other hand, once one larva is found, others tend to follow. Coe (1942), for instance, found that the larva of *Rhingia campestris* is camouflaged by numerous particles of dung and states that, "although a hundred or more *R. campestris* larvae may occur in a single dropping (of cow dung), the most patient and methodical search is necessary to discover them."

Use a sieve to find larvae in decaying vegetation. A sieve with a fine mesh, like that of insect nets, is needed to prevent larvae from being washed away. Convert coarse-meshed garden sieves into fine-mesh ones by placing the entire sieve in a bag of fine netting. Small kitchen sieves can also be used. To use the sieve, place a couple of handfuls of material on it and break up the largest clumps. Pour water on to the sieve to separate fine soil and other material. This can either be done from a watering can or bucket, or partially immerse the sieve in a fast-flowing stream. Allow excess water to drain off and then search through what remains on the sieve for larvae. Movement often gives them away.

3. Techniques

3.1 Examining live larvae

A live hoverfly larva usually needs cleaning before examination with a binocular microscope. To clean a larva, place it on a bed of wet tissue paper in a Petri dish or similar container for a couple of hours. As the larva moves through the wet tissue so the body is cleaned. Alternatively, clean larvae with a few squirts from a wash bottle and a soft brush. Do not use hot water in any cleaning operation as heat can injure. Characters are best studied with a dry specimen so after cleaning remove excess moisture with tissue paper. The end result should be a clean, dry specimen.

Live specimens can be held under the microscope with the fingers. Alternatively, place them in a tube or Petri dish. Over-active specimens can be "quietened down" by placing them in a refrigerator for an hour or so. Do not use a freezer as this will probably kill them. Larvae can withstand dry handling for a few hours. If desiccation is suspected, place the larva on a bed of wet tissue and leave alone for a few hours. Most desiccated larvae have remarkable powers of recovery.

3.2 Examining preserved larva

To examine preserved larvae, remove them from preservative and dry them with tissue paper (see p. 30 for preservation methods). Hold them under the microscope with the fingers. If shaky hands are a problem or larvae need to be held in fixed positions for drawing and close-up photography, place them in a solid watch glass filled with small glass beads or fine sand.

More traditional methods of examining preserved larvae are either to keep them wet i.e. submerged in liquid preservative or to make slide mounts. Integumental characters tend to be obscured by these methods and I have not found them useful. In resolving fine integumental characters it may be helpful to use a stain. Maibach & Goeldlin de Tiefenau (1992) describe a technique using methylene blue which has the advantage of being temporary and suitable for live and preserved specimens.

3.3 Rearing hoverfly larvae

Hoverfly larvae are not difficult to rear. The most vulnerable part of the process is getting them through the first two stages. First and second stage larvae should be handled as little as possible. If they need transferring, this is best done indirectly: on or in their breeding medium, or with a soft paintbrush. Third stage larvae are much more robust and can be handled directly. Except for homopteran predators which may attack one another, larvae can be kept together in the same container but avoid overcrowding. When adding food be careful not to contaminate cultures with newcomers from the field.

Details of how to find hoverfly larvae start on page 9. Below are methods of rearing field-collected larvae, again arranged according to feeding mode.

3.3.1 Phytophagous and mycophagous larvae

Phytophagous and mycophagous larvae are generally easy to rear. They should be collected with their food-plant or fungus. For ease of handling, the plants can be trimmed so that only infested stems or roots are brought back. Plant portions and fungi can be maintained in unsealed plastic bags kept in cool, shaded conditions and moistened periodically. Larvae may need fresh plant material if kept for any length of time. They transfer to new material with few problems and are generally robust to handle. If large active individuals are seen outside the plant or fungus, examine them to see if they have a pair of discs on the dorsal surface of the first abdominal segment (Fig. 2). If these discs are present the larva is probably looking for a place to pupate. Place these larvae in tubes or boxes containing some moist tissue paper or moss and leave well alone in cool, dark conditions.

3.3.2 Homopteran and other predatory larvae

Homopteran predators should be transferred along with portions of homopteran-infested plant and placed in plastic dishes, boxes or bags. Larvae can be reared within these containers which should be kept in cool, shaded conditions. Prey may need adding every few days. It is best to use the same prey species as the predators were collected from, but others can be tried if necessary. Many homopteran predators are capable of accepting a wide range of aphids. Do not overcrowd homopterans or predators as this causes mortality and cannibalism. Further details are given by Rotheray (1989).

Homopteran predators ready to pupate or overwinter will first empty the black material that has accumulated in their hind guts. Larva with empty or nearly empty hind guts (turn larva over to check) should be removed and placed in tubes or boxes containing moist tissue paper or moss. It may be necessary to keep larvae for many months especially if overwintering. To keep conditions fresh, replace the tissue paper or moss every few weeks. If larvae look as if they are a little dry place a drop or two of water on them.

Microdon larvae can be reared with their ant hosts in plastic boxes and other containers. Live cultures of ants can be set up with little trouble and various methods are described in texts dealing with ants. Pontin (1962) describes some simple but effective methods. Try placing *Microdon* larvae in tubes with ant cocoons and see if they eat them. Larvae about to pupate develop the usual pair of discs on the first abdominal segment and such individuals should be transferred to separate tubes containing moist tissue paper or moss.

Volucella larvae are best collected in the autumn when bees and wasps have deserted their nests. Place the larvae, along with a substantial part of the nest, in an unsealed plastic bag. In the spring watch for the formation of puparia and separate them into tubes containing tissue paper or moss.

3.3.3 Saprothagous larvae

Saprothagous larvae can be reared by placing them in tubes or boxes containing some of the medium in which they were found. Most saprothagous larvae shun the light while they are feeding and growing and prefer cool conditions so store them in cold, dark cellars and similar places. If larvae are kept for long periods the medium will need replacing every few

weeks. Saprophagous larvae can take more than a year to develop and will feed throughout the winter. Again it is best to use the same material from which they were collected. But most species will accept alternatives. For example sap run species can be reared on sap run exudate from almost any tree species and the same is true of larvae in rot-holes. There is scope here for some experimentation with diets. Rotting potatoes, turnips and other root vegetables may work as a convenient substitute. Mash up a few raw potatoes and leave exposed outdoors to encourage decay. For saprophagous larvae occurring in decaying vegetation, mashed-up rabbit dung in water has been successfully used as a breeding medium (J. Heal, *pers. comm.*).

Larvae ready to pupate will be found at the surface of the medium or crawling round above it. Confirm that they have the discs on the first abdominal segment which signifies that they are truly ready to pupate; transfer them to tubes and boxes containing moist tissue paper or moss and leave well alone.

With all hoverfly larvae there are two phases in the rearing process that need particular care, pupariation and emergence of the adult. Larvae ready to pupate or overwinter should not be handled roughly. They should be placed individually in tubes or similar containers with a little lightly moistened moss or tissue paper and left well alone in cool, shaded conditions. The puparium is soft at first and it takes a few days to harden. A few days after pupariation the pupal spiracles appear, except in most homopteran predators in which they have been secondarily lost. If pupal spiracles do not appear then either something is wrong or the specimen is parasitised. If something is wrong, then it will usually start to smell and go mouldy and it should be discarded. If not, then wait to see if a parasitoid emerges. Parasitised puparia of homopteran predators can sometimes be recognised by their narrow, dark appearance.

The second vulnerable phase is emergence of the adult. At the start of pupariation fluids are emitted from the anus which stick down the puparium. If the puparium is loose then the emerging adult can find it difficult to drag itself clear and becomes stuck half-in half-out. This can even happen with puparia that are stuck down. Furthermore, the adult needs plenty of room to crawl away, expand its wings and dry off. It will also excrete a mass of whitish fluid. For these reasons loose puparia should be wrapped lightly in dry moss or tissue paper and placed in tubes or boxes with plenty of room for the adult when it emerges. The emerging adult should not be disturbed while it expands its wings. This may take several hours. Emerging adults react badly to light, so keep them shaded. It is good idea to feed recently emerged adults and to keep them alive for a few days. This ensures their colours have strengthened and the integument has fully hardened. It also prevents them from collapsing when pinned in the collection.

Field-collected hoverfly larvae may be parasitised. However not all groups are attacked to the same extent. Homopteran predators suffer the most parasitism and saprophagous groups the least (Table 8). One of the chief reasons for this is that homopteran predators are much more accessible to parasitoids (Shaw and Askew, 1978). Parasitoids make interesting subjects for study in their own right and collecting host records would be a valuable addition to knowledge (see Table 8 for key references to main groups of parasitoids). Even in Britain new species of hoverfly parasitoid are still being discovered (K. Horstmann, *pers. comm.*; Rotheray, 1990b).

Table 8 Common parasitoids of hoverfly larvae and pupae

Host species	Parasitoid	Reference
<i>Cheilosia longula</i>	Ichneumonidae Diplazontinae <i>Bioblapsis mallochi</i>	Rotheray (1990b)
<i>Cheilosia</i>	Ichneumonidae Phygadeuontinae <i>Phygadeuon</i> Braconidae <i>Phaenocarpa</i> <i>Bracon</i>	Rotheray (1988a); Hövmeyer (1993) Rotheray (1988a)
Pipizella - Eupeodes	Ichneumonidae Phygadeuontinae <i>Gelis; Bathytrix;</i> <i>Theroscopus</i> Ichneumonidae Diplazontinae Cynipoidae <i>Melanips</i> <i>Callispidia</i> Pteromalidae <i>Pachyneuron</i> Encyrtidae <i>Bothriothorax</i> <i>Syrphophagous</i> Diapriidae <i>Diapria</i>	Shaw and Askew (1978) Beirne (1941) Fitton & Rotheray (1982) Rotheray (1979); (1984) Shaw & Askew (1978) Rotheray (1985) Rotheray (1981) Weems (1954)
<i>Brachyopa</i>	Eulophidae <i>Tetrastichus brachyopae</i> **	Graham (1991)

<i>Chrysogaster hirtella</i>	Ichneumonidae <i>Rhemobodius bifrons</i>	Rotheray*
<i>Syritta pipiens</i>	Diapriidae <i>Trichopria clavatipes</i>	Notton (1991)
<i>Parhelophilus</i>	Diapriidae Diapria	Hartley (1961)
<i>Eristalis and Myathropa</i>	Phygadeuontinae <i>Rhemobobius</i>	Shaw & Askew (1978)

* unpublished records from individuals stated; ** new to Britain in 1993, material identified by R.R. Askew

3.4 Preserving hoverfly larvae

The best method is to place larvae in cold water and boil slowly for 3 or 4 minutes. This has several beneficial effects: larvae are cleaned; body segments expand and because they are "cooked", they retain a firm shape for ease of handling. A further advantage is that the rectal gills will often expand out of the anal cavity. The rectal gills can be important for species-level identification: they are, for example, used in keys by Hartley (1961) and Doležil (1972).

Third stage larvae that have finished feeding are the best specimens to choose for preservation. In all but the homopteran predators, a pair of differentiated discs appear on the dorsal surface of the first abdominal segment signalling that feeding is over (Fig. 2). Homopteran predators excrete black material from their hind guts which indicates feeding is over. Homopteran predators that are overwintering have also finished feeding.

Immediately after boiling check the thorax to see that it has fully expanded. This is particularly important in *Microdon* and homopteran predators which normally have the prothorax and mesothorax telescoped into the metathorax. If the thorax has not expanded fully, squeeze the larva gently and the segments should unravel (although this requires practice in *Microdon* larvae).

Colour patterns in homopteran predators are difficult to preserve; it is best to write descriptions, take photographs or make drawings before boiling. Alternatively, predatory larvae can be dropped into 60°C water for a few seconds: this kills them and preserves the pattern of fat tissues and some of the colours. Where enough material is available, preserve specimens using both methods. Store larvae in 70% alcohol in plastic-capped or rubber-bunged glass tubes.

4. Functional Morphology

As a group hoverfly larvae are outstandingly diverse. This diversity can teach us much about hoverflies and various ways exist to investigate it. One of these is working out the functions of the numerous morphological features that characterise the diversity. What advantage do *Eupeodes* larvae gain with their U-shaped grasping organs? How do *Criorhina* larvae use their thoracic hooks? What role is played by the lateral lips of long-tailed larvae? Why do *Volucella* larvae have long crochets?

The most direct method of answering these questions is to observe how larvae move, feed and go about their lives. These observations can be followed up by studies of preserved larvae, working out how morphology relates to behaviour. To illustrate this I describe below the functional morphology of one example each of a phytophagous, predatory, saproxylic and saprophagous larva. The scope for studies like these is very wide indeed and apart from being of intrinsic interest, comparative studies of related species can reveal much about the evolutionary pathways followed by hoverfly larvae.

The phytophagous larva of *Cheilosia grossa*, a stem and root tunneller of *Carduus* and *Cirsium* thistles

In early spring, gravid females of *Cheilosia grossa*, search out flowering spikes of certain thistle species which, at that time of year, are only a few centimetres tall. Up to 15 eggs are laid on the tip. Within a few days larvae emerge and begin tunnelling, their presence indicated by a wet, brown stain. Soon they move to their main feeding site, the bulb-like root, which is slowly demolished over the next 2-3 months. If several eggs are laid, overcrowding invariably occurs and some larvae reach the root by the seemingly hazardous tactic of crawling down the outside of the plant and tunnelling back in lower down! *Cheilosia grossa* has an annual life cycle and larvae tunnel out of the root in late August. They overwinter as pupae in the surrounding soil and the cycle starts again in the following spring.

Several larvae feeding together have a dramatic effect on the growth form of the plant. When 1-3 eggs are laid, a normal single-spiked plant develops. More than three and the growing tip is destroyed by the young larvae and the plant loses apical dominance. The plant responds in a characteristic way, it produces several new spikes (Plate 2b). The advantage for *Cheilosia grossa* is that new spikes mean extra food. The large egg batches laid by *Cheilosia grossa* are probably part of an adaptation eliciting this response in the food plant.

The larva of *Cheilosia grossa* is robust, easy to rear and handle and superbly adapted to its way of life (Plate 2a). As is easily demonstrated, it has a remarkable ability to burrow into small spaces. Place the head end of a larva into the tips of two fingers and thumb held firmly together: the force exerted by the larva as it burrows between the fingers is surprising.

Larvae can be cultured in short lengths of thistle stem and their feeding behaviour, in which hook-like mandibles rasp the plant, can be readily observed. Plant particles coat an actively tunnelling larva and are left behind, showing they do not ingest all the tissue they remove.

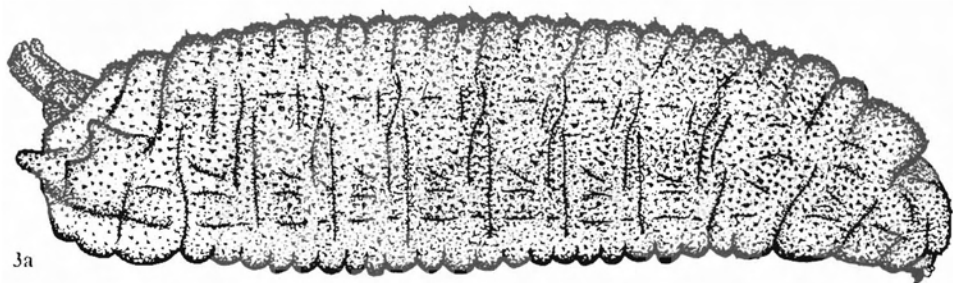
The mandibles consist of one large pair and two smaller pairs of hooks which protrude from the mouth (Fig 3). They are black and heavily sclerotised unlike the much weaker mouth-hooks of *Eumerus*, the evolutionary ancestor of phytophagous hoverflies (Appendix 2). Also significant are the mandibular lobes which have become sclerotised. In *Eumerus* these organs, which lie behind the mandibles, are fleshy and coated in ridges for guiding semi-fluid food into the mouth (Fig. 2). In phytophagous hoverflies such as *C. grossa*, they are black, completely sclerotised and fused to the mouth-hooks (Fig. 3). Their function is now to strengthen the mouth-hooks which have the modified task of rasping relatively solid food. Muscles are attached to the mandibular lobes and the whole structure is mounted on a flexible collar (Fig. 3). This combination of strengthened mouthparts and flexible collar form a highly effective rasping organ capable of great manoeuvrability within confined spaces - an advantage for a tunnelling larva. When tunnelling, the dorsal surface of the prothorax scrapes repeatedly against the plant. For protection, *C. grossa* possesses a lightly sclerotised region, the dorsal plate (Fig. 3).

In relation to *Eumerus*, the thorax of *C. grossa* is deeper and narrower. This is not only obvious from general dimensions but is also shown by the positions of some of the sensilla. The deeper, narrower thorax further enhances manoeuvrability. In *Cheilosia* the shape of the thorax is characteristically modified to suit particular feeding modes such as leaf-mining, mycophagy etc (Rotheray, 1988).

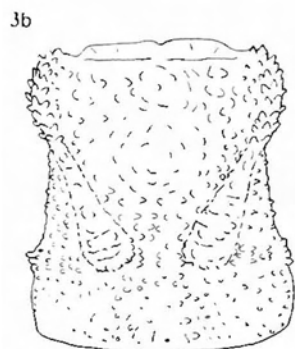
To feed *Cheilosia grossa* must grip the tunnel, otherwise it would slip backwards every time it tried to rasp. The larva maintains position by muscular contractions which forces body fluids forward and expands the body against the sides of the tunnel. Backwardly directed spicules on the sides of the body help anchor it in position (Fig. 3). When tunnelling the larva repeatedly attempts to move forward. However, if it meets an obstruction it is quite capable of reversing out of trouble.

Finally, there is the anal segment. The anal segment of *C. grossa* is similar to that of *Eumerus* except for the prp. The prp is very elaborate with lateral flanges and a coating of nodules (Fig. 3). Other tunnelling *Cheilosia* species possess equally distinctive prps with projections of different kinds (Rotheray, 1988a; 1990a). Such ornamentation probably protects the spiracular openings from becoming blocked.

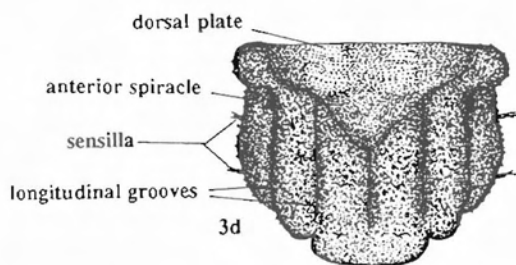
In summary features are present on all parts of the body which adapt the larva of *C. grossa* to a tunnelling way of life. The most radical modifications are in the mouthparts and thorax. These modifications, combined with behavioural features such as crawling down the outside of the plant and a exceptional strategy for manipulating the growth form of the foodplant, show that the larvae of *C. grossa* is highly adapted to its way of life.



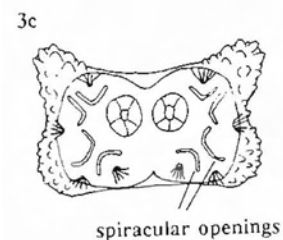
3a



3b



3d

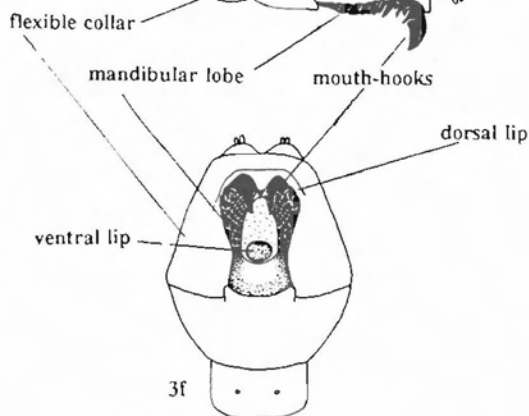


3c

spiracular openings



3e



3f

Fig. 3. *Chetostea grossa*, third stage larva, (a) whole larva, side view, 15mm long, (b) prp, dorsal view. (c) tip of prp; (d) prothorax, dorsal view, (e) mouthparts, side view; (f) mouthparts, ventral view

The predatory larva of *Eupeodes luniger*, an active hunter of aphids on a wide range of plants

Although many families of Diptera have predacious larvae, few hunt prey actively on plants. This is because plant surfaces are extremely hazardous. They are variable and complex in shape making them difficult to search. Their surfaces are hard to grip and there are ever-present dangers of being dislodged by wind or rain, of being dried out by the sun, or of being attacked by natural enemies. Despite these problems and the apparent handicaps of being blind and having no legs, predacious hoverflies are a hugely successful lineage comprising nearly a third of all known species.

Gravid female *E. luniger* locate aphid colonies by sight and smell and oviposit close to or among the prey. Usually single eggs are laid but depending on various circumstances, such as aphid abundance and female age and physiological condition, she may oviposit several times at any one colony.

A few days after oviposition a translucent, yellowish larva breaks out of the egg and begins to search for prey. Moving forward slowly and raising and stretching its thorax it locates prey by touch. Having touched an aphid, the larva catches it, pierces the integument and imbibes its body fluids and other internal tissues. A first stage larva can take several hours to demolish a single aphid. A third stage larva manages this in a couple of minutes and is a formidable hunter.

Unless starving, the third stage larva is primarily active at night. It hides during the day to minimise desiccation and reduce the risk of being found by natural enemies. On night-time forays dozens of aphids are consumed. This pattern of feeding and hiding lasts for between nine and fifteen days. As the larva grows, the hind gut fills with the black digested remains of the prey, easily visible through the translucent body. Only when feeding is over does it empty the hind gut as a shiny black streak. Then it is ready for the next developmental stage - aestivation, overwintering or pupariation.

Eupeodes luniger has 2-3 generations each year and overwinters usually in the pupal stage. This is unusual since most homopteran predators overwinter as third stage larvae. Puparia are either found on the aphid foodplant or in leaf litter beneath such plants.

Hoverfly predators are highly adapted to their way of life. One of their distinctive features are colour patterns. Most diptera larvae, including those of non-predatory hoverflies, lack colour patterns and are usually white or grey. The function of colour patterns in predatory hoverfly larvae seems to be crypsis i.e. camouflaging coloration. This is a defence against visually hunting predators such as birds (Rotheray, 1986). Colour patterns vary. Some species are almost translucent, others are green, brown or otherwise coloured (Plates 4b-10a). Most have disruptive stripes, bars or other markings that break up the body outline making it difficult for predators to recognise characteristic larval shapes. Colour patterns are formed by one or more of the following elements: pigments in the haemolymph and/or the fat; the black hind gut; spicules and markings on the integument.

The colour pattern of the larva of *E. luniger* is quite complex and involves most of these elements (Plate 9a). Dorsally it has a series of pink to pale brown stripes, composed of fat,

running along the body. Overlying these are segmentally arranged, white, triangular-shaped fat bodies. Lateral to these markings are triangular-shaped areas clear of fat through which the black hind gut is visible. Other regions of the body are flecked with white and brown fat particles and on the integument, aggregated clumps of black spicules further enhance the overall mottled brown and white appearance of this larva. Such a colour pattern appears well suited to crypsis on dark backgrounds, particularly twigs and branches of trees and shrubs.

In addition to colour patterns other unique morphological features characterise homopteran predators. The larval thorax of *E. luniger* is highly modified. Its surface is smooth and lacks setae, spicules and sclerotised regions (Fig. 4). Furthermore, the thorax is telescopic with the prothorax retractable within the mesothorax and the mesothorax retractable within the metathorax. When stationary, the anterior margin of the metathorax folds over in front of the larva so protecting the retracted prothorax and mesothorax. In fact the prothorax and mesothorax are rarely seen in live specimens because they are retracted for much of the time.

In the allied genus, *Microdon*, this process of retraction and folding down of the metathorax is taken a step further. In this genus the anterior fold of the metathorax is permanently fixed in a downward position and the prothorax and mesothorax are even narrower and retracted into a "pocket" on the ventral surface of the metathorax. When searching for food, the prothorax protrudes through special mid-dorsal gaps in the margins of the mesothorax and metathorax.

The prothorax of *E. luniger*, has undergone a process of elongation. The defining syrphid character of longitudinal furrows and rows of sensilla (page 5) are present right at the tip of the prothorax behind which is a greatly extended region with the anterior spiracles on the posterior margin of the segment (Fig. 4). In trying to work out where segment boundaries lie, the extreme nature of this elongation has confused many authors including me! It is now clear that the anterior spiracles are prothoacic in position and not situated on the mesothorax as stated in Rotheray and Gilbert (1989).

Apart from elongation, the thorax has undergone other modifications. On the ventral surface are raised pads which probably help to reduce wear during casting. Casts are the characteristic scanning movements of larvae in which the front end of the body is repeatedly stretched forwards and sideways when searching for food. On the antero-lateral margin of the prothorax are a pair of triangular-shaped sclerites which help grip the prey (Fig. 4).

Capturing and holding prey is a specialised process involving all these modifications to the thorax. The narrow elongate shape facilitates casting and the capture of small items of prey. During casting the antenno-maxillary organs project forward and if they touch an aphid, prey capture may occur: sticky saliva pours out to hold the prey; the prothorax retracts to pull round the triangular-shaped sclerites which imbed themselves in the prey anchoring it in position; held firm by saliva and sclerites in the inverted prothorax, the stylets protrude from the mouth to pierce the prey and feeding begins.

To ensure the aphid does not pull itself free, third stage larvae often lift them up (Plate 8a). This also means that alarm pheromones which some aphid species produce when attacked, are harmlessly dispersed above the colony. The success of these techniques is seen in the fact that, unlike other groups of aphid predators, hoverfly larvae often eat their way into

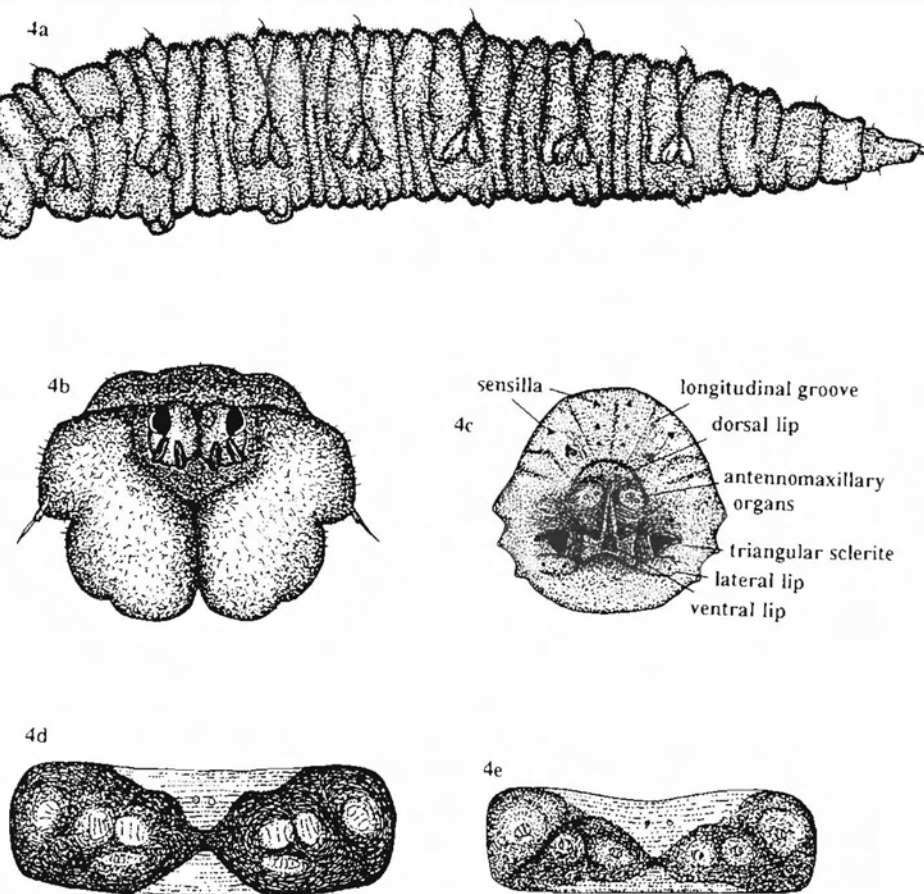


Fig. 4. *Eupeodes luniger*, third stage larva, (a) whole larva, side view, 10mm long, (b) prp and anal lobes, viewed from the end of the larva, (c) prothorax and mouthparts, viewed from the front of the larva, (d) locomotory prominence, 5th abdominal segment; (e) locomotory prominence, 1st abdominal segment

aphid colonies leaving a cleared line behind them, surrounded by undisturbed aphids.

The narrow, retractile, probing thorax of predatory hoverfly larvae with its protective pads, sticky saliva and hook-like sclerites seems a particularly efficient design in the evolution of hoverfly larvae. This is because it is little modified in any of the numerous genera of predacious hoverflies that have subsequently diversified from the original pipizine-like ancestor of the group.

Effective means of capturing prey is but one specialised feature of these larvae. Another speciality is manoeuvrability. Manoeuvrability is considered to be a major barrier to colonisation of plants by insects (Southwood, 1972; Strong et al., 1984). Homopteran predators seem to have the odds stacked against them when it comes to manoeuvrability. Not only do they lack the legs or anal suckers of caterpillars and beetle larvae but they are also blind. Despite this they achieve high levels of locomotive efficiency on plants.

Their success is due to the use of meniscus forces for gripping surfaces. Meniscus forces are created by coating the ventral surface with fluids emitted periodically from the anus, together with saliva from the mouth. Unlike other hoverfly larvae, predatory species have a smooth ventral surface lacking setae or surface sculpture except for a network of shallow grooves. These grooves probably fill with fluids helping to spread meniscus forces across the ventral surface.

In addition there are pairs of locomotory organs on the first six abdominal segments (Fig. 4). These are not true prolegs because they lack musculature and crochets. They work by filling with haemolymph as waves of contraction pass down the body during locomotion. When placed on the substrate the expanded locomotory organ presents a large surface area for contact with the substrate. Apart from locomotory organs there is one other integral feature - the tip of the anal segment. It is very important that the tip of the anal segment grips the substrate when locomotion is initiated otherwise the larva would slip as the wave of contraction passes forward. In non-predatory larvae this is not so important because they are usually buoyed up by liquids or live inside plants. The tip of the anal segment in predatory larvae is modified for gripping. It is large, rounded in profile and has up to three pairs of anal lobes (Fig. 4). It is smooth except for a network of shallow grooves at the extreme tip. Unlike the locomotory organs it is muscular. These modifications are unique to homopteran predators.

Furthermore, the ventral surface has been altered to cope with particular plant structures. *Epistrophe* larvae, for example, are dorso-ventrally flattened with broad, flattened locomotory organs. These larvae are very effective at searching flat substrates such as leaves.

The locomotory organs of *Eupeodes* and *Scaeva* larvae are the most developed of all. They become increasingly large towards the posterior end of the larva. The final two pairs consisting of three/four anal lobes each (Fig. 4). The tip of the anal segment is also large with pairs of downwardly projecting lobes. Together these form a U-shaped grasping organ best appreciated in profile (Plate 9b). *Eupeodes* and *Scaeva* larvae are most effective at moving on cylindrical plant substrates such as stems where they use the U-shaped grasping organ and mouthparts to wrap themselves around the stem and move sideways (Plate 9a).

Most species in these genera feed on conifer aphids where the U-shaped grasping organ may have first developed as a means of locomotion among pine needles, twigs and branches.

The saproxylic larva of *Criorhina berberina*, living in wet decaying heartwood

In the British Isles the beautiful bumble-bee mimic, *Criorhina berberina*, is a fairly widespread woodland hoverfly. Its flies from May to July and is readily seen on flowers. When not at flowers, adults frequent old trees and stumps which males "patrol" and gravid females search for areas of wet decaying heartwood in roots and rot-holes. They lay batches of eggs close to the decay either in cracks and crevices on the bark or on overhanging leaves. Where decaying roots are close to the surface, females oviposit on the ground suggesting that odours from the decay elicit this response from them.

Larvae emerge a few days later and face a perilous journey to find food. This is probably the most vulnerable part of the life cycle involving a high mortality rate. It is no coincidence that in compensation, *Criorhina* are among the most fecund of hoverflies capable of producing hundreds of eggs (F.S. Gilbert, *pers. comm.*). The costs of this egg production are presumably outweighed by the advantages of life in decaying heartwood where larvae are probably free from the vagaries of climate and safe from enemies. Larvae burrow in the wet, decayed wood feeding on micro-organisms and spending up to three years growing and developing. In spring they move up to drier regions to pupate, behind loose bark or in the upper layers of the soil. Two or three weeks later adults emerge.

The larva of *C. berberina* has some exceptional morphological and behavioural features (Fig. 5). In comparison with phytophagous and predatory larvae the thorax is very differently shaped. It is huge, broad and compact. The front part of the prothorax (the anterior fold, Fig. 5) is well developed and coated in sclerotised, backwardly directed spicules. The mouthparts are greatly modified. Gone are rasping hooks and piercing stylets. The hooks are reduced to a trace and are entirely inside the cavity of the mouth. The mandibular lobes are also internal and coat the inside of the mouth. The dorsal, lateral and ventral lips are greatly developed and are coated in setae of various types. These developments are adaptations to filter-feeding on suspended micro-organisms. The broad thorax accommodates a large opening to the mouth, maximising the amount of fluid gathered during feeding lunges. The anterior fold is protected from wear by spicules. The lateral lips help prevent large undigestible fragments from entering the mouth and the dorsal and ventral lips close the mouth to keep food from spilling out.

Another spectacular development are large, black hooks on the thorax (Plate 12f). The particular number, shape and arrangement of hooks is genus-specific (Fig. 14) and *Criorhina* larvae can be recognised by the combination of a central plate bearing one or two pairs of hooks and, just behind, a pair of "cows-horns" (Plate 12f; Fig. 5). A gradual increase occurs in the size and number of hooks in the hypothesised evolutionary sequence: *Tropidia* - *Chalcosyrphus* - *Brachypalpus* - *Brachypalpoides* - *Milesia* - *Spilomyia* - *Criorhina* - *Callicera* - *Temnostoma* (Appendix 2).

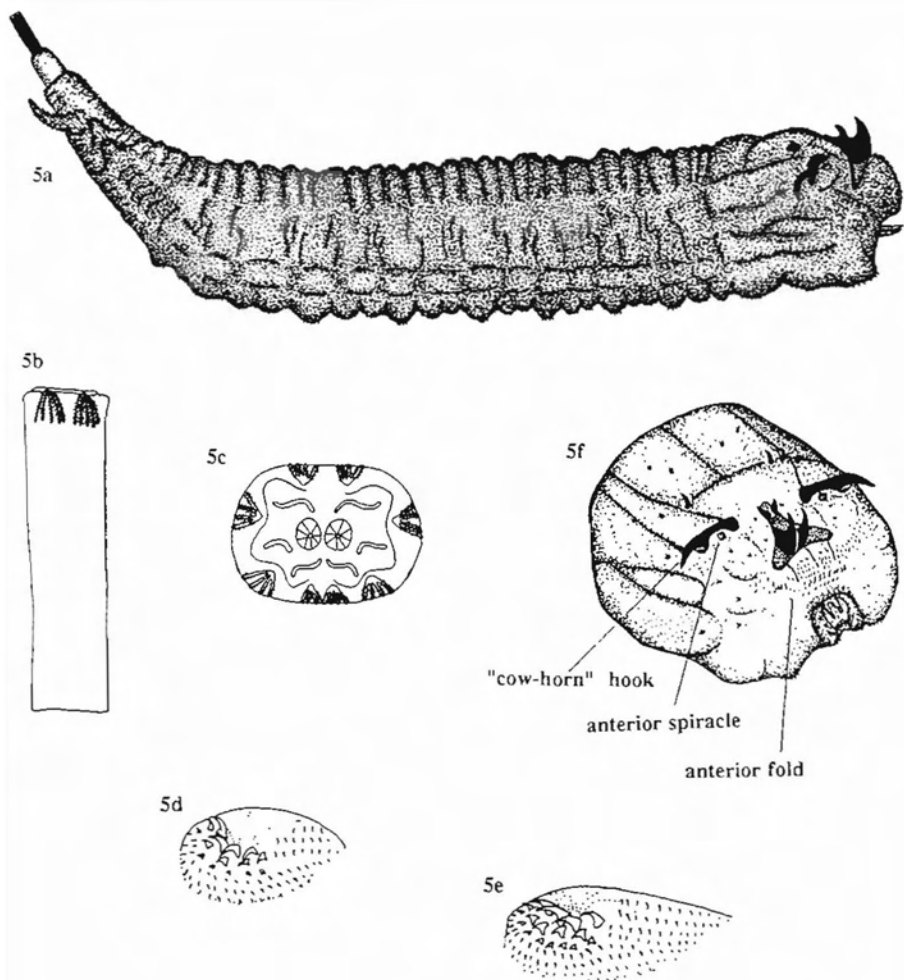


Fig. 5. *Crorhina berbenna*, third stage larva, (a) whole larva, side view, 22mm long, (b) prp. dorsal view; (c) tip of prp. (d) proleg, 6th abdominal segment; (e) proleg, 1st abdominal segment; (f) thorax, antero-lateral view

Where have these hooks come from? A clue to their origin is found in *Tropidia* at the base of the sequence. In this genus spicules occur not just on the anterior fold but have spread in groups over the pro- and mesothorax (Fig. 14b). Some are heavily sclerotised suggesting that, as diversification took place, hooks were elaborated from these spicules.

Associated with the development of hooks are muscles that control their use. Like the hooks themselves, there is a gradual progression in the size and arrangement of these muscles as seen by modifications to the folding pattern on the dorsal and lateral margins of the thorax in the sequence *Tropidia* - *Temnostoma*. In *Tropidia* there are two parallel folds along the lateral margins of the thorax at the level of sensilla 4 and 5. In *Criorhina* larvae there are three folds but the middle one is huge and broad and attached posteriorly in two places (Fig. 5). Anteriorly this fold tapers and ends just behind the "cow-horn" hooks.

In *Criorhina* the development of large centrally positioned hooks on the prothorax has resulted in altered positions for the first three pairs of dorsal sensilla. Usually these sensilla are in longitudinal rows but in these larvae they are displaced by the hooks.

The locomotory organs have also changed. In all but one genus of hook-bearing hoverfly larvae prolegs with crochets are present. They are true "prolegs" because unlike the locomotory organs of predatory larvae they possess musculature. However, the prolegs of *Criorhina* larvae are small with short, pale crochets.

Small prolegs and thoracic hooks are important. *Criorhina* larvae are generally found in the deepest regions of rot-holes and decaying roots where wet decay runs in seams between firmer areas of heartwood. *Criorhina* larvae are well adapted to exploiting these splinter-filled seams. When moving forward the larva repeatedly dips its thorax up and down. This enables splinters of wood to be levered out of the way by the hooks. Nonetheless injuries are common as indicated by small, black, irregular-shaped integumental scars (Plate 12f). Long prolegs and crochets would probably hinder movement in these seams which may account for the reduction in size.

Criorhina larvae appear to represent a transitional stage between those of *Milesia* and *Spilomyia* (not British) which have well developed prolegs and inhabit the more open, liquid areas in decayed wood and *Temnostoma* larvae (also not British) which excavate tunnels through softened but firm heartwood. In *Temnostoma* the trends first evident in *Criorhina* are developed further. The crochets have disappeared altogether and the prolegs are barely discernable. The larva has a huge muscular thorax with a pair of large toothed rasping organs either side of the mesothorax (Plate 13 c,d). In body shape they resemble phytophagous larvae that are adapted to tunnelling (compare Plates 1c,e; 13c,d)

The long-tailed, saprophagous larva of *Myathropa florea*, living in micro-habitats associated mainly with wood.

The most complex hoverfly larvae are those of *Eristalis*, *Helophilus* and allied genera. Termed "rat-" or "long-tailed" because of the elongate anal segment, they are among the largest of hoverfly larvae. They appear late in syrphid evolution with the phylogenetic

sequence hypothesised as: *Sericomyia* - *Mallota* - *Anisimyia* - *Parhelophilus* - *Helophilus* - *Eristalis/Eoseristalis* - *Myathropa* (Appendix 2). All these larvae share the character of a long-tail with the first ring of the anal segment extended more than the second or third rings (Fig. 6) which distinguishes them from other hoverfly larvae with extended anal segments. The long-tail forms a sheath for the highly retractile breathing tube conferring the advantage of respiration with minimum exposure.

Long-tailed larvae were favoured subjects of study for continental anatomists and physiologists at the turn of the century as they grappled with the problem of how the muscle systems worked to extend and retract the breathing tube. In America at about the same time, long-tailed larvae enjoyed a brief period of commercial exploitation as fish bait. But their claim to fame may be earlier than this. Some consider that the "oxen-borne bee" of the ancients and the "bees" observed by Samson swarming out of the body of a lion (Judges, 14,14) were, in fact, *Eristalis tenax*. The logic being that bees would not normally be attracted to carcasses but its hoverfly mimic, *E. tenax*, may have been (Osten Sacken, 1894).

The most ubiquitous long-tailed species is *Myathropa florea* which breeds predominantly in wet micro-habitats associated with wood. It has been reared from a wide range of such habitats including sap-runs, rot-holes, decayed roots (Rotheray, 1990) and under bark (I. Perry, *pers. comm.*). Precariously, it even breeds in shallow, water-filled crevices on the bark of fallen trees (Rotheray, 1990) and seems to accept with equal readiness coniferous as well as deciduous trees. However it appears not to be restricted to such sites, since there are breeding records from wet, cow dung in a plastic pot in a greenhouse (van der Goot, 1987) and wooden water butts (Coe, 1953).

In the British Isles adult *M. florea* start to appear in spring and can be found in every month until October/November. Larvae may take two or more years to develop depending on whether oviposition is in spring or autumn (Hartley, 1961).

Like *C. berberina* the mouthparts of the larva of *M. florea* are adapted for filter-feeding (Roberts, 1970). The chief difference between the mouthparts of *C. berberina* and *M. florea* are in the greater size and development of the latter species. Externally the dorsal, ventral and lateral lips are large and well developed. The lateral lips are coated in specialised setae from those at the tip which are long, fine and densely aggregated to those at the base which are broad and spatulate (Fig. 6). The mesothoracic prolegs are also very large. Between them and the mouth is a smooth "feeding-channel" (Fig. 6).

To feed, the thorax is thrust into the liquid and food enters the the channel. The thorax contracts and, prevented from escaping by the mesothoracic prolegs and lateral lips, the food is forced into the open mouth. The various internal filtering mechanisms that separate the food are meticulously described by Roberts (1970). The specialised setae coating the lateral lips not only help prevent food from escaping but may also help prevent the feeding-channel becoming blocked by large particles.

As with other long-tailed larvae, the prothorax of *M. florea* has two innovative features. First, the thorax is broader and larger and has extra folds (Fig. 6). The larger thorax presumably enhances the amount of food gathered with each lunge. The anterior fold is

coated in protective spicules, a feature shared by many other larvae including *Criorhina*. Second, the anterior spiracles are large and are completely retractile within specialised pockets of the integument (Fig. 6). Associated muscles control the movement of the anterior spiracles in and out of these pockets. In the other main aquatic group, the chrysogasterines, the problem of protecting anterior spiracles has been solved in a more radical manner by reducing them to vestigial non-functional remnants or by doing away with them altogether.

Prolegs are highly developed in rat-tailed larvae. Apart from the mesothoracic prolegs, there are 6 pairs on the first six abdominal segments (Fig. 6). Each proleg consists of a conical projection with a smooth, indented tip. The indentation is where muscles are attached. At the tip is a row of long, curved crochets below which are two or more rows of smaller crochets. When the muscles contract, the proleg is inverted and the primary crochets are grouped together within the proleg. When extended the crochets expand out of the proleg to engage the substrate.

The position of the primary crochets changes towards the rear of the body. From a transverse row on the posterior margin of segment one they change to a lateral row on the outside of the proleg on segment six (Fig. 6). This change in orientation is a feature of *Eristalis*, *Eoseristalis* and *Myathropa*. However in *Helophilus*, *Parhelophilus* and *Anasimyia* the crochets on segment 6 appear on the anterior margin of the proleg i.e. as if the crochets have moved round to the other side of the proleg. In addition, many species in all these genera have one or more crochet-like spicules between the prolegs on segment 6. These developments help prevent the body from floating to the surface when respiring. Greig (1989) shows that in *M. florea* air in the breathing tube makes larvae buoyant. Under these circumstances a means of gripping the substrate, particularly at the posterior end, is necessary to prevent the body from floating to the surface.

The long-tail appears smooth but at various points sensilla project (Fig. 6). These correspond to the lappets and sensilla pairs 10 and 11. That considerable elongation of the anal segment has occurred is indicated by the positions of these latter sensilla. They occur, on the long tail rather than just behind the anal opening as in other groups.

Segment 7 is also extended. It is a feature of syrphid larvae that the dorsal parts of body segments overlap the ventral parts and this trend reaches its greatest development in long-tailed larvae. The dorsal part of segment 7 extends over the anal segment to the base of the long tail and has tapered to such an extent that sensilla 2 is almost directly behind, rather than being lateral to, sensilla one as in other groups. At the tip of the long-tail is the prp which has four groups of water-repellant setae between the spiracular slits. At the surface of the water these setae splay out and enable the prp to float.

As a group, long-tailed larvae include generalists and specialists which exploit an incredibly wide range of micro-habitats from water-pockets in tropical forest bromeliads to peat-filled pools high on mountains. They seem to occur in almost every type of wet decaying organic material. In many ways these large, aquatic larvae can be considered as occupying the same ecological role as those other large, aquatic, filter-feeders, the baleen whales.

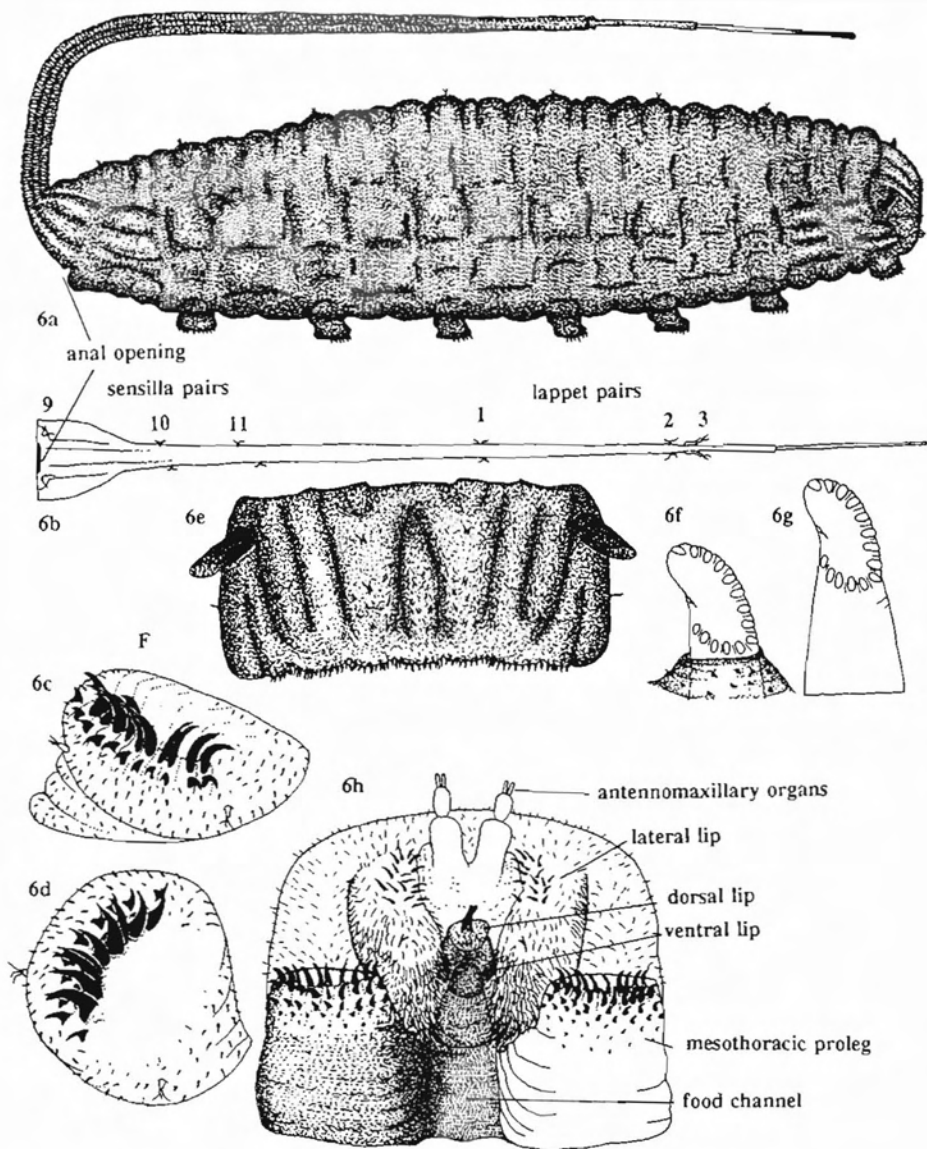


Fig. 6. *Myathropa florea*, third stage larvae. (a) whole larvae, side view, 23mm to base of tail + 28mm long tail, (b) anal segment, ventral view, (c) proleg, 1st segment, (d) proleg 6th segment, showing change in orientation of crochets, F = front of larva; (e) prothorax, dorsal view; (f) partially retracted anterior spiracle; (g) anterior spiracle, dorsal view, (h) mouthparts, ventral view

5. Using hoverfly larvae for biocontrol and conservation

Homopteran predators have long been recognised as important natural enemies of aphids. Indeed it was Erasmus Darwin, grandfather of Charles, who first suggested using them against these difficult pests. However, despite demonstrations of their ability to control aphids (eg Chambers and Adams, 1986), hoverfly predators are frequently ignored. Where research has been undertaken, it is dominated by laboratory-based studies of just two species, *Episyrphus balteatus* and *Eupeodes corollae*.

Hoverfly larvae may have been by-passed because of the influence of certain older studies suggesting that larvae appear too late or are too scarce to bring about control. I believe these studies are unrepresentative. Larval abundance is often underestimated because of two behavioural correlates of crypsis: feeding at night and dispersal when satiated. Night feeding is a well known feature of cryptic animals which thereby avoid visually searching predators such as insectivorous birds (Edmunds, 1974). Under most circumstances hoverfly larvae feed at night (Rotheray, 1986). Another means of avoiding predators is to hide during daytime (Edmunds, 1974). When satiated, hoverfly predators tend to disperse from the aphid colony and hide during the day in leaf curls and other crevices on plants (Rotheray, 1986). These adaptations make hoverfly larvae unobtrusive and easy to underestimate. The problem has an obvious solution - sample aphid colonies at night.

Hoverfly predators have a number of useful features when it comes to aphid control. In comparison with other aphid predators there are larger numbers of species to choose from, each with individual characteristics with many being specialised to hunt particular plants. For example many species of *Eupeodes* and *Scaeva* are specialised hunters of the foliage of conifers. Other species, such as *Epistrophe*, are specialised to search flat leaves of trees and shrubs. Others, like *Sphaerophoria*, prefer ground layer aphids. Furthermore, hoverfly predators hunt stealthily and do not cause aphids to scatter only to reappear elsewhere. Hoverfly predators have variable oviposition responses, sometimes batching their eggs and sometimes not (Rotheray and Dobson, 1987). Some oviposit in a density-dependent fashion while others do not (Chandler, 1968). These features, combined with their high powers of mobility both as adults and larvae, make them adept at finding small colonies and wiping them out. Their true value in this respect will not be realised until more research is done.

Phytophagous hoverfly larvae have potential for weed control. Although phytophagous hoverflies are poorly known, one European species, *Cheilosia grossa* (= *corydon*), has already been selected and imported into the USA in an attempt to control accidentally introduced thistles (Rizza, *et. al.*, 1988). Several more species are under scrutiny for similar projects. Some mycophagous/phytophagous hoverflies such as the bulb flies, *Eumerus* and *Merodon*, are themselves subjects of control programmes and recently *Cheilosia vulpina* has been reported as a pest of artichokes in France (Brunel and Cadou, 1990).

For both predatory and phytophagous hoverflies there are pioneering studies to be undertaken to aid their use in biocontrol. At the very minimum, rearing data are badly needed, particularly for phytophagous species. Behavioural interactions between predators and prey (see Rotheray, 1989) and phytophages and food-plant (see page 31) are also required if

hoverfly larvae are to be evaluated properly. Evaluation is necessary because only by understanding the behaviour and ecology of potentially useful species can the most effective be utilised.

Hoverfly larvae play other useful roles apart from controlling pests and weeds. Mention has been made of the brief period when *Eristalis tenax* was exploited commercially for fish bait. It could play that role again. Saprophagous hoverflies that specialise on decaying vegetation might also be used as a source of protein and at the same time help in the breakdown and recycling of various kinds of organic waste. In Central America a project of this kind has been under investigation to recycle coffee pulp, otherwise a source of pollution, using the tropical saprophagous hoverfly, *Ornidia obesa* (Lardé, 1989).

On another level, the natural distribution and abundance of hoverflies is used to evaluate habitats for their importance to conservation. For example certain hoverflies are indicators of ancient woodlands (Stubbs, 1982; Whiteley, 1987; Speight, 1989) while others indicate the quality of wetland sites (Whiteley, 1987).

Most attempts to use hoverflies as indicators rely on sightings of adults. As Stubbs (1982) points out, however, adults of many hoverflies are highly mobile and widespread which limits their value as indicators. This is not so with egg-laying females and larvae which are likely to be confined to breeding sites. Their presence is a better sign that the species is established in a site. Unfortunately egg-laying females are difficult to distinguish from other females but larvae are much easier to deal with. The use of larvae in assessments of habitats has hardly begun. The chief barrier is finding and identifying larvae, and I hope that the present guide will serve in this respect.

There are practical advantages too. Many species take more than a year to develop so larvae can be sampled at any time. Many occur in clearly defined sites such as rot-holes, sap runs, pond margins etc so quantitative assessment is possible using standardised techniques. Long-term monitoring of breeding sites is therefore possible offering insight into how sites might be changing.

Some rare hoverflies are in need of conservation. Not only are these species of intrinsic interest as examples of specialised life histories in threatened habitats, but many are large and colourful. Such hoverflies can be used as "flagships" with their conservation of benefit to other species. For example, in Scotland the RDB category 1 species, *Hammerschmidtia ferruginea*, breeds under the bark of fallen aspen trees and branches. It is one of the largest and most distinctive species of about thirty flies that utilise this breeding site including seven other Red Data Book species. A conservation programme aimed at conserving *Hammerschmidtia ferruginea* would conserve these other species as well.

The key to making hoverflies maximally useful for biocontrol and conservation depends on larval stages and breeding sites. It is only by advancing knowledge on these fronts that the potential of hoverflies for both fields of endeavour will be fully realised.

6. Identification of hoverfly larvae

The following keys to European hoverfly genera are based on the third stage larva. Most second stage larvae can also be identified. The keys are provisional since the larval stages within some genera are entirely unknown eg *Chamaesyphus*. If a larva appears not to key out, it could belong to one of these genera. Identification will then depend on rearing it through to the adult stage. Having reached a name in the keys check the identification using the section on generic accounts starting on page 64.

Certain genera are either included in two keys or occur twice in the same key. This is to account for possible misinterpretations. For example *Ferdinandea* and *Rhingia* larvae have very reduced mouth-hooks that, according to how they are preserved, may protrude slightly making it possible that individuals will fit both sides of the first couplet in Key V. Thus they are included in both parts of the key. *Caliprobola* and *Myolepta* are dealt with similarly on account of the variable length of the anal segment as are *Brachyopa* and *Hammerschmidtia* because of the variation in appearance of crochets within individuals of certain species.

Details on how to prepare larvae for identification are given on page 26. Briefly, use a binocular microscope in good light with clean, dry specimens held gently in the fingers or in a container with glass beads or dry sand.

Key I - p 46, main groups

Key II - p 47, *Microdon*, Plate 3c-e

Key III - p 48, homopteran predators, Plates 4b-10a

Key IV - p 54, larvae with hooks on the thorax, mostly saproxylic species, Plates 11c; 12 d,e; 13a,c,e

Key V - p 57, mostly larvae with mouth-hooks, phytophages, mycophages and some saprophages

Key VI - p 59, *Volucella* in bee and wasp nests and short-tailed saprophagous larvae, Plates 10b-f; 11; 12a,b

Key VII - p 61, mostly long-tailed saprophagous and saproxylic larvae, Plates 13b,f; 14

Key I Main Groups

I larva with band of setae around the margin of the body, a flat ventral surface and a domed dorsal surface; prothorax and mesothorax narrow and telescoped into a pocket on the ventral surface of metathorax **Microdon** (Plate 3c-e) **Key II**
in and around ant nests

- not like this **2**

2 larva with colour pattern (Plates 4b-10a); anal segment without lappets; pair of triangular-shaped sclerites either side of the mouth (Fig. 4) **Key III**
*predators of mostly soft-bodied Homoptera, eg aphids, coccids and psyllids. Notable exceptions are **Parasyphus nigratarsis** (Plate 7c) which feeds on chrysomelid beetle larvae and **Xanthrandrus comtus** (Plate 4b) which feeds on gregarious caterpillars see Table 2 for other exceptions*

Key III

(predatory larvae with colour patterns)

Rotheray and Gilbert (1989) provide a key to third stage larvae and puparia of European genera of predatory larvae based extensively on characters of the posterior respiratory process (prp; Fig. 2). The following keys use a combination of structural characters and colour patterns to take advantage of the colour plates.

Key III.1 p. 48 main groups

Key III.2 p. 48 green larvae

Key III.3 p. 49 larvae with dorsal projections

Key III.4 p. 50 larvae with longitudinal stripes and overall colour pattern other than green

Key III.5 p. 50 translucent larvae

Key III.6 p. 51 larvae with specific markings and structural characters not covered in keys III.2-5

Key III.1 (Main Groups)

- 1 overall colour of larva green, eg Plates 4a,5a Key III.2
- overall colour otherwise 2
- 2 larva with dorsal projections (view from side), Plate 10a Key III.3
- larva without dorsal projections (view from side) 3
- 3 larva with longitudinal dorsal stripes, Plates 4c,5d,7d,e Key III.4
- larva without longitudinal stripes 4
- 4 larva translucent with white, yellow or pale brown markings, Plates 5f,6a-c,e,8c,d Key III.5
- not like this Key III.6

Key III.2 (green larvae)

- 1 larva with a mid-dorsal white, yellow or pinkish stripe (eg Plate 7f) 2
- larva without a mid-dorsal stripe 3
- 2 larva sub-cylindrical in cross-section; prp broader than long
. *Scaeva* (Plate 9d) p.87
wide range of aphids on herbaceous plants and trees

- larva dorso-ventrally flattened; prp longer than broad *Epistrophe* (Plate 7f) p.71
aphids mostly on trees and shrubs
- 3 larva with a pair of rounded projections at the tip of the anal segment (Plate 5a-c)
..... *Pipiza* (in part) p.84
mostly on low herbaceous plants and aphig galls including those on trees
- larva lacking a pair of rounded projections 4
- 4 prp with a posterior projection (Fig. 7) *Xanthandrus* (Plate 4b) p.91
predator on mostly gregarious microlepidopteran larvae
- prp lacking a posterior projection 5
- 5 upper-lateral stripes present (Plate 4c-f); body with chevron-like markings and flecked
with particles of fat *Platycheirus scutatus* (Plate 4e,
shows overwintering specimens which have darkened and lost their otherwise bright
green colour) p.85
associated with a wide range of ground layer aphids
- upper-lateral stripes and chevrons absent 6
- 6 larva with white fat body not forming dorsal stripes (Plate 4b); prp broader than
long *Melanostoma* p.78
leaf litter and ground layer plants, diet uncertain, rare at aphid colonies
- larva with fat body forming a pair of dorsal stripes (sometimes inconspicuous); prp
longer than broad *Sphaerophoria* (Plate 5e) p.87
associated with a range of ground layer aphids

Key III.3 (larvae with dorsal projections)

- 1 anal segment with a pair of long tapering projections *Dasysyrphus* (Plate 8e,f) p.70
arboreal aphids
- anal segment lacking a pair of long projections 2
- 2 larva brown with a white crescent-shaped marking (Plate 6d)
..... *Melangyna arctica* p.77
Pterocallis ulni on *Ulnus* (Rotheray 1988b)
- larva not like this 3
- 3 tip of anal segment with a transverse row of 4 bristle-like projections behind the prp

(Fig. 8); small larva about 7mm long *Paragus*
(Plate 9e, this preserved specimen is darker than it would be in life) p.82
ground layer plants and shrubs

- tip of anal segment without a row of 4 transverse projections; large larva between 9 and 17mm long 4
- 4 prp tapering and longer than broad at tip 5
- prp not tapering and broader than long or about as broad as long 6
- 5 larva with a broad white marking with a greenish brown fringe, like a bird dropping (Plate 8b) *Meligramma triangulifera* p.78
aphids on shrubs and trees
- larva uniform dark brown or black *Meligramma guttatus* p.78
aphids on Acer
- 6 body coated in setae; prp with inwardly sloping spiracular plates *Didea*
(Plate 9f, this preserved specimen is darker than it would be in life) p.71
arboreal aphids including those on pines
- body lacking setae, coated in black triangular spicules; prp with spiracular plates not sloping inwardly towards each other *Eriozona* (Plate 10a) p.72
pine aphids

Key III.4 (larvae with longitudinal stripes and overall colour pattern other than green)

- 1 prp about as broad as long; basal region pale 2
- prp longer than broad; basal region dark
. *Parasyrphus* in part (Plate 7d,e) p.83
arboreal aphids, particularly those on pines
- 2 larva more or less square in cross section with the two dorsal stripes not merging smoothly at the head end (Plate 5d) *Baccha* p.64
aphids on low growing herbaceous plants, particularly those in shady conditions
- larva subrectangular in cross section with dorsal stripes merging smoothly at the head end (Plate 4c,f) *Platycheirus* in part p.85
ground layer aphids, but diet of some species uncertain

Key III.5 (translucent larvae)

- 1 anal segment with a pair of rounded projections at the tip of the anal segment; larva

- uniformly translucent white *Trichopsomyia flavitarsis* p.90
in galls of the psyllid, Livia juncorum on Juncus articulatus
- anal segment lacking a pair of rounded projections at the tip; larvae not uniformly translucent white, mottled to some extent 2
- 2 prp without dorsal spurs (Fig. 9) 3
- prp with dorsal spurs (Fig. 10) 4
- 3 larva with upper lateral stripes; spiracular openings short-oval in shape, not much longer than broad *Platycheirus* in part (Plate 4f) p.85
in ground layer, diet of some species uncertain
- larva without upper-lateral stripes; spiracular openings narrow, several times longer than broad *Episyrphus balteatus* (Plate 5f) p.72
a very wide range of ground layer and arboreal aphids
- 4 prp with a basal rim (Fig. 11) *Meliscaeva auricollis* p.79
ground layer aphids and those on shrubs
- prp without a basal rim 5
- 5 basal region of prp below bulbous shiny tip broader than long; white, yellow/red or brown colour pattern with 4 or 5 pairs of chevrons (Plate 6 a-c) . *Syrphus* p.89
a very wide range of ground layer and arboreal aphids
- basal region of prp below bulbous tip longer than broad 6
- 6 larva very translucent with 3 or 4 white ill-defined chevrons (Plate 6e)
. *Melangyna cincta* p.77
arboreal aphids, particularly Phyllaphis fagi (L.) on Fagus
- colour pattern not like this 7
- 7 larva with 5 or 6 pairs of yellow or brownish spots with narrow yellow (turning brown in diapause) zig-zag markings in front (Plate 7c)
. *Parasyrphus nigratarsis* p.83
predator of chrysomelid beetle larvae on Alnus and Salix
- larva with broad white, yellowish or pale brown chevrons (Plate 8c,d)
. *Leucozona* p.77
ground layer and arboreal aphids

Key III.6 (larvae with other markings and structural characters not covered in keys III.2-5)

1	prp dome-shaped in side view lacking a central depression	2
-	prp angular in side view with a central depression at the tip	3
2	prp with wavy spiracular openings (Fig. 12) <i>Xanthogramma</i> p.92 <i>in ant nests (Table 2)</i>	
-	prp with slightly curving spiracular openings <i>Doros</i> p.71 <i>possibly in ant nests (Table 2)</i>	
3	prp sloping backwards (Fig. 13); larva yellowish-brown in overall colour <i>Meliscaeva cinctella</i> p.79 <i>arboreal aphids including those on pines</i>	
-	not like this	4
4	prp lacking dorsal spurs (Fig. 9)	5
-	prp with dorsal spurs (Fig. 10)	10
5	anal segment with 2 pairs of short fleshy projections behind the prp; prp broader than long with short spiracular openings not extending over the side <i>Rohdendorphia (not British)</i> <i>mountains</i>	
-	anal segment without such projections; prp longer than broad or if not, spiracular openings long, extending over the side	6
6	prp with long, conspicuous inter-spiracular setae, at least half as long as the spiracular openings	7
-	prp with short, inter-spiracular setae, less than half as long as the spiracular openings	9
7	larva lacking a pair of rounded projections at the tip of the anal segment; larva flattened in cross-section <i>Pipizella</i> p.84 <i>ant-attended root aphids</i>	
-	larva with a pair of rounded projections at the tip of the anal segment; larva more subcylindrical in cross-section	8
8	body coated in spine-like setae <i>Pipiza</i> (Plate 5a-b) p.84 <i>mostly on low herbaceous plants and aphid galls including those on trees</i>	
-	body coated in blunt, round-tipped setae <i>Heringia</i> including <i>Neocnemodon</i> (Plate 5c) p.76 <i>aphid and adelgid galls on trees</i>	

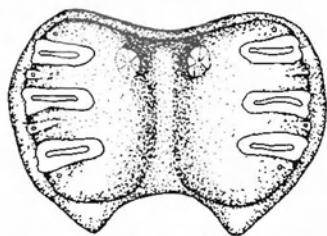


Fig. 7. *Xanthandrus comtus*, tip of prp showing posterior projections.

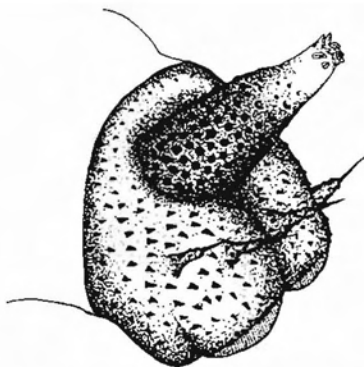


Fig. 8. *Paragus*, tip of anal segment showing transverse row of 4 setae.



Fig. 9. *Platycheirus*, prp, dorsal view.

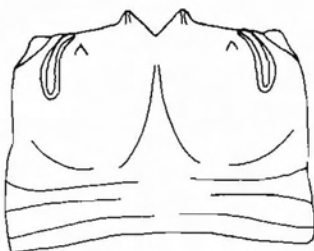


Fig. 10. *Syrphus*, prp, dorsal view showing dorsal spurs.



Fig. 11. *Meliscaeva auricollis*, prp, dorsal view showing basal rim

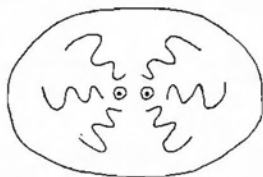


Fig. 12. *Xanthogramma*, tip of prp

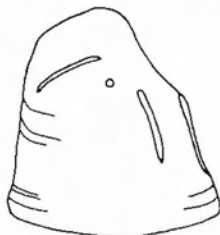


Fig. 13. *Meliscaeva cincitella*, prp, side view

- 9 prp less than 2x as long as broad at base; larva flattened in cross-section and mottled orange and brown *Meligramma euchroma* p.78
known from fruit tree aphids
- prp less than 2x as long as broad at base; larva subcylindrical in cross-section and sandy coloured *Eupeodes nielseni* (Plate 9c) p.74
aphids on pines
- 10 body coated in short spine-like setae or body smooth; spiracular openings greater than 6x as long as broad *Chrysotoxum* p.69
associated with ant nests
- body coated in dome-like papillae; spiracular openings less than 3x as long as broad 11
- 11 larva brown with a white crescent-shaped marking (Plate 6d)
. *Melangyna arctica* p.77
Pterocallis ulni on *Ulnus*
- larva not like this 12
- 12 larva dark brown with 4 or 5 square-shaped white markings
(Plate 7a) *Melangyna quadrimaculata* p.77
adelgids on *Abies*
- larva not like this 13
- 13 larva white, sometimes with a light brown fringe (Plate 7b)
. *Melangyna umbellatarum* p.77
aphids on *Umbelliferae*
- larva with 4 or 5 white blotch-like markings with an orange-brown fringe (Plate 6f) *Melangyna lasiophthalma* p.77
aphids on *shrubs* and *trees*

Key IV

(larva with hooks on the thorax)

- 1 thorax with a single pair of backwardly directed hooks on the anterior margin of prothorax (Fig. 14a); anal segment dorso-ventrally flattened with sensilla of first lappet on two separate projections (Fig. 15); small larva, up to 12mm long
. *Neoscia* (Plate 11c) p.82
ponds, streams, bogs etc in *decaying vegetation*
- thorax usually with more than a single pair of hooks but if a single pair is present they are not situated on the anterior margin of the prothorax; anal segment

- subcylindrical with sensilla of first lappet not on two separate projections; large larva, more than 12mm long 2
- 2 anterior margin of mesothorax with a row of mostly small hooks not much larger than spicules on anterior fold (Fig. 14b); a few similar hooks on the dorsal and lateral margins of the thorax *Tropidia* p.90
ponds, streams, bogs etc in decaying vegetation
- hooks elsewhere on the thorax, not forming a row on the anterior margin of the mesothorax 3
- 3 one hook lateral to each anterior spiracle and below this another separate hook (Fig. 14d); upper row of spicules on anterior fold larger than the rest (Fig. 14d) *Brachypalpus* (Plate 12d) p.65
rot-holes, under bark
- hooks arranged differently 4
- 4 two red-brown hooks lateral to each anterior spiracle (Fig. 14e); larva with a moderately long tail as in Plate 12c *Brachypalpoidea lenta* p.65
in wet, decaying heartwood of deciduous trees
- hooks black and more than two hooks on the thorax 5
- 5 two hooks lateral to each anterior spiracle and below these, on a separate base, another small hook (Fig. 14c); larva somewhat dorso-ventrally flattened with a short tail as in Plate 11f *Chalcosyrphus* p.67
under bark
- hooks arranged differently 6
- 6 two groups of hooks just behind and lateral to the anterior spiracles each group comprising 3-4 hooks of which outer hook largest (Fig. 14f); prolegs partially fused to form a single oval structure. *Callicera* (Plate 13e) p.66
rot-holes
- hooks arranged differently; prolegs forming pairs of oval structures 7
- 7 mid-dorsal part of prothorax with a "Y" or triangular-shaped hook base (Fig. 14i); Plate 12f); a pair of "cow horn" shaped, laterally directed hooks behind the anterior spiracles (Plate 12f) *Criorhina* (Plate 12e) p.70
decaying roots, rot-holes
- "prothorax without a Y" or triangular-shaped hook base 8

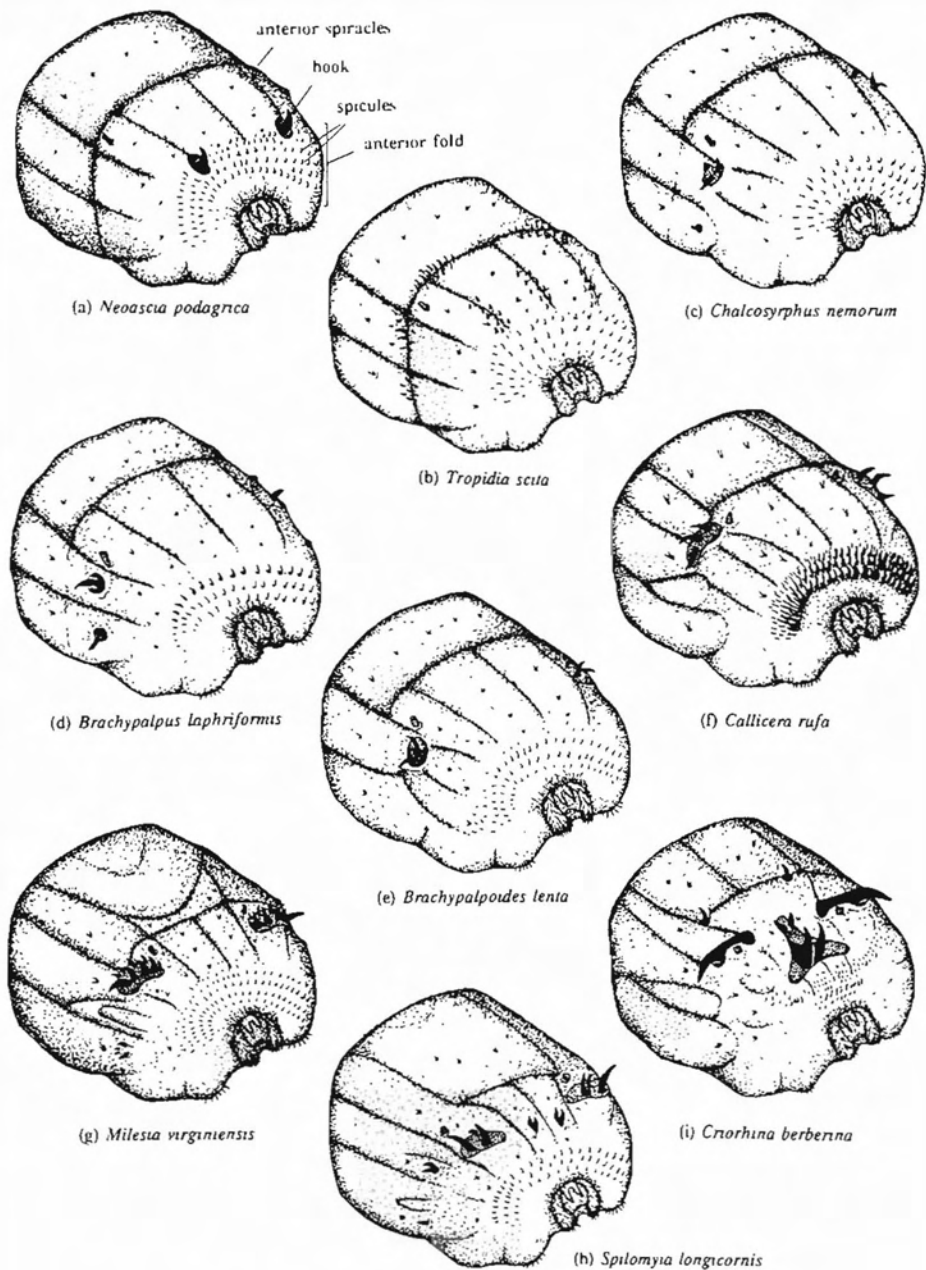


Fig. 14. Thoraces of hook-bearing larvae, antero-lateral views

- 8 larva short and compact (Plate 13c); a pair of large rasps consisting of 4-5 rows of blunt-tipped hooks lateral to the anterior spiracles (Plate 13d); crochets absent *Temnostoma* (Plate 13c,d) not British, p.90
tunnelling firm, moist wood in logs and fallen branches
- larva not short and compact (Plate 13a); lacking rasps, crochets present 9
- 9 two large groups of hooks just anterior to the anterior spiracles each comprising a primary row of 3-4 large hooks, a second row of intermediate hooks and a third row of small inconspicuous hooks (Fig. 14g); a small group of 4-6 hooks below each of these groups of hooks (Fig. 14g) *Milesia* (Plate 13a) not British p.81
rot-holes
- thorax with four groups of hooks (Fig. 14h) *Spilomyia* not British p.88
rot-holes

Key V
(Phytophages, mycophages and some saprophages)

- 1 black mouth-hooks protruding from mouth (Fig. 3); anterior fold short (less than half length of dorsum of prothorax) 2
phytophages, mycophages (Plates 1-2)
- mouth-hooks not protruding from mouth, mouthparts internal (Fig. 6); anterior fold long (more than half length of dorsum of prothorax) 9
saprophages (Plates 3a-b;10b-f;11a-b)
- 2 mandibular lobes fleshy (Fig. 2) 3
- mandibular lobes black and sclerotised (Fig. 3) 7
- 3 anal segment with middle pair of lappets divided into two (Fig. 2)
. *Eumerus* (Plate 1a) p.74
in pockets of fungal decay in bulbs
- anal segment with three pairs of lappets 4
- 4 anal segment with a narrow, terminal ring (Plate 2c); dorsal surface of abdomen coated in setae of varying sizes and densities *Cheilosia* p.67
Cheilosia longula and Cheilosia scutellata in fruiting bodies of fungi
- anal segment without narrow terminal ring and setae, if present, on dorsum of abdomen not of varying sizes and densities 5
- 5 sensilla pairs 1 and 2 on dorsal surface of abdominal segment 7 borne on conspicuous stick-like or fleshy projections 6

- sensilla pairs 1 and 2 on dorsal surface of abdominal segment 7 not borne on conspicuous projections *Cheilosia* p.67
decaying roots in non-woody plants, the only species to date known with this habit is Cheilosia pagana in association with Anthriscus sylvestris (Stubbs, 1980)
- 6 dorsal surface of abdominal segments 6 and 7 with sensilla pairs 1 and 2 borne on stick-like, black projections (Plate 3a); body coated in upright, spike-like setae *Rhingia* (Plate 3a) p.86
cow dung
- dorsal surface of abdominal segment 7 with sensilla pairs 1 and 2 borne on fleshy projections, those on segment 6 not on projections; body coated in short, fleshy flattened setae *Ferdinandea* (Plate 3b) p.75
sap runs
- 7 larva with a longitudinal anal slit i.e. parallel to the length of the body *Portevinia maculata* (Plate 1c-d) p.86
tunnelling in bulbs of Allium ursinum
- larva with a transverse anal slit i.e. at right angles to the length of the body 8
- 8 anal segment with middle pair of lappets divided into two (Fig. 2) *Merodon* (Plate 1b) p.79
tunnelling in bulbs
- anal segment with up to three pairs of lappets *Cheilosia* (Plates 1e-f;2) p.67
tunnelling in roots and stems, leaf-mining etc, see Table 2
- 9 prp about as long as broad with a mid-point ridge or groove (compare Plates 3a,b with 10b-f & 11a,b) 10
- prp longer than broad lacking a mid-point ridge or groove 11
- 10 dorsal surface of abdominal segments 6 and 7 with sensilla pairs 1 and 2 borne on stick-like, black projections (Plate 3a); body coated in upright, spike-like setae *Rhingia* (Plate 3a) p.86
cow dung
- dorsal surface of abdominal segment 7 with sensilla pairs 1 and 2 borne on fleshy projections, those on segment 6 not on projections; body coated in short, fleshy flattened setae *Ferdinandea* (Plate 3b) p.75
sap runs
- 11 anterior spiracles absent or reduced and inconspicuous; anterior fold with pale setae; body subcylindrical in cross-section

- *Chrysogaster, Lejogaster, Orthonevra* in part
Plate 10f;11a-b) p.69
in ponds, ditches, bogs etc feeding in decaying vegetation
- anterior spiracles conspicuous (Fig. 2); anterior fold with darkened spicules; body somewhat dorso-ventrally flattened 12
- 12 sensilla pairs 1 and 2 separated by an oblique groove on abdominal segments 2-6; setae on dorsal surface of abdominal segments 1-7 not forming transverse rows .
 *Hammerschmidtia ferruginea* (Fallén) (Plate 10e) p.75
under bark and in sap runs of Populus tremula L.
- sensilla pairs 1 and 2 not separated by an oblique groove on abdominal segments 2-6; setae on dorsal surface of abdominal segments 1-7 forming 4 transverse rows or setae absent; *Brachyopa* (Plate 10b-d) p.64
sap runs, under bark

Key VI

(*Saprophages in decaying vegetation and decaying wood, predators/saprophages in bee and wasp nests*)

- 1 primary row of crochets on abdominal prolegs sclerotised brown or black and arranged as a transverse row; anterior fold with less than 10 sclerotised spicules
 *Volucella* (Plates 3f;4a) p.91
bee and wasp nests
- primary row of crochets on abdominal prolegs pale and weakly sclerotised but if black and sclerotised then arranged in a curved, not a transverse row; anterior fold with more than 10 sclerotised spicules or spicules absent 2
- 2 anal segment extended up to about combined length of abdominal segments 6 and 7 (turn larva over and check using ventral surface) (Plates 10f-11d;12-13); 3
- anal segment extended more than combined length of abdominal segments 6&7 (turn larva over and check using ventral surface) (Plates 10b-e;11e-f) 7
- 3 anterior spiracles absent or reduced and inconspicuous
 *Chrysogaster, Lejogaster, Orthonevra* in part
 (Plates 10f;11a-b) p.69
in ponds, ditches, bogs etc feeding in decaying vegetation
- anterior spiracles conspicuous (Fig. 2) 4
- 4 prolegs not projecting from the ventral surface, view from side 5

- prolegs projecting from the ventral surface, view from side 6
- 5 sensilla pairs 1 and 2 separated by an oblique groove on abdominal segments 2-6; setae on dorsal surface of abdominal segments 1-7 not forming transverse rows *Hammerschmidtia ferruginea* (Fallén) (Plate 10e) p.75
under bark and in sap runs of Populus tremula L.
- sensilla pairs 1 and 2 not separated by an oblique groove on abdominal segments 2-6; setae on dorsal surface of abdominal segments 1-7 forming 4 transverse rows or setae absent; *Brachyopa* (Plate 10b-d) p.64
sap runs, under bark
- 6 anterior fold with evenly sized spicules about as long as setae on the surface of the body; prolegs bar-shaped with crochets as a transverse row facing mostly forwards on abdominal segments 1-5; larva small, less than 4mm wide
. *Syritta* (Plate 11e) p.89
decaying vegetation as in compost, manure etc
- anterior fold with spicules of varying sizes, many larger than setae on the surface of the body; prolegs oval-shaped with crochets forming curved rows and facing out to the lateral margins of the body from abdominal segment 1 to 5; larva large, usually more than 4mm wide *Xylota in part* (Plate 11f&12b) p.92
under bark, sap runs, rot holes, decaying tree roots; Xylota segnis also in decaying vegetation
- 7 anterior spiracles absent or reduced and inconspicuous
. *Chrysogaster, Lejogaster, Orthnevro* in part
(Plate 10f;11a-b) p.69
in ponds, ditches, marshes, bogs etc feeding in decaying vegetation
- anterior spiracles conspicuous (Fig. 2) 8
- 8 anal segment with basal (first) pair of lappets divided at tip (Fig. 15); small larva, less than 12mm long 9
- anal segment with basal pair of lappets not divided at tip (first two pairs may be reduced) 10
- 9 anterior margin of prothorax with a pair of hooks (Fig. 14a)
. *Neosascia* (Plate 11c) p.82
ponds, ditches, marshes, bogs etc feeding in decaying vegetation
- anterior margin without a pair of hooks *Sphagina* (Plate 11d) p.88
under bark, sap runs
- 10 anal segment with three pairs of equally long lappets
. *Xylota in part* (Plate 12a) p.92
rot-holes, decaying tree roots, under bark

- anal segment with third (distal) pair of lappets longer than the first two pairs 11
- 11 anal segment with evenly-spaced lappets 12
- anal segment with unevenly spaced lappets (distance between third pair and first two pairs greater than the distance between the first two pairs) 13
- 12 anterior fold without spicules; anal segment coated with wart-like papillae, many bearing long terminal setae (Fig. 16) *Myolepta* Plate 13f, p.82
rot-holes
- anterior fold with spicules; anal segment not coated with wart-like papillae
. *Pocota* Plate 12c, p.85
- 13 anal segment less than half as long as body from tip of prothorax to posterior margin of abdominal segment 7; body dorso-ventrally flattened in cross-section
. *Certana* not British p.67
sap-runs
- anal segment more than half as long as body; body subcylindrical in cross-section
. *Caliprobola* (Plate 13b) p.66
decaying tree roots (Caliprobola)

Key VII

(saproxylic and saprophagous larvae with extended anal segments, including long-tailed larvae)

- 1 anterior spiracles about as tall as broad, flat-tipped and not retractile into pockets on the thorax 2
- anterior spiracles retractile longer than broad, pointed at tip and retractile into pockets on the thorax (Fig 6) 4
- 2 anterior fold without spicules; anal segment coated with wart-like papillae, many bearing long terminal setae (Fig. 16) *Myolepta* Plate 13f, p.82
rot-holes
- not like this 3
- 3 anal segment about half as long as length of body (Plate 13b); ventral surface with a pair of fleshy projections immediately behind anal opening *Caliprobola* p.66
decaying tree roots
- anal segment more than half length of body (Plate 14a); ventral surface without a pair of projections immediately behind anal opening *Sericomyia* p.87
bogs, moorland pools

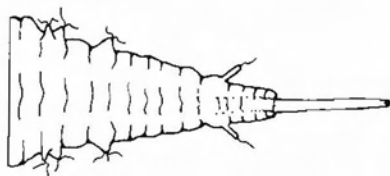


Fig. 15. *Neosascia podagrica*, anal segment, ventral view showing 1st pair of lappets divided into two.

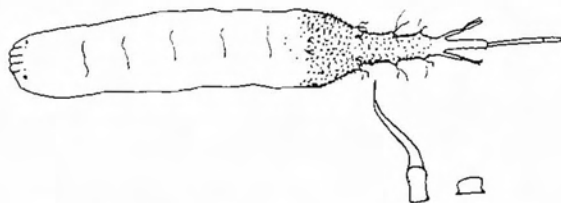


Fig. 16. *Myolepta luteola*, whole larva, dorsal view showing papillae at posterior end.

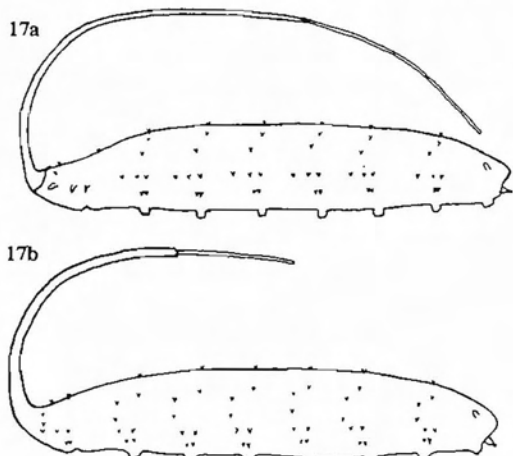


Fig. 17. Long-tailed larvae, (a) *Mallota cimibiciformis*, showing sensilla 4-6 forming a line and lateral projections at the base of the tail; (b) *Eristalis tenax* showing sensilla 4 above sensilla 5 and 6.

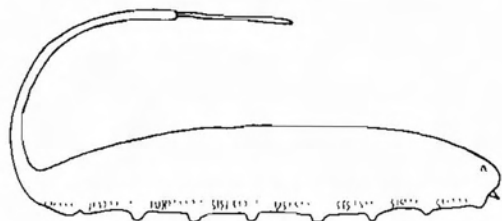


Fig. 18. *Anasimyia lineata*, whole larva showing lower lateral line of setae.

- 4 abdominal segments 2-7 with sensilla 4-6 in the same horizontal plane (Fig. 17a); abdomen smooth, not coated in setae *Mallota* (Plate 14b) p.77
- abdominal segments 2-6 with sensilla 4 above 5 and 6 (Fig. 17b) (segment 7 with sensilla 4-6 in the same horizontal plane); abdomen usually coated in setae . . . 5
- 5 last pair of prolegs with the curved tips of most of the large, primary crochets facing forwards to the front of the larva 6
- last pair of prolegs with the curved tips of most of the primary crochets facing out to the lateral margins of the larva 8
- 6 ventral surface with 3 pairs of projections between the anal opening and the base of the long tail *Helophilus* (Plate 14d) p.76
wet manure, ponds, ditches, marshes etc
- ventral surface without 3 pairs of projections between the anal opening and the "tail" 7
- 7 abdomen with a line of pubescence along the lower lateral margin (Fig. 18) *Anasimyia* (Plate 14c) p.64
ponds, marshes etc
- abdomen with pubescence absent or more evenly distributed, not reduced to a lower lateral line *Parhelophilus* p.83
ponds, marshes etc
- 8 transverse row of spicules just in front of last pair of prolegs *Eristalinus* p.73
ponds, marshes etc (sepulchralis); rotting seaweed (aeneus)
- no transverse row of spicules just in front of last pair of prolegs, although a few scattered spicules may be present between the prolegs 9
- 9 anterior spiracles pale brown; prolegs with crochets in two main rows with evenly sized spicules below *Myathropa florea* (Plate 14f) p.81
rot-holes including those in pines, large sap-runs, decaying tree roots, water filled cavities in bark of fallen trees etc
- anterior spiracles dark brown; prolegs with crochets in three rows with spicules gradually becoming smaller below *Eristalis* (Plate 14e), *Eoseristalis* p.73
wet manure, ponds, ditches, wet silage, marshes, bogs etc

7. Generic Accounts

Anasimyia Schiner, 1864 (Plate 14c)

Overall appearance. A long-tailed larva with retractile anterior spiracles; lateral margins of abdominal segments with a line of setae (Fig. 18); last pair of prolegs with most of the large primary crochets facing towards the front of the body.

Confirming characters. Anterior fold with spicules; prolegs with primary row of about 6 crochets; some crochet-like spicules between, not in front of, the last pair of prolegs.

Related taxa. Distinguished from other long-tailed larvae by the line of setae along the lateral margins of the body.

Biology. Larva living in pools and ponds where decaying vegetation, particularly *Typha*, accumulates.

Baccha Fabricius, 1805 (Plate 5d)

Overall appearance. Larva sub-rectangular in cross-section; a thin line of white fat along the dorso-lateral margins and a pair of mid-dorsal lines of white fat, one of which always extends forward more than the other, compare Plate 4c with 5d.

Confirming characters. Dorsal sensilla with one apical seta; prp broader than long and without dorsal spurs; spiracular openings not extending over the sides of the prp.

Related taxa. Larva most similar to *Platycheirus* from which it differs in that one of the mid-dorsal lines of fat always extends forward more than the other.

Biology. Associated with a range of ground layer aphids in shaded sites eg the bramble aphid, *Sitobion fragariae* on *Rubus* (Rosaceae).

Brachyopa Meigen (Plate 10b-d)

Overall appearance. Larva somewhat dorso-ventrally flattened with mouth-hooks and mandibular lobes internal; sides of body with gradually elongating projections; prp long and narrow and base coated in nodules; anterior fold coated in numerous spicules; abdominal segments 2-7 with up to four transverse rows of setae (reduced in *Brachyopa insensilis*).

Confirming characters. Prolegs not well developed and a few crochets may or may not be discernable; in dorsal view anal segment with two tapering rings; two pairs of lappets on the basal ring and one pair on the distal ring.

Related taxa. Larva most similar to *Hammerschmidtia* and *Chrysogaster*. *Hammerschmidtia*

is separated from *Brachyopa* in that it is coated completely in setae and sensilla one of abdominal segments 2-7 is separated from two by an integumental fold such that sensilla one is anterior to two. *Chrysogaster* is separated from *Brachyopa* in that it lacks an anterior fold coated in sclerotised spicules and has reduced anterior spiracles or anterior spiracles absent.

Biology. Larvae either occur in sap runs or in accumulations of decaying sap under bark where they feed probably on bacteria and other micro-organisms. *Brachyopa bicolor* is known from sap runs on *Aesculus*, *Fagus* and *Quercus*. *Brachyopa insensilis* is found in sap runs on a variety of trees, particularly *Aesculus*. *Brachyopa pilosa* is a disjunct species which seems to prefer sap runs on *Populus tremula* in Scotland but is on *Quercus* and *Fagus* in southern England. *Brachyopa scutellaris* is found on various trees including *Fraxinus*, *Taxus* and *Ulmus* but always in sap runs close to the ground.

Notes. *Brachyopa* larvae appear to have a remarkable ability to withstand desiccation which may help them survive periods when sap runs dry out, for example, during winter. They occur often in huge numbers with small and large larvae present together suggesting there is considerable overlap between stages and larval development may take more than one season. *Brachyopa insensilis* is the most common species as a larva and is easily distinguished from other British species by the relative lack of setae in transverse rows and by being coated evenly in dark blotches of various sizes. *Brachyopa bicolor* has strictly aligned setae in the transverse rows whereas in *B. pilosa* and *B. scutellaris* these setae are in approximate alignment with some setae forward of others. *Brachyopa scutellaris* can be separated from *B. pilosa* by the prp which is less than twice as long as the last pair of lappets. In *B. pilosa* the prp is three or more times longer than the last pair of lappets.

Brachypalpoidea lenta (Meigen, 1822)

Overall appearance. A short-tailed larva with mouth-hooks and mandibular lobes internal; prolegs with crochets well developed; thorax with two groups of 2 large, evenly sized hooks, each group lateral to the anterior spiracle (Fig. 14e); hooks red-brown in colour.

Confirming characters. Anterior fold coated in a narrow band of 4-5 rows of spicules, those in the second row the largest; 3 pairs of lappets, middle pair smallest; sclerotised plate at base of hooks with several spicules and on inner margin a large hook-like spicule.

Related taxa. Most similar to *Brachypalpus*, *Chalcosyrphus* and *Xylota*. *Brachypalpoidea lenta* differs from all these taxa in having two groups of 2 red-brown hooks on the thorax.

Biology. Larva found in decaying heartwood of *Fagus*, particularly in live trees with exposed decay at ground level.

Brachypalpus Macquart, 1834 (Plate 12d)

Overall appearance. A short-tailed larva subcylindrical in cross-section; mouth-hooks internal; anterior fold with a narrow band of 3-4 rows of spicules, those in the first row the

largest; lateral margins of mesothorax with two pairs of large backwardly directed hooks, one separated and below the other (Fig. 14d);

Confirming characters. Prolegs with 7 or 8 primary crochets; anal segment with three pairs of lappets, first two pairs about the same size, third pair longest.

Related taxa. Similar to *Tropidia* and other hook-bearing hoverfly larvae. The two pairs of hooks on the lateral margins of the thorax separate *Brachypalpus* from these other taxa.

Biology. Larvae are found in rot-holes of deciduous trees.

Caliprobola speciosa Rossi, 1790 (Plate 13b)

Overall appearance. A subcylindrical, relatively long-tailed larva with mouth-hooks internal; first two pairs of lappets at base of extended anal segment, third pair at tip; anal segment extended to about 75% of body length.

Confirming characters. Anterior fold with 5-7 rows of sclerotised spicules; thorax lacking hooks although spicules may be present; body coated in fine setae including segment 7 and anal segment; prolegs small with 7 or 8 primary crochets; anterior spiracles not retractile.

Related taxa. Similar to *Myolepta* and *Lejota* from which *Caliprobola* may be distinguished by the long section of the anal segment between the middle and third pairs of lappets which is about 6x as long as the section between the first and middle pairs of lappets.

Biology. Larva found in decaying heartwood of *Fagus* trees, particularly old stumps where they may be deep in the roots.

Callicera Panzer, 1809 (Plate 13e)

Overall appearance. Larva with an extended anal segment bearing a pair of fleshy projections; prolegs partially fused forming a single oval structure on abdominal segments 1-6; thorax with two groups of 3-4 hooks lateral to the anterior spiracles.

Confirming features. Mouth-hooks internal; anterior fold with a narrow band of densely aggregated thin spicules that become shorter from front to back; prp with transverse spiracular openings.

Related taxa. With the arrangement of the hooks on the thorax and the partially fused prolegs *Callicera* larvae are unlikely to be confused with any other taxon.

Biology. Larvae in rot-holes. *Callicera rufa* is found in rot-holes on *Pinus* and recently in a rot-hole on *Larix* (Iain MacGowan, pers. comm.). *Callicera aurata* (= *aenea*) and *C. spinolae* both breed in rot-holes on *Fagus*. However a broader range of trees is likely to be used by all these species.

Notes. *Callicera spinolae* is distinguished from the other two species in having a series of longitudinal stripes running down the prp. *Callicera rufa* can be separated from *C. aurata* in that the former species has a broad band of nodules just below the tip of the prp. In the latter species this region of the prp is smooth with only scattered nodules.

Ceriana Rafinesque, 1815 [not British]

Overall appearance. a dorso-ventrally flattened larva with a slightly extended anal segment; mouth-hooks internal; anterior fold coated in spicules; body coated in setae of variable sizes and densities.

Confirming characters. Prolegs small with 5 or 6 primary crockets; anal segment with 3 pairs of lappets; thorax without hooks although spicules are present.

Related taxa. Larva similar to *Xylota* from which it differs in having the body coated in variable sizes and densities of setae.

Biology. Larvae found in sap runs.

Chalcosyrphus Curran, 1925

Overall appearance. A short-tailed, slightly dorso-ventrally flattened larva; mouth-hooks internal; thorax with two groups of 1-2 black hooks, each group lateral to the anterior spiracle; below these hooks and separate from them there may be a smaller single black hook (*C. nemorum*).

Confirming characters. Anterior fold with a narrow band of 3-4 rows of spicules, second row with the largest spicules; prolegs small with 6 to 8 primary crochets; anal segment slightly extended (like *X. segnis* in Plate 11f) with three pairs of evenly sized lappets.

Related taxa. Similar to *Tropidia* and other hook-bearing hoverfly larvae. The one or two groups of hooks on the lateral margins of the thorax and dorso-ventrally flattened shape with a barely extended anal segment distinguishes *Chalcosyrphus* from these taxa.

Biology. Larvae are found in sap runs and under bark in accumulations of decaying sap.

Cheilosia Meigen, 1822

Overall appearance. From the larval point of view this large genus is not easy to characterise unless it is divided into groups based on feeding modes. All species possess mouth-hooks, but sometimes they are reduced and inconspicuous; prolegs are absent and the anterior fold is without spicules.

Feeding Mode

(i) **Mycophagous** (Plate 2c,d). One pair of small and inconspicuous mouth-hooks; mandibular lobes soft and fleshy; dorsal lip with a setal fringe; dorsal surface of abdomen with rows of long and short setae; tip of anal segment with an extended "ring" (Plate 2c).

Biology. Larvae found in the fruiting bodies of fungi. Infested fungi often lose their shape and appear as brown smudges on the ground. Searching these fungal remnants in which 50+ individuals may be present, is the best way to find larvae (Rotheray, 1990a).

(ii) **Semi-liquid fungal decay of plants.** The only species known with this feeding mode is *Cheilosia pagana* (Meigen) but undoubtedly other species are involved. Mouth-hooks small and inconspicuous; mandibular lobes soft and fleshy; dorsal lip with a setal fringe; dorsally, body coated in evenly-sized setae; tip of anal segment without an extended "ring".

Biology. The only rearing record for *C. pagana* is from decaying roots of *Anthriscus sylvestris* (Umbelliferae). Larvae were collected on 1.x.1978 (Stubbs, 1980). The larva is described by Rotheray (1990).

(iii) **Tunnelling in roots and stems** (Plate 1e,f; 2a,b). This is the most common feeding mode. Up to four pairs of mouth-hooks, usually one main pair and smaller ones behind; black, sclerotised mandibular lobes; dorsal lip smooth, lacking setae; posterior end may be contracted, flattened and obliquely angled forming an anal plate (Plate 1f); prp often with ridges, bars and projections; larva often with spicules (sclerotised setae) on the lateral margins of the thorax for gripping the tunnel and sometimes with a dorsal plate (sclerotised region on the surface of the prothorax) to reduce wear.

Biology. The nine species known with this feeding mode are restricted to particular plants (Table 1). Most of tunnelling larvae are best collected in August and September (page 9). For life histories of some of these species see Rotheray (1988a; 1991)

(iv) **Leaf-mining** (Plate 2e,f). Six pairs of mouth-hooks; black, sclerotised mandibular lobes; dorsal lip with setal fringe; integument with a dense covering of upright pubescence; prp with three pairs of straight, oval-shaped spiracular openings (other species with more than three and/or wavy openings).

Biology. Foodplants for *Cheilosia fasciata* and *Cheilosia semifasciata*, the two leaf-mining species known are given in Table 1. The life history of *C. fasciata* is considered by Hövemeyer (1987 and 1993) and the larva described by Rotheray (1990). The larva of *C. semifasciata* is described by Rotheray (1988).

(v) **Cambium and sap-feeding in pines.** One huge pair of mouth-hooks; black, sclerotised mandibular lobes; dorsal lip with setal fringe; prothorax with a dorsal plate; anterior part of body with a pair of dorso-lateral ridges; first abdominal segment with a pair of fleshy,

dorsal projections; anal segment extended about a third to twice body length depending on species.

Biology. The larvae of this group excavate cavities in the sapwood of pines. They gain entry to the cambium through wounds and emergence holes created by bark beetles. Immersed in pine resin, the extended anal segment projects to the outside for respiration. In Europe this feeding mode is represented by *Cheilosia morio* (Tragardh, 1923; Hellrigl, 1992). A number of species are known from the USA where the feeding mode was first described (Burke, 1905).

***Chrysogaster* Meigen, 1803; *Orhonevra* Macquart, 1829 & *Lejogaster* Rondani, 1857**
(Plates 10f, 11a,b)

This group is being revised by Alain Maibach and Pierre Goeldlin de Tiefenau of the Musée Zoologique, Lausanne, Switzerland. Generic limits are changing on the basis of larval and adult characters and I am unable to include these changes as they are in the process of being published. However the group as a whole is easy to distinguish.

Overall appearance. Larva subcylindrical with internal mouth-hooks; anterior spiracles reduced or absent; dorsal surface of abdomen with rows of setae; anterior fold with pale lightly sclerotised setae, rather than dark, heavily pigmented spicules; tip of prp tapered.

Confirming characters. Mesothoracic prolegs and lateral lips enlarged, projecting well below the thorax; lower lateral margin of abdomen with a prominent ridge fringed with long setae; prolegs small with crochets weakly developed, usually absent on posterior prolegs; crochets, when present, forming a transverse row across the proleg.

Related taxa. The group is most similar to *Brachyopa* from which they are separated by the reduced or absent anterior spiracles, lack of pigmented spicules on the anterior fold and tapered prp.

Biology. Larvae of this group are aquatic being found in accumulations of decaying vegetation and mud in pools, ponds and slow-moving streams. Some species, like *C. hirtella*, have remarkably thin and pointed prp's which are adapted for piercing the air spaces of aquatic plants for respiration (Varley, 1937; Hartley, 1958).

***Chrysotoxum* Meigen, 1803**

Overall appearance. Larvae are probably pale to dark brown in colour; body coated in short unsclerotised pubescence; dorsal sensilla borne on conspicuous basal projections; prp dark in colour, nodulate basally and with dorsal spurs; spiracular openings extending down the sides of the prp; a pair of well developed anal lobes at tip of anal segment, appearing as rounded downwardly directed projections.

Confirming characters. The larval stages of this genus are poorly known and study of

additional material with doubtless reveal better distinguishing characters. The larva of *Chrysotoxum bicinctum* (L.) and the puparium of *Chrysotoxum verralli* have only been studied.

Related taxa. Similar to *Didea*, *Eupeodes* and *Leucozona* from which *Chrysotoxum* may be distinguished by the longer than broad prp and the presence of large rounded anal lobes.

Biology. The precise feeding habits of *Chrysotoxum* are unknown. Larvae seem to be associated with ants with reports of females ovipositing about nests (Rotheray and Gilbert, 1989) and puparia being found under stones close to nests (Speight, 1976). They may feed on ant-attended root aphids like *Pipizella* larvae. A larva of *C. bicinctum* was reared on pea aphids in the laboratory (J.C. Hartley, *pers. comm.*).

Cnemonon , see *Heringia*

Criorhina Meigen, 1822 (Plate 12e,f)

Overall appearance. A short-tailed, subcylindrical larva with mouth-hooks internal; dorsally prothorax with one or two large pairs of hooks on a Y or triangular-shaped hook base (Plate 12f); behind each of the anterior spiracles is a large laterally directed hook, like a pair of cow horns (Plate 12f).

Confirming characters. Other pairs of smaller hooks may also be present on the thorax (Fig. 14i); a slightly extended anal segment bearing three pairs of lappets, middle pair smallest; prolegs reduced with small pale crochets.

Related taxa. With the Y or triangular-shaped hook base on the prothorax and the "cow horns" *Criorhina* larvae are unlikely to be confused with those of any other taxon.

Biology. Larvae found in decaying heartwood of various trees, particularly *Fagus*, including old stumps where they may be deep underground in decaying roots. They also occur in rot-holes.

Dasysyrphus Enderlein, 1938 (Plate 8e,f)

Overall appearance. Sub-triangular in cross-section with serrate lateral margins and segmentally arranged mid-dorsal projections; anal segment with a pair of long tapering projections.

Confirming characters. Body with patchily distributed spicules; prp dark at base, nodulate and with dorsal spurs; colour pattern mottled brown, grey and pink, like bark.

Related taxa. Similar to *Didea*, *Erizona*, *Eupeodes* and *Paragus*. *Dasysyrphus* larvae are immediately distinguished from all these taxa by the long tapering projections of the anal

segment.

Biology. Larva are mostly arboreal on both coniferous and deciduous trees. *Dasysyrphus tricinctus* is recorded as feeding on sawfly caterpillars (Table 2) but I have found it regularly on aphid-infested *Acer pseudoplatanus* foliage.

Notes. *Dasysyrphus* larvae rest during daytime on twigs and branches where their bark-like colour pattern makes them very difficult to spot (Goeldlin, 1974; Rotheray, 1986).

***Didea* Macquart, 1834** (Plate 9f)

(includes *Megasyrphus annulipes*, see Rotheray and Gilbert (1989))

Overall appearance. Larva with serrate lateral margins and mid-dorsal projections; prp black and broader than long; spiracular plates sloping inward towards each other and dorsal spurs weakly developed.

Confirming characters. Larva large, up to 12mm long and 4mm wide; body coated in long, thin, tapering spicules; mottled brown and black, like bark.

Related taxa. Similar to *Eriozona* and *Dasysyrphus* from which *Didea* differs in having a coating of long, thin spicules and inwardly sloping spiracular plates.

Biology. Associated mostly with aphids on conifers. Also known from other arboreal aphids such as those on *Salix*.

***Doros* Meigen, 1803**

Larva unknown but descriptions of puparia are given by Speight (1988) for two European species, including *D. conopseus* which occurs in Britain. The puparia are similar to those of *Xanthogramma* from which they differ in having straight spiracular openings on the prp. *Xanthogramma* has wavy spiracular openings.

Biology. ?Associated with ants in wood (Lundbeck, 1916).

Eoseristalis, see *Eristalis*

***Epistrophe* Walker, 1852** (Plates 7f, 8a)

Overall appearance. Green dorso-ventrally flattened larva without serrate lateral margins and a pale mid-dorsal stripe; overwintering larva loses much of the green colour;

Confirming characters. Prp up to 3x as long as broad, pale in colour with dorsal spurs; body coated in dome-like papillae.

Related taxa. The flattened shape and green colouration make larvae of this genus very distinctive. *Scaeva* larvae can be green with a pale stripe but they are sub-cylindrical in cross-section.

Biology. Larva associated with aphids on trees but also occurring on shrubs and tall herbs. *Epistrophe grossulariae* (Meigen) is only known from aphids on *Acer pseudoplatanus*.

Notes. Individual larvae of *E. grossulariae* seem to have a range of emergence times. In Scotland some go over into two or even three years before emerging as adults. Variable times as a third stage larva may be more common in this group than recognised currently, perhaps accounting for swings in abundance characteristic of some species.

Epistrophella, see *Melangyna*

Episyphus Matsumura and Adachi, 1917 (Plate 5f)

Overall appearance. Oval in cross-section; translucent with short, rather shapeless, white fat bodies covering the hind gut and sometimes with conspicuous red malpighian tubules; body coated in dome-like papillae; spiracular openings black-lined.

Confirming characters. Prp about as long as broad and dorsal spurs absent; spiracular openings extending over the sides of the prp.

Related taxa. Larva most similar to *Meliscaeva*, *Syrphus* and *Melangyna cincta*. *Episyphus* differs from the latter two taxa in the position of sensilla 11 on the ventral surface of abdominal segments 1-7. In *Episyphus* this sensilla is situated on the locomotory prominence but in the other taxa it is situated just forward of each locomotory prominence. It differs from *Meliscaeva* in lacking a basal rim to the prp (view in profile, Fig. 11).

Biology. One of the most polyphagous hoverfly predators. Reared from a very wide range of ground layer and arboreal aphids.

Notes. This species migrates from southern Europe in the spring and reaches northern Europe in the summer, breeding as it goes. In the autumn it re-migrates south and overwinters as an adult. Migrants arrive in Britain in late June/July just when new colonies of summer-occurring aphids are starting to build up. It usually has one generation in Britain but, depending on conditions, a few adults overwinter here and a small spring generation may result.

Eriozona Schiner, 1860 (Plate 10a)

Overall appearance. Larva with serrate lateral margins and mid-dorsal projections; body coated in thick, black triangular-shaped spicules;

Confirming characters. Larva large, up to 15mm long and 5mm wide; prp black and broader than long; spiracular plates more or less level and dorsal spurs weakly indicated.

Related taxa. Larva similar to that of *Didea* from which it is separated by the presence of black triangular spicules and level spiracular plates.

Biology. In Czechoslovakia the larva of *Eriozona syrphoides* is known from *Picea* feeding on *Cinara* aphids (Kula, 1983).

Eristalinus Rondani, 1845

Overall appearance. A long-tailed larva (Plate 14) with internal mouth-hooks and retractile anterior spiracles; transverse row of spicules just in front, not between, the last pair of prolegs; anterior spiracles brown; prolegs with crochets in 2 main rows.

Confirming characters. Larva without a line of setae along the lower lateral margins although some setae may be present close to sensilla; last pair of prolegs with most of the large primary crochets facing the lateral margins of the body.

Related taxa. Similar to other long-tailed larvae but differs from them in the presence of a row of spicules just in front of the last pair of prolegs.

Biology. *Eristalinus sepulchralis* occurs in accumulations of decaying vegetation in ponds, pools and marshes and also in wet manure. *Eristalinus aeneus* occurs along shorelines in rock pools containing large amounts of decaying seaweed.

Eristalis Latreille, 1804, Eoseristalis Kanervo, 1938

Overall appearance. A long-tailed larva (Plate 14) with internal mouth-hooks and retractile anterior spiracles; anterior spiracles dark brown; prolegs with crochets in 3 or more rows.

Confirming characters. Larva without a line of setae along the lower lateral margins although some setae may be present close to sensilla; last pair of prolegs with most of the large primary crochets facing towards the lateral margins of the body.

Related taxa. Similar to *Myathropa* but differs from that taxa by having dark brown anterior spiracles. In *Myathropa* the anterior spiracles are pale brown. No consistent characters have been found to separate *Eoseristalis* from *Eristalis* although at the species level, good characters seem to exist, see the keys of Hartley (1961) and Doležil (1972).

Biology. Associated with wet decaying organic material, particularly accumulations of decaying vegetation in ponds and mud and farmyard manure or silage.

Eumerus Meigen, 1822 (Plate 1a)

Overall appearance. A larva with mouth-hooks, fleshy mandibular lobes and middle pair of lappets divided into two small projections.

Confirming features. Dorsal lip with a setal fringe; prp at tip of barely extended anal segment; antenno-maxillary organs on flattened, oval-shaped lobes; prolegs absent.

Related taxa. Larva most similar to *Merodon* (Plate 1b) and mycophagous *Cheilosia* (Plate 2c). *Eumerus* differs from *Merodon* in having fleshy mandibular lobes and from mycophagous *Cheilosia* in lacking an extended "ring" at the tip of the anal segment.

Biology. Larvae living in plant bulbs. They survive best when fungal decay is present (Creager and Spruijt, 1935). With mouthparts adapted to imbibing semi-liquid food, they feed probably on the products of the decay. Many larvae are usually present in each infested bulb.

Notes. Few *Eumerus* species have been reared so there may be feeding sites other than bulbs. Of the four in Britain *Eumerus strigatus* and *Eumerus tuberculatus* are known in the larval stage where they are sometimes pests of *Narcissus* bulbs (Amaryllidaceae) and are known as the "lesser bulb flies" on this account (Hodson, 1927, 1932; Hartley, 1961). *Merodon equestris* also feeds on bulbs and is known as the "large bulb fly". *Eumerus* larvae are best found by digging up bulbs in late spring. Infested bulbs are often soft because of the decayed interior. *Eumerus* larvae may inoculate and spread fungal growth through the bulb.

Eupeodes Osten Sacken, 1877 (Plate 9a-c) (= *Metasyrphus* Matsumura, 1917)

Overall appearance. Sub-cylindrical in cross-section; mottled white and brown (or sandy coloured, *Eupeodes nielseni*, Plate 9c) without mid-dorsal and lateral stripes of fat; body coated in clumps of spicules of variable sizes and colour.

Confirming features. Metathorax with a ventral row of long setae; locomotory organs consisting of 2-4 lobes each; tip of anal segment with 3 pairs of lobes; prp short with spiracular openings mounted on ridges almost reaching the base of the prp.

Related taxa. Similar to *Scaeva* from which *Eupeodes* may be distinguished by its clumps of spicules giving the integument the appearance of light and dark patches.

Biology. Most *Eupeodes* larvae are associated with conifer aphids but two of the commonest species, *Eupeodes corollae* and *Eupeodes luniger* have moved away from conifers and are found on a wide range of ground layer aphids.

Notes. *Eupeodes* and *Scaeva* larvae are adept at moving on cylindrical structures. This proficiency may have developed as a means to increase locomotive efficiency on pine needles. On other plants they specialise in catching prey on stems, raised leaf veins etc.

Fagisyrrhus, see *Melangyna*

Ferdinandea Rondani, 1844 (Plate 3b)

Overall appearance. Larva with one pair of small, inconspicuous mouth-hooks mostly inside the mouth; ventral surface of the anal segment with one transverse fold between the anal opening and the tip of the segment; abdominal segment 7 with sensilla 1-6 on fleshy, rounded papillae.

Confirming features. Ridged mandibular lobes almost all inside the mouth; dorsal lip with a setal fringe; anal segment with three pairs of equal-sized lappets; prolegs absent and the anterior fold is without spicules; prp with a mid-point constriction.

Related taxa. Larva similar to *Eumerus*, *Cheilosia* and *Rhingia*. Differs from *Eumerus* in having three pairs of lappets. Differs from *Cheilosia* in having internalised mandibular lobes and one fold between the anal opening and the tip of the segment and from *Rhingia* in having fleshy rounded papillae supporting sensilla 1-6 on abdominal segment 7. In *Rhingia* these sensilla are supported on black, stick-like papillae.

Biology. Larvae found in sap-runs on deciduous trees, particularly *Quercus*. Also found in sap-runs associated with caterpillar of the Goat Moth, *C. cossus*. Larvae often numerous when present. They are adept at manoeuvring themselves into small spaces under the bark and remaining hidden deep within the sap. Barrel-shaped puparia, by contrast, are easy to find in crevices and under pieces of loose bark near the sap run.

Notes. Of the two British species the larva of *Ferdinandea cuprea* is the better known (Hartley, 1961; Dušek and Láška, 1988). *Ferdinandea ruficornis* has been reared from a *Cossus* sap run on *Populus* (Lundbeck, 1916) but the larva is undescribed.

Hammerschmidtia Schummel, 1834 (Plate 10e)

Overall appearance. Mouth-hooks and mandibular lobes internal; sides of body with gradually elongating projections; somewhat dorso-ventrally flattened; prp long and narrow and base coated in nodules; anterior fold coated in numerous spicules; abdominal segments 2-7 coated in setae.

Confirming characters. Prolegs not well developed and a few crochets may or may not be discernable; in dorsal view anal segment with two tapering rings with two pairs of lappets on the first and one pair on the second.

Related taxa. Larva most similar to *Brachyopa* and *Chrysogaster*. *Hammerschmidtia* is separated from *Brachyopa* in that it is coated completely in setae and sensilla one of abdominal segments 2-7 is separated from sensilla two by an integumental groove such that sensilla one is anterior to two. *Hammerschmidtia* differs from *Chrysogaster* in that it has a band of sclerotised spicules on the anterior fold and well developed anterior spiracles.

Anterior spiracles are reduced or absent in *Chrysogaster*.

Biology. Larvae either occur in sap runs or, more frequently, in accumulations of decaying sap under bark of fallen *Populus tremula* (Rotheray, 1991).

Helophilus Meigen, 1822 (Plate 14d)

Overall appearance. A long-tailed larva with internal mouth-hooks and retractile anterior spiracles; anterior spiracles pale brown; anal segment in the region before the narrow "tail" with three pairs of ventro-lateral fleshy projections; prolegs with crochets in 3 or more rows.

Confirming characters. Larva without a line of setae along the lower lateral margins although some setae may be present close to sensilla; last pair of prolegs with most of the large primary crochets facing towards the front of the body.

Related taxa. Similar to other long-tailed larvae but differs from them by having 3 pairs of fleshy projections behind the anal opening.

Biology. Associated with wet decaying organic material, particularly accumulations of decaying vegetation in ponds and mud and farmyard manure or silage.

Heringia Rondani, 1856 (Plate 5c)

(includes *Cnemodon* Egger, 1865 and *Neocnemodon* Geoffe, 1944, see Rotheray and Gilbert, 1989) (Plate 5c)

Overall appearance. Tip of the anal segment with a pair of rounded projections; body coated in round-tipped papillae; larva brown.

Confirming characters. Spiracular openings not extending over the sides of the prp; prp lacking dorsal spurs; inter-spiracular setae long and conspicuous (more than half the length of a spiracular opening).

Related taxa. Similar to *Pipiza* but differs in not having the body coated in pubescence. The short prp (less than 2x long as broad) of the larva of *Triglyphus primus* distinguishes it from *Heringia* where the prp is 2-6x long as broad.

Biology. Associated with *Schizoneura* aphids on *Ulmus* and *Pemphigus* aphids on *Populus* (Dušek and Křístek, 1959), *Dreyfusia piceae* on *Abies* (Delucchi *et al.*, 1957) and *Eriosoma lanigerum* on *Malus*.

Lejogaster, see *Chrysogaster*

Leucozона Schiner, 1860 (Plate 8c,d)

Overall appearance. Larva with flattened lateral margins giving the body a sub-triangular cross-section; lateral margins smooth, not serrate; larva translucent with white or cream chevrons and stripes;

Confirming characters. Prp about as long as broad with dorsal spurs and pale brown in colour.

Related taxa. Similar to *Syrphus* from which it differs in having a prp which is about as broad as long (broader in *Syrphus*) and *Chrysotoxum* from which it differs probably in colour pattern.

Biology. *Leucozона lucorum* is known from arboreal and ground layer aphids. *Leucozона (Ischyrosyrphus) laternaria* is associated with *Caveriella* aphids on umbellifers. *Leucozона (Ischyrosyrphus) glauca* is associated with ground layer aphids (Dušek and Láška, 1962).

Mallota Meigen, 1822 (Plate 14b)

Overall appearance. A long-tailed larva with retractile anterior spiracles; abdominal segments 2-7 with sensilla 4-6 all in a row (Fig. 17); abdomen smooth without a coating of setae.

Confirming characters. Lateral margins of abdominal segment 7 just before the "tail" with three, short, fleshy projections (view from above); mandibles and mandibular lobes internal.

Related taxa. Distinguished from other long-tailed larvae by the smooth integument and abdominal segments 2-7 with sensilla 4-6 all in a row.

Biology. Found in rot-holes of various deciduous trees. Several larvae often found together in rot-holes small and large, low and high on trees.

Megasyrphus, see *Didea*

Melangyna Verrall, 1901 (Plates 6d-f,7a,b) (includes *Fagisyrphus*, see Rotheray and Gilbert, 1989)

Overall appearance. Larva with flattened lateral margins giving the body a sub-triangular cross-section; lateral margins smooth, not serrate; larvae with various species-specific colour patterns involving particularly chevrons and rectangular blocks, see Plates 6d-f,7a,b).

Confirming characters. Prp up to twice as long as broad, matt at base, shining at tip; spiracular openings mostly black-lined and about half their length extending over the side of the prp; *Melangyna umbellatarum* may have extensive brown markings along the posterior

dorsal margins in addition to being white as in Plate 7b.

Related taxa. Most similar to *Parasyrphus* from which the species-specific colour patterns distinguish *Melangyna* species.

Biology. Larvae appear to have clear preferences for particular aphids - *Melangyna arctica* from *Pterocallis ulnii* on *Alnus*; *Melangyna cincta* from *Phyllaphis fagi* on *Fagus* (and isolated records from aphids on *Quercus*, *Acer* and *Tilia*; *Melangyna quadrimaculata* from adelgids on *Abies*; *Melangyna umbellatarum* from *Cavariella* aphids on umbellifers.

Melanostoma Schiner, 1860

Overall appearance. Larva oval in cross-section; shining translucent green like *Xanthandrus comtus* (Plate 4b); dorsal sensilla on slightly raised, dome-shaped papillae lacking apical setae.

Confirming characters. Prp broader than long and without dorsal spurs; spiracular openings not extending over the sides of the prp.

Related taxa. Similar to *Xanthandrus*, *Platycheirus* and *Sphaerophoria*. It differs from larvae of the latter two genera in lacking apical setae to the dorsal sensilla and from *Xanthandrus* in lacking posterior projections to the prp (Fig. 7).

Biology. Larvae are sometimes encountered in leaf litter and ground layer aphid colonies, but feeding habits are uncertain.

Notes. One of the biggest gaps in knowledge is the feeding habits of *Melanostoma* larvae. In the laboratory they readily accept a wide range of aphids but, in the field, larvae are practically absent from aphid colonies which is curious for such abundant species. A possible feeding site is leaf litter where they could be generalised predators. Systematic study in the field is necessary to solve the problem.

Meligramma Frey, 1946 (Plate 8b) (includes *Epistrophella*, see Rotheray and Gilbert, 1989)

Overall appearance. Larva dorso-ventrally flattened in cross-section with serrate lateral margins; prp dark in colour and heavily nodulated; dorsal spurs present except in *Meligramma euchroma*.

Confirming characters. Species-specific colour patterns, orange and white (*M. euchroma*), black (*Meligramma guttata*) and white pinkish-brown and black, like a bird dropping (*Meligramma triangulifera*, Plate 8b).

Related taxa. Similar to *Melangyna* and *Didea*. *Meligramma* differs from the former genus in having serrate margins and from the latter genus in not having inwardly sloping spiracular plates.

Biology. *Meligramma guttata* has only been reared from aphids on *Acer pseudoplatanus* (Dixon, 1960; F. Gilbert, pers. comm.). The other two British species are known from a range of aphids particularly on fruit trees and shrubs.

Meliscaeva Frey, 1946

Overall appearance. Oval in cross-section; translucent with short, rather shapeless accumulations of white fat bodies covering the hind gut (*Meliscaeva auricollis*) or translucent yellowish brown (*Meliscaeva cincitella*).

Confirming characters. Body coated in dome-like papillae; prp with dorsal spurs even if small; spiracular openings black-lined and extending over the sides of the prp.

Related taxa. Similar to *Episyrphus*, *Syrphus* and *Melangyna cincta*. *Meliscaeva* differs from the latter two taxa in the position of sensilla 11 on the ventral surface of abdominal segments 1-7. In *Meliscaeva* this sensilla is situated on the locomotory prominence but in *Syrphus* and *Melangyna* it is situated just forward of each locomotory prominence. It differs from *Episyrphus* in having a basal rim to the prp (view in profile, Fig. 11). The prp of *M. cincitella* is unique in that it slopes away posteriorly which makes it easy to recognise (Fig. 13).

Biology. *Meliscaeva auricollis* can be found among aphid colonies on shrubs such as *Berberis* and *Sarothamnus* (Dixon, 1960) and aphids on flowers and stems of umbellifers; it is also known from the psyllid, *Pyslla alni* on *Alnus glutinosa*. *Meliscaeva cincitella* is known from arboreal aphids on various trees such as *Quercus*, *Picea*, *Pinus*, *Malus* and *Sambucus*.

Merodon Meigen, 1803 (Plate 1b)

Overall appearance. Larva with mouth-hooks; black, sclerotised mandibular lobes and middle pair of lappets divided into two small projections.

Confirming characters. Dorsal lip smooth, lacking setae; tip of anal segment angled obliquely towards head (view in profile); prolegs absent and anterior fold without spicules.

Related taxa. Larva most similar to *Eumerus* (Plate 1a) and *Cheilisia* (Plates 1 e, f & 2). *Merodon* differs from *Eumerus* in having black sclerotised mandibular lobes and from *Cheilisia* in having an anal segment with middle pair of lappets divided into two small projections.

Biology. Living in plant bulbs. Apart from *Narcissus*, *Merodon equestris*, the only British species in the genus, attacks a variety of plants in gardens including *Hippeastrum*, *Amaryllis*, *Haemanthus*, *Sprekelia*, *Hymenocallis*, *Brunsvigia*, *Eucharis*, *Cyrtanthus*, *Nerine*, *Crinum*, *Vallota*, *Leucorum*, *Eurycles*, *Glanthus* (Amaryllidaceae) *Lachenalia*, *Cardiocrinum*, *Scilla*, *Galtonia*, *Hyacinth* (Liliaceae) and *Kaempferia* (Zingiberaceae) (A.J. Halstead, pers. comm.).

It has also been recorded from *Habranthus* (Amaryllidaceae) (Chittenden, 1911). It can be a pest and is known to horticulturalists as the "large bulb fly".

Notes. Of the many *Merodon* species occurring in Europe few have been reared. *Merodon equestris* is most easily found by digging up bulbs in late spring. Infested bulbs are often soft because of the hollowed interior.

Metasyrphus, see *Eupeodes*

Microdon Meigen, 1803 (Plate 3c-e)

Overall appearance. Perhaps the most distinctive syrphid larva despite having been identified as a mollusc during the 19th century! The hemispherical shape in cross-section and marginal band of setae are characteristic.

Confirming characters. Gap in marginal bands of setae at front end of body; prothorax and mesothorax elongate, narrow and retracted into the metathorax on the ventral surface and are not seen unless the larva is moving when they project through the gap in the middle of anterior margin of the metathorax (place the larva on a sheet of glass and view from beneath); antenno-maxillary organs sharply pointed; prolegs absent.

Related taxa. Similar to predatory larvae and *Volucella* but the hemispherical shape and marginal bands of setae distinguish *Microdon* from these taxa.

Biology. Donisthorpe (1927) suggests, in his authoritative book, that *Microdon* larvae feed on solid pellets ejected from the hypopharyngeal pockets of ants. It is now clear, however, that nearctic *Microdon* larvae are predators of ant pupae (Duffield, 1981; Garnett *et al.*, 1985). Predation of ant pupae has also been observed in *M. eggeri* (G.E. Rotheray, unpublished observations and *M. mutabilis* (Boyd Barr *pers. comm.*). The likelihood of this being true of other European species is high but needs confirming.

Notes. The very distinctive features of *Microdon* larvae are probably adaptations to prevent the larva from being bitten by ants. *Microdon mutabilis* is distinguished from other British species in having the reticulate pattern of setae confined to a wide band round the margin (Plate 3e). In the two other British species the entire upper surface is coated in a reticulate arrangement of setae. *Microdon devius* can be distinguished from *M. eggeri* in having a denser coating of setae such that the reticulate pattern consists of cells as large as, or larger, than the diameter of the prp (compare Plate 3c with 3d) and the ventral surface is coated with fine setae.

Microdon mutabilis, the most widespread species, is known from a variety of ant species often, but not exclusively, associated with wet, boggy habitats eg *Formica lemani*, *Formica fusca*, *Lasius niger* and *Myrmica ruginodis*. The larva of *Microdon eggeri* is usually found in association with *Lasius niger* and *Formica rufa* ants under bark of well decayed *Betula* and

Pinus stumps and logs. This species appears to have a disjunct distribution occurring in Scotland and southern Britain and also Ireland (Stubbs and Falk, 1983). *Microdon devius*, the rarest of the three species, is associated with *Lasius flavus* ants on chalk grassland in England.

***Milesia* Latreille, 1804** (Plate 13a) [not British]

Overall appearance. A short-tailed larva with mouth-hooks and mandibular lobes internal; prolegs with crochets well developed; thorax with two large groups of hooks either side of the anterior spiracles (Fig. 14g); hooks in the first group in 3 or more rows with a smaller group of two main hooks separated and below.

Confirming characters. Anterior fold coated in a narrow band of 4-5 rows of spicules, those in the middle rows the largest; one pair of lappets at the tip of the anal segment, first two pairs close to each other and reduced to slight bulges.

Related taxa. Similar to other hook-bearing taxa but differs from them in having hooks arranged in three rows in the first group either side of the anterior spiracles.

Biology. Larva found in decaying heartwood of deciduous trees, including rot-holes.

Notes. In the absence of European material, the above description is based on an American species, *Milesia virginensis*. The similarity in characters between species in other genera with European and American representatives suggests that European species are unlikely to differ very much from congeners in America.

***Myathropa* Rondani, 1845** (Plate 14f)

Overall appearance. A long-tailed larva with internal mouth-hooks and retractile anterior spiracles; anterior spiracles pale brown; prolegs with crochets in 2 rows.

Confirming characters. Larva without a line of setae along the lower lateral margins although some setae may be present close to sensilla; last pair of prolegs with most of the large primary crochets facing towards the lateral margins of the body.

Related taxa. Similar to *Eristalis* but differs from that taxa by having pale brown anterior spiracles. In *Eristalis* the anterior spiracles are dark brown.

Biology. Associated with wet decaying vegetation in rot-holes and in decaying heartwood of a wide variety of trees. Also occurs deep underground in decaying tree roots. Occurs in all main microhabitats associated with wet decay in trees from sap-runs to rot-holes. Often the most common species encountered in rot-holes and decaying heartwood.

Myolepta Newman, 1838 (Plate 13f)

Overall appearance. Larva 15 to 17mm long, sub-cylindrical in cross-section with a narrow extended anal segment about half body length; mouth-hooks internal; anterior fold without sclerotised spicules; body coated in fine setae except for segment 7 and anal segment which are coated in papillae at the tip of which are tufts of setae (Fig. 16).

Confirming characters. Prolegs small with 7 or 8 primary crochets some of which increasingly face out to the lateral margins of the body towards the posterior end; anal segment with 3 pairs of equidistant lappets.

Related taxa. Similar to *Pocota*, *Lejota* and *Caliprobola*. It differs from all these taxa in lacking a spicule band on the anterior fold of the prothorax and having the abdominal segment 7 and the anal segment coated in papillae bearing tufts of setae.

Biology. Larvae in rot-holes of deciduous trees.

Neoascia Williston, 1886 (Plate 11c)

Overall appearance. Larva small, up to 6mm long, dorso-ventrally flattened with an extended anal segment; mouth-hooks internal; anterior fold coated with spicules; dorsally prothorax with a pair of large, backwardly directed hooks.

Confirming characters. Prolegs small with 4 or 5 main crochets; anal segment with 3 pairs of lappets but the first pair of lappets, at the base of the "tail", divided into two at the tip like the letter "Y".

Related taxa. Similar to *Chrysogaster*, *Sphegina* and *Syrriua*. It differs from all these genera in possessing a pair of large hooks on the prothorax.

Biology. The few breeding records are from wet manure in farmyards and from decaying vegetation round the margins of ponds.

Neocnemodon, see *Heringia*

Orthonevra, see *Chrysogaster*

Paragus Latreille, 1804 (Plate 9e: the larva illustrated is a preserved specimen; in life it would have been much paler and mottled, like Plate 9a)

Overall appearance. Larva small, up to 8mm long; oval in cross-section but flattened posteriorly; mottled white and brown; dorsal sensilla borne on fleshy projections; a row of 4 setae on fleshy projections on the anal segment behind the prp (Fig. 8).

Confirming characters. Prp up to twice as long as broad with tall, prominent dorsal spurs; spiracular openings short not extending over the sides of the prp and mounted on tall, dark ridges; ventral surface with sensilla 11 on a separate fold anterior to the locomotory prominences.

Related taxa. Similar to *Dasysyrphus*, *Didea*, *Scaeva* and *Eupeodes*. It differs from these taxa in having a row of 4 setae on fleshy projections behind the prp on the anal segment.

Biology. Known from a range of ground layer and arboreal aphids. *Paragus* (*Pandasyopthalmus*) *haemorrhous* has been known to breed in urban areas (John Dobson, pers. comm.).

Parasyrphus Matsumura, 1917 (Plate 7c-e)

Overall appearance. Body hemispherical in cross-section and narrow with either longitudinal stripes (Plate 7d,e) or chevrons (Plate 7c, *Parasyrphus nigratarsis*).

Confirming characters. Prp up to 3x as long as broad with dorsal spurs, nodulate in basal half and usually pale brown.

Related taxa. Those species with longitudinal stripes are superficially similar to *Baccha* and *Platycheirus* but differ from such genera in having a longer than broad prp with dorsal spurs. *Parasyrphus nigratarsis* resembles *Syrphus* but differs in having a longer than broad, nodulated prp.

Biology. Larvae are mostly arboreal on adelgids and pine aphids. *Parasyrphus punctulatus* has a wider prey range including aphids on *Rosa* spp. and *Fagus*. *Parasyrphus nigratarsis* feeds exclusively on eggs, larvae and pupae of leaf beetles (Chrysomelidae) associated with *Alnus* and *Salix* (Schneider, 1953).

Parhelophilus Girschner, 1897

Overall appearance. A long-tailed larva with internal mouth-hooks and retractile anterior spiracles; anterior spiracles pale brown; anal segment in the region before the narrow "tail" without three pairs of ventro-lateral fleshy projections; prolegs with crochets in 3 or more rows.

Confirming characters. Larva without a line of setae along the lower lateral margins although some setae may be present close to sensilla; last pair of prolegs with most of the large primary crochets facing towards the front of the body.

Related taxa. Similar to other long-tailed larvae but differs from them in having most of the primary crochets of the last pair of prolegs facing forwards and lacking a line of setae along the lower lateral margins and lacking 3 pairs of fleshy projections behind the anal opening.

Biology. Associated with accumulations of decaying vegetation, particularly *Typha*, in ponds and slow-moving streams.

***Pipiza* Fallén, 1810** (Plate 5a,b)

Overall appearance. Tip of the anal segment with a pair of rounded projections; body coated in unsclerotised pubescence; spiracular openings not extending over the sides of the prp; prp lacking dorsal spurs.

Confirming characters. Inter-spiracular setae long and conspicuous (more than half the length of a spiracular opening); larva green or brown, sometimes with an underlying pale fat body (Plate 5a).

Related taxa. Similar to *Heringia* and *Trichopsomyia*. *Pipiza* differs from *Heringia* in having the body coated in pubescence rather than round-tipped papillae. *Pipiza* differs from *Trichopsomyia* in colour pattern. *Trichopsomyia flavitarsis* (the only species studied) is translucent creamy-white in colour. *Pipiza* species are either green or dark brown.

Biology. *Pipiza austriaca* has been reared from *Caveriella* aphids on *Heracleum sphondylium* (Umbelliferaceae). *Pipiza noctiluca* has also been reared from this aphid and from a range of ground-layer and arboreal aphids. *Pipiza festiva* (not British) is associated with *Pemphigus* aphids on *Populus* (Dušek and Křístek, 1959). *Pipiza luteitarsis* has been reared from *Schizoneura* aphids which curl *Ulmus* leaves (Rotheray, 1987).

Notes. The larva of *Triglyphus primus* is similar to *Pipiza* but has not been studied by me. It appears to be specific to galls induced by the aphid, *Cryptosiphum artemisiae*, on *Artemisia vulgaris* (Leclercq, 1944; Sedlag, 1967).

***Pipizella* Rondani, 1856**

Overall appearance. (Only *Pipizella viduata* (= *varipes*) examined). Larva flattened in cross-section with the rounded projections at the tip of the anal segment short and inconspicuous; body coated in round-tipped pubescence.

Confirming characters. Dorsal sensilla borne on club-tipped papillae; prp lacking dorsal spurs; inter-spiracular setae long and conspicuous (more than half the length of a spiracular opening); larva dark brown.

Related taxa. Similar to *Pipiza* and *Trichopsomyia* but *Pipizella* differs from these taxa in being flattened with very short rounded projections at the tip of the anal segment.

Biology. Associated with root-feeding aphids on umbelliferous plants (Heeger, 1858; Dixon, 1959).

Platycheirus Lepeletier and Serville, 1828 (Plate 4c-f)

(includes *Pyrophaena* Schiner under which it is synonymised: Vockeroth, 1990)

Overall appearance. Sub-rectangular in cross-section with a thin, sometimes interrupted, line of fat along either side of the upper and lower lateral margins; prp broader than long and without dorsal spurs; spiracular openings not extending over the sides of the prp.

Confirming characters. Various coloured larvae, usually mottled cream and pale brown except *P. scutatus* (Meigen) which is green sometimes with a purplish tinge but turning brown in diapause; larva "spotty" with particles of fat; dorsal sensilla with an apical seta; abdominal segments with sensilla 11 on the locomotory prominences, not anterior to them and separated from them by a groove.

Related taxa. Similar to *Baccha* from which it differs in that the mid-dorsal lines of fat always meet together at the anterior end of the larva (Plate 4c). In *Baccha* (Plate 5d) one line always extends further forward than the other.

Biology. A range of feeding strategies occur in this diverse genus from generalised predators to those specialised to feed on one or two aphids. Most species feed within the ground layer. Like *Melanostoma* the adults of such species as *Platycheirus albimanus*, *Platycheirus clypeatus* and *Platycheirus granditarsa* are common but larvae are rare at aphid colonies. They may be generalised predators in the leaf litter but this needs investigation. *Platycheirus manicatus* and *Platycheirus peltatus* may accept a wide range of aphids within the shaded, moist sites gravid females seem to prefer. *Platycheirus scutatus* is, possibly the most polyphagous aphid predator in the genus. Specialists include *Platycheirus fulviventris* feeding on *Hyalopterus pruni* on monocotyledonous plants in wetlands (Rotheray and Dodson, 1987), *Platycheirus immarginatus* (Zetterstedt) and *Platycheirus perpallidus* on *Trichocallis cyperi* aphids associated with *Carex* (Cyperaceae) also in wetlands.

Notes. Two groups of larvae occur in this genus based on the arrangement of the mid-dorsal fat bodies. Those species such as *P. fulviventris* (Plate 4c) have broad, longitudinal lines of fat running down the centre of the larva with inconspicuous chevrons. Others, like *P. scutatus* (Plate 4e) have conspicuous chevrons lacking longitudinal lines of fat. A great deal more needs to be discovered about the larval biology of *Platycheirus* species and there is considerable potential for comparing species having different feeding strategies. One of the biggest gaps in knowledge is the feeding habits of common species like *P. albimanus* and *P. clypeatus*.

Pocota Lepeletier and Serville, 1828 (Plate 12c)

Overall appearance. A short-tailed, subcylindrical larva with internal mouth-hooks; extended part of anal segment broad, not much less than half body width; thorax lacking hooks although spicules may be present.

Confirming characters. Spicule band occupying more than 50% of the anterior fold; body coated in fine setae; prolegs small with 7 or 8 primary crochets; anal segment with 3 pairs

of equidistant lappets, third pair at tip the longest, first two pairs on short, inconspicuous projections.

Related taxa. Similar to *Xylota* and *Myolepta*. *Pocota* differs from *Xylota* in having one pair of long lappets on the anal segment, all 3 pairs are long in *Xylota*. *Pocota* differs from *Myolepta* in having a spicule band on the anterior fold.

Portevinia Goffe, 1944 (Plate 1c,d)

Overall appearance. Larva with mouth-hooks; black, sclerotised mandibular lobes; a flattened posterior end and anal opening parallel to the longitudinal axis of the body.

Confirming characters. Dorsal lip smooth, lacking setae; flattened posterior end with tufts of setae round its raised margin; prolegs absent and anterior fold without spicules.

Related taxa. Larva most similar to *Merodon* and *Cheilosia*. It differs from both these genera by the longitudinal anal opening. *Cheilosia albitarsis* (Plate 1e), *Cheilosia antiqua* (Plate 1f) and *Merodon equestris* (Plate 1b) also possess a flattened posterior end although not as extreme as *Portevinia*.

Biology. Living in plant bulbs. The larvae of the only British species, *Portevinia maculata*, tunnels the bulbs of *Allium ursinum* (Liliaceae) (Speight, 1986; Rotheray, 1991). The best time to find them is to dig up the cigar-shaped bulbs from January to early March. It is at this time of year that larvae are actively growing and developing.

Rhingia Scopoli, 1763 (Plate 3a)

Overall appearance. Three pairs of black, stick-like lappets present; abdominal segments 6-8 with dorsal sensilla 1-6 on long black, stick-like papillae; one pair of small, inconspicuous mouth-hooks which do not protrude from the mouth; ridged mandibular lobes internal, on either side of the mouth.

Confirming characters. Dorsal lip with a setal fringe; body coated conspicuously in stiff, upright pubescence; ventral surface of the anal segment with one fold between the anal opening and the tip of the segment; prolegs are absent and the anterior fold is without spicules.

Related taxa. Similar to *Cheilosia* and *Ferdinandea*, differs from both in having black, stick-like papillae at the posterior end of the body.

Biology. The only larva known is that of *Rhingia campestris*. Larvae of this species were found in cow dung by Coe (1942) who also gives details of its biology.

Notes. Adult *Rhingia campestris* are often seen far away from cattle raising the possibility that larvae develop in the dung of other species or even in material such as wet, compost.

Within cow dung the larva of *R. campestris* is well camouflaged being coated in fragments of dung (Coe, 1942).

Scaeva Fabricius, 1805 (Plate 9d)

Overall appearance. Sub-cylindrical in cross-section; green, brown or pink with broad mid-dorsal and thin lateral stripes; body evenly and sparsely coated in spicules of uniform size and colour; prp short with spiracular openings mounted on ridges almost down to the base of the prp.

Confirming characters. Metathorax with a ventral row of long setae; locomotory organs in front of anal opening consisting of four lobes each; tip of anal segment with 3 pairs of lobes.

Related taxa. Similar to *Eupeodes* from which *Scaeva* is distinguished by its even, rather than aggregated, coating of spicules and the broad mid-dorsal white stripe. It is distinguishable from other green coloured larvae by the short prp with spiracular openings almost down to its base.

Biology. *Scaeva pyrastris* is found on a wide range of ground layer and, less frequently, arboreal aphids. *Scaeva selentica* is associated with pine aphids.

Sericomyia Meigen, 1803. (Plate 14a)

Overall appearance. A long-tailed larva with short, non-retractile, dark brown anterior spiracles; prolegs small and weakly developed; thorax large, conspicuously broader than the abdomen (view from above).

Confirming characters. Dorsum of prothorax with 3 pairs of longitudinal grooves; dorsal lip without setae; body coated sparsely in pubescence.

Related taxa. Distinguished from other long-tailed larvae by the presence of non-retractile anterior spiracles and the small prolegs.

Biology. Larvae associated with peaty pools in moorland habitats (Bloomfield, 1897; Hartley, 1961).

Sphaerophoria Lepeletier and Serville, 1828 (Plate 5e)

Overall appearance. Oval in cross-section; bright green with pale, dorsal stripes; prp usually longer than broad and without dorsal spurs; spiracular openings not extending over the sides of the prp.

Confirming characters. Body coated in dome-like papillae; abdominal segments with

sensilla 11 on the locomotory prominences, not anterior to them and separated from them by a groove; dorsal sensilla with an apical seta.

Related taxa. Similar to *Melanostoma*, *Xanthandrus* and green coloured *Pipiza*. It differs from the former two genera in having dorsal sensilla with apical setae and from the latter in lacking a pair of rounded projections at the tip of the anal segment.

Biology. Associated with a range of ground layer aphids.

Sphegina Meigen, 1822 (Plate 11d)

Overall appearance. A short-tailed larva between 6 and 8 mm long; dorso-ventrally flattened; mouth-hooks internal; prothorax without a pair of large, backwardly directed hooks; anal segment with first pair of lappets at base of extended part of anal segment, divided at tip.

Confirming characters. Profegs small with 4 or 5 primary crochets; lateral sensilla on projections which become longer towards the end of the body; anterior fold coated with spicules.

Related taxa. Larva most similar to *Neoascia* and *Syritta*. It differs from *Neoascia* in lacking a pair of large hooks on the prothorax and from *Syritta* in being dorso-ventrally flattened with an extended anal segment.

Biology. Larvae found in accumulations of decaying sap under bark, usually in wet situations such as damp, shaded woodland and in partially submerged wood in streams and pools. *Sphegina clunipes* has also been recorded from sap runs.

Spilomyia Meigen, 1803 [not British]

Overall appearance. A short-tailed larva with mouth-hooks and mandibular lobes internal; profegs with crochets well developed; thorax with four groups of hooks, one group in an antero-dorsal position on the prothorax, second group in front of the anterior spiracles, third group below and lateral to the anterior spiracles and fourth group below the third (Fig. 14h).

Confirming characters. Anterior fold coated in a narrow band of 4-5 rows of spicules, those in the middle rows the largest; one pair of lappets at the tip of the anal segment, first two pairs close to each other and reduced to slight bulges.

Related taxa. Similar to other hook-bearing taxa but differs from them in having four groups of hooks.

Biology. Larva found in decaying heartwood of deciduous trees, including rot-holes.

Notes. In the absence of European material, the above description is based on four

American species. The similarity in characters between species in other genera with European and American representatives suggests that European species are unlikely to differ very much from congeners in America.

Syritta Lepelletier and Serville, 1828 (Plate 11e)

Overall appearance. A short-tailed, subcylindrical larva about 12mm long; mouth-hooks internal; anterior fold coated with evenly spaced spicules about as long as setae on the dorsal surface of the body; prothorax without a pair of large, backwardly directed hooks.

Confirming characters. Prolegs small with 5 or 6 primary crochets arranged as a transverse row across the segment; anal segment with 3 pairs of lappets, first two pairs equal in length, third pair at tip longest.

Related taxa. Similar to *Sphegina* and *Xylota*. *Syritta* differs from *Sphegina* in having a shorter anal segment (compare Plate 11 d with e) and an undivided first pair of lappets. It differs from *Xylota* in having evenly sized spicules on the anterior fold of the prothorax and having crochets arranged as transverse rows across the body. In *Xylota* the crochets are in curved rows and the spicules on the anterior fold vary in size.

Biology. Larva found in various kinds of wet, decaying matter including, compost, manure and silage but not in pools and ponds.

Syrphus Fabricius, 1775 (Plate 6a-c)

Overall appearance. Oval in cross-section anteriorly, broadening posteriorly; translucent with white (Plate 6a), red and yellow (Plate 6b) or brown (Plate 6c) chevrons; prp broader than long with dorsal spurs.

Confirming characters. Abdominal segments with sensilla 11 anterior to, and separated from the locomotory prominence by a groove; tip of anal segment with three pairs of lobes; spiracular openings more than 6x as long as broad with about half their length extending over the side of the prp and sometimes black-lined.

Related taxa. Similar to *Episyrphus*, *Meliscaeva* and *Melangyna cincta* (Fallén) from which *Syrphus* differs by having a prp that is broader than long with about half the length of the spiracular openings extending down its sides.

Biology. Associated with a wide range of ground layer and arboreal aphids.

Notes. *Syrphus ribesii* is often very abundant at aphid colonies. From November to April overwintering larvae of all three British species are readily found in leaf litter beneath previously aphid-infested *Acer pseudoplatanus* trees. The larvae of individual species are very similar but can be separated though a key provided by Dušek and Láška (1964).

***Temnostoma* Lepeletier and Serville, 1828** (Plate 13c,d)

[not British]

Overall appearance. Larva sub-cylindrical in cross-section; contracted at both anterior and posterior ends (Plate 13c); mouth-hooks internal; extreme modifications to the thorax with metathorax and mesothorax partially fused and both enlarged; prothorax narrow and all three thoracic segments directed ventrally; lateral to each of the anterior spiracles is a large oval-shaped hook base bearing rows of hooks (Plate 13d).

Confirming characters. Prolegs reduced and crochets absent; anal segment contracted to form an anal plate with a large prp at its centre.

Related taxa. With its contracted shape, modified thorax, huge hooks and absence of crochets *Temnostoma* larvae are quite unlike those of any other hook-bearing taxon.

Biology. Larvae burrow in moist decayed wood using their hooks as rasping organs operated in a forwards and backwards motion by huge muscles housed in the mesothorax and metathorax. *Temnostoma* larvae have been found in fallen *Alnus* or *Betula* logs, more than 10cm in diameter, lying in wet, boggy conditions. The larvae tunnel from the lower part of the log forming circular tunnels running at right-angles to the grain of the wood.

***Trichopsomyia* Williston, 1888**

Overall appearance. Tip of the anal segment with a pair of rounded projections; colour pattern translucent creamy-white; spiracular openings not extending over the sides of the prp; prp lacking dorsal spurs.

Confirming characters. Inter-spiracular setae long and conspicuous (more than half the length of a spiracular opening); body coated in unsclerotised pubescence.

Related taxa. Similar to *Heringia*, *Pipiza* and *Pipizella*. *Trichopsomyia* can be readily distinguished from these taxa by its pale colour pattern.

Biology. Predator of the psyllid, *Livia juncorum* in the galls this psyllid forms on *Juncus articulatus* (Juncaceae).

***Tropidia* Meigen, 1822**

Overall appearance. Larva up to 15mm long, sub-cylindrical with a slightly extended anal segment, like *X. segnis*, Plate 11f; mouth-hooks internal; anterior fold coated in spicules of various sizes and these extending on to the prothorax and lateral and dorsal margins of the mesothorax (Fig. 14b).

Confirming characters. Prolegs small with 5 or 6 crochets; anal segment with 3 pairs of lappets.

Related taxa. Similar to *Xylota* from which it differs in having a row of spicules on the antero-dorsal margin of the mesothorax just behind and between the anterior spiracles.

Biology. Larva are probably in accumulations of decaying vegetation and mud at the margins of ponds and ditches but this needs confirmation (Decler and Rotheray, 1991).

Volucella Geoffroy, 1762 (Plates 3f;4a)

Overall appearance. Mouth-hooks and mandibular lobes internal; prothorax narrow with a few, large sclerotised spicules on the anterior fold; prolegs with crochets arranged in a transverse row present on the mesothorax and the first six abdominal segments.

Confirming characters. There are two main morphological groups within *Volucella*. The first, containing all the British species except *V. inanis*, is characterised, in addition to the characters noted above, by having very long crochets which are longer than the prolegs; transverse rows of setae on the dorsal aspect of the abdomen and lateral margins with long tapering projections (Plate 3f). The second group, containing *V. inanis*, is characterised by dorso-ventral flattening; a smooth body surface lacking transverse rows of setae and lateral projections (Plate 4a).

Related taxa. Similar to *Brachyopa*, *Hammerschmidia* and to the predacious larvae from which it differs in having well developed prolegs with long crochets.

Biology. Except for *Volucella inflata*, *Volucella* larvae are found in vespine (social wasp) nests. Most species are predator/scavengers of vespine larvae and pupae. The long crochets are probably an adaptation to move upsidedown across wasp combs. *Volucella inanis* has gone one step further and is an ectoparasite of vespine larvae (Rupp, 1989). The larva of *V. inflata* has been found in a sap run on *Quercus* (Miles, pers. comm.). The larva is undescribed and whether it feeds on the material of the sap run or is a predator of other insect larvae within the sap run is unknown.

Xanthandrus Verrall, 1901 (Plate 4b)

Overall appearance. Larva shining translucent green; dorsal sensilla on slightly raised, dome-shaped papillae lacking apical setae; prp with a posterior projection just below the tip (Fig. 7).

Confirming characters. Spiracular openings not extending over the sides of the prp; larva oval in cross-section; prp broader than long, without dorsal spurs.

Related taxa. Similar to *Melanostoma*, *Platycheirus* and *Sphaerophoria*. It differs from larvae of the latter two genera in lacking apical setae to the dorsal sensilla and from the former genus in possessing posterior projections to the prp.

Biology. A predator of various hyponemeutid and tortricid caterpillars (Lepidoptera)

(Chapman, 1906; Lyon, 1968). Not often reared in this country but recent records include *Ancylis apicella* (Tortricidae) on *Frangula alnus* (Rhamnaceae) in Cumbria (Shaw and Rotheray, 1990) and *Caloptilia syringella* (Gracillariidae) on *Fraxinus excelsior* (Oleaceae) in Perthshire (Rotheray and Bland, 1992).

Notes. Lyon (1968) includes a few aphids in his list of prey for this species but aphid predation seems unlikely. It is one of the two main exceptions to the general rule that larvae of this group feed on soft-bodied Homoptera. The other exception is *Parasyrphus nigritarsis* [see under *Parasyrphus*].

Xanthogramma Schiner, 1860

Overall appearance. Larva oval in cross-section; prp smooth, rounded and dome-like in profile (Fig. 12) and lacking dorsal spurs; spiracular openings long and wavy (Fig. 12).

Confirming characters. Larva oval in cross-section; vestiture of close-set dome-like papillae; abdominal segments with sensilla 11 separated from locomotory prominence by a groove and anterior to it;

Related taxa. Larva probably similar to *Doros* from which it differs in having wavy spiracular openings (straight in *Doros*).

Biology. According to Holldobler (1929) the larva of *Xanthogramma citrofasciatum* is probably fed by workers of *Lasius* ants in whose colonies the larvae are found. However this is uncertain and needs confirmation. Alternatively they may feed on root aphids associated with the ant colonies.

Xylota Meigen, 1822 (Plates 11f,12a,b)

Overall appearance. A short-tailed larva varying according to species from about about 12 to 15 mm long; sub-cylindrical with a very short (Plate 11f) to a more extended (Plate 12a) anal segment; mouth-hooks internal; anterior fold coated with spicules of varying sizes, many longer than setae on the dorsal surface of the body; thorax without hooks.

Confirming characters. A few aggregated spicules on the lateral margins of the thorax beyond the anterior fold; prolegs small with 5 or 6 primary crochets often arranged in a curved row; anal segment with 3 pairs of lappets.

Related taxa. Similar to *Sphegina* and *Tropidia*. *Xylota* differs from *Sphegina* in having variously-sized spicules on the anterior fold and having crochets which are arranged in curved, not transverse rows. *Xylota* differs from *Tropidia* in lacking a row of spicules on the antero-dorsal margin of the mesothorax just behind and between the anterior spiracles.

Biology. A range of feeding habits, associated mostly with trees, are known within this genus. *Xylota segnis* feeds in decaying sap under bark and in sap runs created by the bark

weevil, *Hylobius abietus*. It is also found outside microhabitats associated with trees, in silage (Hartley, 1961) and in decomposing potatoes (Blackith and Blackith, 1989). *Xylota coeruleiventris* has been found in sap-filled tunnels of the bark weevil, *Hylobius abietus*. *Xylota sylvarum* feeds in decayed heartwood of various trees including deep underground in tree roots and above ground in rot-holes. *Xylota tarda* has been found in sap runs on *Populus* and *X. xanthocnema* in rot-holes.

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Appendix 1. Summary of larval feeding modes for the genera dealt with in this guide (order of genera follows Appendix 2)

Genus	Feeding mode	Larval habitat
<i>Eumerus</i>	mycophagous/ phytophagous	fungal decay in plant bulbs
<i>Cheilisia</i>	mycophagous/ phytophagous	fungal decay in plant roots; fruiting bodies of fungi; leaf-miners; stem & root tunnellers; sap/cambium feeders in pines
<i>Merodon</i>	phytophagous	plant bulbs
<i>Portevinia</i>	phytophagous	plant bulbs
<i>Ferdinandea</i>	saprophagous	sap runs
<i>Rhingia</i>	saprophagous	cow dung
<i>Pipizella</i> to <i>Eupeodes</i> (see Appendix 2)	predacious	soft-bodied homoptera
<i>Xanthandrus</i>	predacious	caterpillars
<i>Parasyrphus</i> (in part)	predacious	beetle larvae
<i>Microdon</i>	predacious	ant pupae in ant nests
<i>Volucella</i>	predacious/ saprophagous	bee & wasp nests; sap runs
<i>Brachyopa</i>	saprophagous	sap runs; decaying sap under bark

<i>Hammerschmidtia</i>	saprophagous	decaying sap under bark
<i>Chrysogaster</i> <i>Orthonევრა</i> <i>Lejogaster</i>	saprophagous	wet decaying vegetation in ponds, ditches marshes, bogs
<i>Neoascia</i>	saprophagous	wet decaying vegetation in ponds, ditches; wet manure
<i>Syritta</i>	saprophagous	wet decaying vegetation & manure
<i>Xylota</i>	saprophagous	wet decaying vegetation; decaying sap under bark; rot-holes; decaying heartwood
<i>Ceriana*</i>	saprophagous	sap runs
<i>Tropidia</i>	saprophagous	ponds, ditches
<i>Chalcosyrphus</i> <i>Brachypalpus</i> <i>Brachypalpoides</i> <i>Spilomyia*</i> <i>Milesia*</i>	saprophagous	decaying sap under bark; rot holes decaying heartwood
<i>Callicera</i> <i>Pocota</i> <i>Myolepta</i> <i>Mallota</i>	saprophagous	rot-holes
<i>Criorhina</i>	saprophagous	decaying heartwood
<i>Caliprobola</i>	saprophagous	decaying tree roots
<i>Lejota</i>	saprophagous	?decaying tree roots
<i>Temnostoma*</i>	saprophagous	tunnelling in firm moist wood
<i>Sericomyia</i>	saprophagous	wet decaying vegetation on moorlands
<i>Anasimyia</i> <i>Parhelophilus</i>	saprophagous	wet decaying vegetation in ponds, ditches,

<i>Helophilus</i> <i>Lejops</i>		bogs, marshes; wet manure (some)
<i>Eristalinus</i>	saprophagous	wet decaying vegetation in ponds, ditches, decaying seaweed
<i>Eristalis</i>	saprophagous	wet decaying vegetation & manure
<i>Myathropa</i>	saprophagous	rot-holes; sap runs; under bark; decaying heartwood & decaying vegetation

* genera not in Britain

Appendix 3. Literature references to British and European species descriptions of hoverfly larvae or puparia within genera dealt with in this guide arranged alphabetically according to genera

Species	Reference
<i>Anasimyia lineata</i> (Fabricius)	Hartley (1961)
<i>Anasimyia lunulata</i> (Meigen)	Hartley (1961)
<i>Anasimyia transfuga</i> (L.)	Hartley (1961)
<i>Baccha elongata</i> (Fabricius)	Dixon (1960) Dušek & Láška (1960) Goeldlin de Tiefenau (1974)
<i>Brachyopa bicolor</i> (Fallén)	Krivosheina & Mamaev (1967) Rotheray (1991)
<i>Brachyopa insensilis</i> Collin	Krivosheina & Mamaev (1967) Rotheray (1991)
<i>Brachyopa pilosa</i> Collin	Krivosheina & Mamaev (1967) Rotheray (1991)
<i>Brachypalpus laphriformis</i> (Fallén)	Rotheray (1991)
<i>Brachypalpus valgus</i> (Panzer)	Dušek & Láška (1988)
<i>Caliprobola speciosa</i> (Rossi)	Girschner (1884) Rotheray (1991)
<i>Callicera aurata</i> (Rossi) (= <i>aenea</i> (F.))	Rotheray (1991)
<i>Callicera rufa</i> Schummel	Coe (1938) Dixon (1960) Hartley (1961)
<i>Chalcosyrphus (Xylotina) nemorum</i> (Fabricius)	Hartley (1961)
<i>Chalcosyrphus (Xylotodes) eunotus</i> (Loew)	Maibach & Goeldlin de Tiefenau (1992a)
<i>Cheilosia albipila</i> Meigen	Rotheray (1988a)

<i>Cheilosia albitarsis</i> Meigen	Rotheray (1991)
<i>Cheilosia antiqua</i> Meigen	Rotheray (1991)
<i>Cheilosia bergenstammi</i>	Smith (1979)
<i>Cheilosia canicularis</i> (Panzer)	Dušek (1962) Rotheray (1990a)
<i>Cheilosia fasciata</i> Schiner & Egger	Dušek & Láska (1962) Rotheray (1990a)
<i>Cheilosia fraterna</i> (Meigen)	Rotheray (1988a)
<i>Cheilosia grossa</i> (Fallén)	Dušek & Láska (1962) Rotheray (1988a)
<i>Cheilosia longula</i> (Zetterstedt)	Rotheray (1990a)
<i>Cheilosia morio</i> (Zetterstedt)	Trägårdh (1923)
<i>Cheilosia omissa</i> Becker	Dušek (1962)
<i>Cheilosia pagana</i> (Meigen)	Rotheray (1990a)
<i>Cheilosia proxima</i> (Zetterstedt)	Rotheray (1988b)
<i>Cheilosia semifasciata</i> Becker	Rotheray (1988)
<i>Cheilosia scutellata</i> (Fallén)	Rotheray (1990a)
<i>Cheilosia variabilis</i> (Panzer)	Dušek (1962) Rotheray (1990a)
<i>Chrysogaster hirtella</i> Loew	Varley (1935; 1937) Hartley (1958; 1961) Dixon (1960)
<i>Chrysogaster solstitialis</i> (Fallén)	Hartley (1961)
<i>Chrysotoxum elegans</i> Loew	Dušek & Láska (1962)
<i>Chrysotoxum festivum</i> (L.)	Speight (1976)
<i>Chrysotoxum verralli</i> Collin	Dixon (1960)
<i>Cnemodon</i> , see <i>Heringia</i>	

<i>Criorhina berberina</i> (Fabricius)	Hartley (1961) Rotheray (1991)
<i>Criorhina floccosa</i> (Meigen)	Rotheray (1991)
<i>Criorhina ranunculi</i> (Panzer)	Rotheray (1991)
<i>Dasysyrphus albosrianius</i> (Fallén)	Scott (1939) Brauns (1953) Bitsch (1955) Dixon (1960) Goeldlin de Tiefenau (1974)
<i>Dasysyrphus postclaviger</i> (Stys & Moucha)	Goeldlin de Tiefenau (1974)
<i>Dasysyrphus lunulatus</i> (Meigen)	Rotheray (1987)
<i>Dasysyrphus tricinctus</i> (Fallén)	Dixon (1960)
<i>Dasysyrphus venustus</i> (Meigen)	Dušek & Láska (1962) Rotheray (1987)
<i>Didea</i> (= <i>Megasyrphus</i>) <i>annulipes</i> (Zetterstedt)	Goeldlin de Tiefenau (1974)
<i>Didea fasciata</i> Macquart	Heiss (1938) Dixon (1960)
<i>Doros profuges</i> (Harris) (= <i>conopseus</i> Fabricius)	Speight (1988)
<i>Eoseristalis abusivus</i> Collin	Hartley (1961)
<i>Eoseristalis arbustorum</i> (L.)	Hartley (1961)
<i>Eoseristalis horticola</i> (Degeer)	Doležil (1972)
<i>Eoseristalis interrupta</i> (Poda) (= <i>nemorum</i> auctt. nec. Linnaeus)	Hartley (1961) (as <i>nemorum</i> L.)
<i>Eoseristalis intricarius</i> (L.)	Hartley (1961)
<i>Eoseristalis pertinax</i> (Scopoli)	Hartley (1961)
<i>Eoseristalis rupium</i> (Fabricius)	Doležil (1972) Maibach & Goeldlin de Tiefenau (1991a)
<i>Epistrophe eligans</i> (Harris)	de Meijere (1916)

	Krüger (1926) Brauns (1954) Dixon (1960) Dušek & Láška (1961) Goeldlin de Tiefenau (1974)
<i>Epistrophe grossulariae</i> (Meigen)	Rotheray (1986a)
<i>Epistrophe liophthalma</i> (Schiner & Egger)	Goeldlin de Tiefenau (1974)
<i>Epistrophe nitidicollis</i> (Meigen)	Dušek & Láška (1959) Dixon (1960) Goeldlin de Tiefenau (1974)
<i>Epistrophe ochrostoma</i> (Zetterstedt)	Goeldlin de Tiefenau (1974)
<i>Epistrophella</i> , see <i>Meligramma</i>	
<i>Episyrphus balteatus</i> (Degeer)	Vimmer (1925) Krüger (1926) Scott (1939) Fielding (1953) Dixon (1960) Goeldlin de Tiefenau (1974)
<i>Eriozona syrphoides</i> (Fallén)	Kula (1983)
<i>Eristalinus aeneus</i> (Scopoli)	Metcalf (1913) Klein-Krautheim (1936) Dixon (1960) Hartley (1961)
<i>Eristalinus sepulchralis</i> (L.)	Hartley (1961)
<i>Eristalis tenax</i> (L.)	Batelli (1879) Buckton (1895) Metcalf (1913) Vimmer (1925) Gäbler (1930; 1932) Klein-Krautheim (1936) Smart (1948) Dixon (1960) Hartley (1961)
<i>Eumerus strigatus</i> Fallén	Hodson (1927; 1932) Vimmer (1931)

	Balachowsky & Mesnil (1936) Heiss (1938) Kanervo (1942) Dixon (1960) Hartley (1961)
<i>Eumerus tuberculatus</i> Rondani	Hodson (1927; 1931; 1932) Balachowsky & Mesnil (1936) Kanervo (1942) Dixon (1960)
<i>Eupeodes</i> (= <i>Metasyrphus</i>) <i>corollae</i> (Fabricius)	Vimmer (1925) Scott (1939) Fielding (1953) Dixon (1960)
<i>Eupeodes latifasciatus</i> (Macquart)	Dušek & Láška (1960)
<i>Eupeodes latilunulatus</i> (Collin)	Dixon (1960)
<i>Eupeodes luniger</i> Meigen	Bhatia (1939) Scott (1939) Fielding (1953) Dixon (1960)
<i>Eupeodes neilseni</i> (Dušek & Láška)	Rotheray (1988b)
<i>Eupeodes</i> (<i>Lapposyrphus</i>) <i>lapponicus</i> (Zetterstedt)	Goeldlin de Tiefenau (1974)
<i>Fagisyrphus</i> , see <i>Melangyna</i>	
<i>Ferdinandea cuprea</i> Scopoli	Krüger (1926) Krivosheina & Mamaev (1967) Hartley (1961) Dušek & Láška (1988)
<i>Hammerschmidtia ferruginea</i> (Fallén)	Krivosheina & Mamaev (1967) Rotheray (1991)
<i>Helophilus hybridus</i> Loew	Hartley (1961)
<i>Helophilus pendulum</i> (L.)	Klein-Krautheim (1936) Dixon (1960) Hartley (1961)
<i>Helophilus trivittatus</i> (Fabricius)	Doležil (1972)

<i>Heringia curvinervis</i> Strobl	Dušek & Láška (1960)
<i>Heringia heringia</i> (Zetterstedt)	Dušek & Láška (1959)
<i>Heringia</i> (= <i>Cnemodon</i>) <i>latitarsis</i> Egger	Dušek & Láška (1960)
<i>Heringia</i> (= <i>Neocnemodon</i>) <i>vitripennis</i> (Meigen)	Delucchi et al. (1957)
<i>Lejogaster metallina</i> (Fabricius)	Hartley (1961)
<i>Lejogaster splendida</i> (Meigen)	Hartley (1961)
<i>Leucozona</i> (<i>Ischyrosyrphus</i>) <i>glaucius</i> (L.)	Dušek & Láška (1962)
<i>Leuzona</i> (<i>Ischyrosyrphus</i>) <i>laternaria</i> (Müller)	Rotheray (1988b)
<i>Leucozona lucorum</i> (L.)	Dixon (1960)
<i>Mallota cimbiciformis</i> (Fallén)	Coe (1953a) Dixon (1960) Hartley (1961)
<i>Megasyrphus</i> , see <i>Didea</i>	
<i>Melangyna arctica</i> (Zetterstedt)	Rotheray (1988b)
<i>Melangyna cincta</i> (Fallén)	Dixon (1960) [misidentified as <i>grossulariae</i> , see Rotheray 1986a] Dušek & Láška (1962)
<i>Melangyna lasiophthalma</i> (Zetterstedt)	Goeldin de Tiefenau (1974)
<i>Melangyna quadrimaculata</i> (Verrall)	Rotheray (1988b)
<i>Melangyna umbellatarum</i> (Fabricius)	Dixon (1960)
<i>Melanostoma mellinum</i> (L.)	Metcalf (1916)
<i>Melanostoma scalare</i> (Fabricius)	Dušek & Láška (1959) Dixon (1960)
<i>Meligramma</i> (= <i>Epistrophella</i>) <i>euchroma</i> (Kowarz)	Dušek & Láška (1959) Goeldin de Tiefenau (1974)
<i>Meligramma guttata</i> (Fallén)	Dixon (1960)
<i>Meligramma triangulifera</i> (Zetterstedt)	Heiss (1938) Dixon (1960)

	Goeldlin de Tiefenau (1974)
<i>Meliscaeva auricollis</i> Meigen	Scott (1939) Dixon (1960)
<i>Meliscaeva cinctellus</i> (Zetterstedt)	Scott (1939) Dixon (1960)
<i>Merodon equestris</i> Fabricius	Hodson (1932a) Hartley (1961) Dixon (1960)
<i>Metasyrphus</i> , see <i>Eupeodes</i>	
<i>Microdon devius</i> (L.)	Vimmer (1925) Dixon (1960) Rotheray (1991)
<i>Microdon eggeri</i> Mik	Andries (1912) Dixon (1960) Hartley (1961)
<i>Microdon mutabilis</i> (L.)	Hecht (1899) Andries (1912) Dixon (1960)
<i>Myathropa florea</i> (L.)	Beling (1888) Krüger (1926) Klein-Krautheim (1936) Dixon (1960) Hartley (1961) Krivosheina & Mamaev (1967)
<i>Myolepta luleota</i> Gmelin	Becher (1882) Dušek & Láška (1960) Hartley (1961)
<i>Myolepta potens</i> (Harris)	Rotheray (1991)
<i>Neoascia meiculosa</i> (Scopoli) (= <i>aenea</i> Meigen)	Hartley (1961)
<i>Neoascia podagrica</i> (Fabricius)	Hartley (1961) Dušek & Láška (1962)
<i>Neocnemodon</i> , see <i>Heringia</i>	
<i>Orthonevra brevicornis</i> Loew	Hartley (1961)
<i>Orthonevra splendens</i> Meigen	Hartley (1961)

<i>Paragus albifrons</i> (Fallén)	Goeldlin de Tiefenau (1974)
<i>Paragus haemorrhous</i> Meigen	Goeldlin de Tiefenau (1974)
<i>Paragus majoranae</i> Rondani	Goeldlin de Tiefenau (1974)
<i>Paragus quadrifasciatus</i> Meigen	Goeldlin de Tiefenau (1974)
<i>Parasyrphus lineola</i> (Zetterstedt)	Goeldlin de Tiefenau (1974)
<i>Parasyrphus nigratarsis</i> (Zetterstedt)	Kellér (1917) Kanervo (1946) Schneider (1953)
<i>Parasyrphus punctulatus</i> (Verrall)	Rotheray (1987)
<i>Parasyrphus vittiger</i> (Zetterstedt)	Goeldlin de Tiefenau (1974)
<i>Parhelophilus frutetorum</i> (Fabricius)	Hartley (1961)
<i>Parhelophilus versicolor</i> (Fabricius)	Hartley (1961)
<i>Pipiza austriaca</i> Meigen	Goeldlin de Tiefenau (1974)
<i>Pipiza bimaculata</i> Meigen	Dušek & Láška (1959)
<i>Pipiza festiva</i> Meigen	Dušek & Láška (1959)
<i>Pipiza luteitarsis</i> (Zetterstedt)	Rotheray (1987)
<i>Pipiza noctiluca</i> (L.)	Dixon (1960)
<i>Pipizella viduata</i> (L.) (= <i>varipes</i> Meigen)	Heeger (1858) Dixon (1960)
<i>Platycheirus (Pachysphyria) ambiguus</i> (Fallén)	Dušek & Láška (1959) Goeldlin de Tiefenau (1974)
<i>Platycheirus albimanus</i> (Fabricius) (= <i>cyaneus</i> Müller)	Fielding (1953) Dixon (1960)
<i>Platycheirus angustatus</i> (Zetterstedt)	Rotheray (1988b)
<i>Platycheirus clypeatus</i> (Meigen)	Fielding (1953) Dixon (1960)

<i>Platycheirus fulviventris</i> (Macquart)	Rotheray & Dobson (1987)
<i>Platycheirus immarginatus</i> Zetterstedt	Goeldlin de Tiefenau (1974)
<i>Platycheirus manicatus</i> (Meigen)	Dunn (1949) Fielding (1953) Dixon (1960) Goeldlin de Tiefenau (1974)
<i>Platycheirus ovalis</i> Becker	Goeldlin de Tiefenau (1974)
<i>Platycheirus peltatus</i> (Meigen)	Fielding (1953) Dušek & Láska (1960) Goeldlin de Tiefenau (1974)
<i>Platycheirus perpallidus</i> Verrall	Maibach & Goeldlin de Tiefenau (1991)
<i>Platycheirus scambus</i> (Staeger)	Fielding (1953) Rotheray (1988b)
<i>Platycheirus scutatus</i> (Meigen)	Krüger (1926) Bhatia (1939) Scott (1939) Fielding (1953) Dixon (1960)
<i>Pocota personata</i> (Harris)	Aubertin (1928) Dixon (1960) Rotheray (1991)
<i>Portevinia maculata</i> (Fallén)	Speight (1986) Rotheray (1991)
<i>Rhingia campestris</i> Meigen	Krüger (1926) Coe (1942) Hammer (1942) Dixon (1960) Hartley (1961)
<i>Scaeva pyrastris</i> (L.)	Krüger (1926) Bhatia (1939) Scott (1939) Brauns (1954) Dixon (1960) Goeldlin de Tiefenau (1974)

<i>Scaeva selenitica</i> (Meigen)	Scott (1939) Brauns (1953) Dixon (1960)
<i>Sericomyia lappona</i> L.	Hartley (1961)
<i>Sphaerophoria menthastri</i> (L.)	Rotheray (1987)
<i>Sphaerophoria rueppelli</i> (Wiedemann)	Bhatia (1939)
<i>Sphaerophoria scripta</i> (L.)	Bhatia (1939) Dixon (1960) Goeldlin de Tiefenau (1974)
<i>Sphegina clunipes</i> Fallén	Hartley (1961) Krivosheina & Mamaev (1967)
<i>Sphegina elegans</i> (Schummel) (= <i>kimakowiczi</i> Strobl)	Hartley (1961)
<i>Sphegina verecunda</i> Collin	Hartley (1961)
<i>Syritta pipiens</i> L.	Beling (1882) Krüger (1926) Hodson (1931) Heiss (1938) Dixon (1960) Hartley (1961)
<i>Syrphus ribesii</i> (L.)	Vimmer (1925) Krüger (1926) Bhatia (1939) Scott (1939) Fielding (1953) Dixon (1960) Dušek & Láška (1964) Goeldlin de Tiefenau (1974)
<i>Syrphus torvus</i> Osten-Sacken	Heiss (1938) Scott (1939) Dixon (1960) Dušek & Láška (1964)
<i>Syrphus vitripennis</i> Meigen	Scott (1939) Fielding (1953) Dixon (1960) Dušek & Láška (1964)

<i>Temnostoma apiforme</i> (Fabricius)	Hequist (1957) Krivosheina & Mamaev (1962)
<i>Temnostoma bombylans</i> (Fabricius)	Krivosheina & Mamaev (1962)
<i>Temnostoma vespiforme</i> (L.)	Stammer (1933) Krivosheina & Mamaev (1962)
<i>Triglyphus primus</i> Loew	Sedlag (1967)
<i>Tropidia scita</i> (Harris)	Decler & Rotheray (1990)
<i>Volucella inanis</i> (L.)	Dixon (1960) Hartley (1961) Rupp (1989)
<i>Volucella bombylans</i> (L.)	Künckel d'Herculais (1875) Vimmer (1925) Smith (1955)
<i>Volucella pellucens</i> (L.)	Künckel d'Herculais (1875) Lundbeck (1916) Krüger (1926) Dixon (1960) Hartley (1961)
<i>Volucella zonaria</i> (Poda)	Dixon (1960)
<i>Xanthandrus comtus</i> (Harris)	Chapman (1905) Silvestri (1907) Lundbeck (1916) Lucchese (1942) Lyon (1968)
<i>Xanthogramma festivum</i> (L.) (= <i>citrofasciatum</i> Degeer)	Hölldobler (1929) Speight (1990)
<i>Xanthogramma pedissequum</i> (Harris)	Beling (1882) Dixon (1960)
<i>Xylota florum</i> (Fabricius)	Dušek & Láska (1960)
<i>Xylota segnis</i> L.	Hartley (1961)
<i>Xylota sylvarum</i> L.	Dixon (1960) Hartley (1961) Krivosheina & Mamaev (1967)

Xylota tarda (Meigen)

Rotheray (1991)

Xylota xanthocnema Collin

Hartley (1961)

Glossary of morphological terms used to describe hoverfly larvae

Anal lobe A rounded section at the tip of the anal segment, delimited by grooves and best seen in ventral view; characteristic of homopteran predators, Fig. 4.

Anal opening Anus.

Anal plate An obliquely angled, flat end to the body resulting from contraction of the anal segment and, sometimes, the 7th abdominal segment; best developed in *Portevinia maculata*, Plate 1c.

Anal segment The last segment of the body with the anal opening on the ventral surface and the prp on the dorsal surface, Fig. 2.

Antenno-maxillary organs Pairs of sensory organs on the head of hoverfly larvae appearing just above the mouth and borne on fleshy projections, Figs. 2-6.

Anterior fold The area between the antenno-maxillary organs and the front margin of the prothorax often coated in spicules of various types; poorly developed in phytophagous larvae, well developed in short and long-tailed larvae, Fig. 14.

Anterior spiracles The respiratory organs of the front end of the body, appearing as a pair of sclerotised brown or black structures either side of the dorsal surface of the prothorax, Fig. 2. In *Eristalis* and most long-tailed larvae the anterior spiracles are, for protection, retractile into specialised pockets on the prothorax, Fig. 6.

Chevron Sergeant-stripe pattern of fat on the dorsal surface of homopteran predators, sometimes triangular in shape, Plates 4e, 6a, e, 7c, 8b.

Crochet A sclerotised hook on the rim and sides of a proleg; occurring in rows, the largest are the primary crochets, Fig. 6.

Discs Appearing as a pair of differentiated "spots" on the integument on the dorsal surface of the 1st abdominal segment, Fig. 2. They only appear when the larva has finished feeding in the third stage and is preparing to pupate. It is through these discs that the pupal spiracles will protrude soon after pupariation. In many homopteran predators these discs have been secondarily lost, see Rotheray and Gilbert (1989).

Dorsal lip An area of integument between the mouth and the antenno-maxillary organs often bearing setae, Figs. 2, 6.

Dorsal plate A lightly sclerotised region on the dorsal surface of the prothorax in tunnelling *Cheilosia* larvae, Fig. 3.

Dorsal projection A fleshy projection of the dorsal surface of the abdomen, Plate 10a.

Dorsal scar A circular pit at the edge of a spiracular plate on the prp, Fig. 2.

Dorso-ventral flattening A larva that is flattened from above, Plate 7f.

Feeding channel A wide, open groove between the mesothoracic prolegs and the lateral lips in long-tailed larvae along which suspended food travels before entering the mouth, Fig. 6.

Fleshy projection A general term for a soft extension of the integument, tapered or rounded, may or may not bear sensilla, Plates 3f,8e,f.

Fold An area on the surface of the integument delimited by grooves; folds and grooves form regular patterns on larvae, Fig 2.

Groove An excavated line in the integument separating folds; folds and grooves form regular patterns on larvae, Fig. 2.

Hook A large sclerotised, usually black spike on the thorax of certain saproxylic larvae, Plate 12f; Fig. 14.

Integument The "skin".

Inter-spiracular setae Hair-like processes between the spiracular openings of the prp, Fig. 2.

Lappet A fleshy projection of the anal segment bearing sensilla, up to four pairs are present, Fig. 2.

Lateral lips A pair of lobe-like fleshy structures either side of the mouth but part of the prothorax and often coated in specialised setae, Figs. 2&6.

Locomotory organs General term for the locomotory prominences and prolegs.

Locomotory prominences Paired structures on the ventral surface of the abdomen and thorax involved in locomotion; distinguished from prolegs in that they do not contain musculature, Fig. 4

Long-tailed larva A term of convenience referring to larvae having a particularly extended anal segment, Plate 14.

Longitudinal grooves A series of grooves on the dorsal surface of the prothorax, one of the defining features of hoverfly larvae, Fig. 2.

Mandibular lobes A pair of ridged structures along each side of the mouth; in *Eumerus* they are fleshy and external (Fig. 2), in many *Cheilosia* they are sclerotised (Fig. 3) and in many short and long-tailed larvae they are internal within the mouth and form part of a filtration system for separating food.

Mesothorax Second segment of the thorax, Fig. 2.

Metathorax Third segment of the thorax, Fig. 2.

Mouth-hooks Black sclerotised hooks at the leading edge of the mouth, Fig. 3.

Papilla A small, fleshy projection of the integument, Fig. 8.

Posterior breathing tube See posterior respiratory process.

Posterior respiratory process (prp) One of the defining features of hoverfly larvae resulting from the fusion of the two breathing tubes at the rear end and appearing as a sclerotised brown or black structure from the dorsal surface, or the tip, of the anal segment, Fig. 2.

Proleg Paired projections from the ventral surface of the mesothorax and first six abdominal segments of the abdomen, musculature present (look for an indentation at the tip where muscle fibres are attached on the inside); crochets usually present, Fig. 6.

Prothorax The first segment of the thorax, Fig. 2.

Prp See posterior respiratory process

Pubescence A general term for the coating of setae over the body or a part of it.

Pupal spiracles A pair of brown, sclerotised structures projecting from the front end of the puparium and coated in spiracular openings.

Rectal gills Fleshy organs not seen unless they are protruding from the anal opening. They are involved in salt regulation and vary in shape from species to species.

Sensilla (pl), sensillum (s) Microscopic sensory pits forming regular patterns on each of the segments, usually borne on basal papillae and surrounded by setae, Fig. 2.

Setae (pl) seta (s) A small "hair".

Short-tailed larva A term of convenience referring to larvae having an extended anal segment, Plate 12.

Spicule A sclerotised seta, appearing as a small, dark hook.

Spiracular opening The point on the prp where the breathing tubes open to the air, Fig. 2.

Spiracular plate The paired regions at the tip of the prp bearing the spiracular openings.

Subcylindrical Referring to the slightly less-than-perfect cylindrical shape of a larva in cross-section.

Tail A term of convenience referring to the extended anal segment.

Ventral lip A spherical-shaped organ at the rear margin of the mouth, Fig. 2.

Vestiture A general term for the coating of setae over the body or a part of it.

References

- Aguilar, J. D' and Coutin, R. 1988. *Cheilosia caerulescens* Meigen, ravageur des Joubarbes (Dipt. Syrphidae). *Bulletin de la Société Entomologique de France*, **92**, 307-309.
- Andrewes, H. W. 1944. *Chilosia albipila* Meigen bred. *Entomologist's Record and Journal of Variation*, **56**, 71.
- Andries, M. 1912. Zur Systematik, Biologie and Entwicklung von *Microdon* Meigen. *Zeitschrift für Wissenschaftliche Zoologie*, **103**, 300-361.
- Aubertin, D. 1928. The larva of *Pocota apiformis* Schrank. *The Entomologist*, **61**, 151-152.
- Balachowsky, A. and Mesnil, L. 1936. *Les insectes nuisibles aux plantes cultivées*. 2 Paris.
- Batelli, A. 1879. Contribuzione all'Anatomie ed alla Fisiologia della larva dell *Eristalis tenax*. *Bulletin Societe Entomologie Italia*, **11**, 77-120.
- Becher, E. 1882. Ueber die ersten Stände einiger Syrphiden und eine neue *Myiolepta* Art. *Wiener Entomologische Zeitung*, **1**, 249-254.
- Beirne, B. P. 1941. British species of Diplazonini (Bassini auctt.) with a study of the genital and postgenital abdominal sclerites in the male (Hym.: Ichneumonidae). *Transactions of the Royal Entomological Society of London*, **91**, 661-712.
- Beling, T. 1882. Beitrag zur Metamorphose zweiflügeliger Insekten aus den Familien Tabanidae, Leptidae, Asilidae, Empididae, Dolichopodidae und Syrphidae. *Archiv für Naturgeschichte*, **48**, 186-240.
- Beling, T. 1888. Beitrag zur Metamorphose zweiflügeliger einiger Insekten aus den Familien Tabanidae, Empididae und Syrphidae. *Verhandlungen des Zoologisch-Botanischen Gesellschaft in Wien*, **38**, 1-4.
- Bhatia, M. L. 1939. Biology, morphology and anatomy of aphidophagous syrphid larvae. *Parasitology*, **31**, 78-129.
- Bitsch, J. 1955. Sur la larve de *Syrphus albostrigatus* Fall. (Dipt. Syrphidae). *Bulletin de la Société Entomologique de France*, **60**: 18-23.
- Blackith, R. E. and Blackith, R. M. 1989. Diptera reared from decaying potatoes in Ireland. *Irish Naturalists' Journal*, **23**, 71-72.
- Blackman, R. L. 1974. *Aphids*. Ginn., London.
- Bloomfield, E. N. 1897. Habits of *Sericomyia borealis* Fln. *Entomologist's monthly Magazine*, **8**, 222-223.
- Brauns, A. 1953. Beiträge zur Ökologie und wirtschaftlichen Bedeutung der aphidivorer Syrphidenarten (Diptera). *Bericht Entomologischer*, **3**, 278-303.
- Brindle, A. 1965. Taxonomic notes on the larvae of British Diptera No 20 - The Sepsidae. *The Entomologist*, **98**, 137-140.
- Brischke, C. G. 1880. Ueber Fliegenmaden aus *Scrophularia nodosa* u. *Pteris aquilina*. *Entomologische Nachrichten Berlin*, **6**, 56.
- Britten, H. 1916. *Mallota cimbiciformis* Fln., bred from rotten wood. *Transactions Entomological Society of London (Proceedings)*, **1916**, 83-84.
- Brunel, E. and Cadou, D. 1990. Description de la larve et de la puppe de *Cheilosa vulpina* Meigen (1822), mineuse de racine d'Artichaut (*Cynara scolymus* L.) en Bretagne. *Bulletin de la Société Entomologique de France*, **95**, 121-129.
- Buckton, G. B. 1895. *The Natural History of Eristalis tenax or The Drone Fly*. Macmillan, London.
- Burke, H. E. 1905. Black Check in Western Hemlock. *U.S.D.A. Bureau of Entomology. Circular No 61*, 1-10.

- Buxton, P. A. 1955. British Diptera associated with fungi. III. Flies of all families from about 150 species of fungi. *Entomologist's monthly Magazine*, **96**, 61-94.
- Carpenter, G. H. 1913. Injurious insects and other animals observed in Ireland during the year 1912. *Economical Proceedings of the Royal Dublin Society*, **2**, 79-104.
- Carter, C. I. 1971. *Conifer Woolly Aphids (Adelgidae) in Britain*. Forestry Commission Bulletin No. 42, London.
- Chambers, R. L. and Adams, T. H. L. 1986. Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids in winter wheat: an analysis of field populations. *Journal of Applied Ecology*, **23**, 895-904.
- Chandler, A. E. F. 1968. The relationship between aphid infestations and oviposition by aphidophagous Syrphidae (Diptera). *Annals applied biology*, **61**, 425-434.
- Chapman, T. A. 1905. Some observations on *Hastula hyerana* Mill. *Entomologist's monthly Magazine*, **26**, 149-157.
- Chapman, T. A. 1906. Food and habits of *Xanthandrus comtus* Harris. *Entomologist's monthly Magazine*, **27**, 14.
- Chittenden, F. 1911. A Note on the Habits of the Narcissus Fly. *Journal Royal Horticultural Society*, **37**, 122-123.
- Claussen, C. 1980. Die Schwebfliegenfauna des Landesteils Schleswig in Schleswig-Holstein (Diptera, Syrphidae). *Supplement zu Faunistisch-Ökologische Mitteilungen*, **1**, 3-79.
- Coe, R. L. 1938. Rediscovery of *Callicera yerburyi* Verrall (Diptera: Syrphidae); its breeding habits, with a description of the larva. *The Entomologist*, **71**, 97-102.
- Coe, R. L. 1942. *Rhingia campestris* Meigen (Dipt., Syrphidae) an account of its life-history and descriptions of the early stages. *Entomologist's monthly Magazine*, **78**, 121-130.
- Coe, R. L. 1953. *Diptera, Syrphidae. Handbooks for the Identification of British Insects*, **10(1)**. Royal Entomological Society, London.
- Coe, R. L. 1953a. *Mallota cimbiciformis* Fallén (Diptera, Syrphidae) breeding in Hyde Park, London. Its larva and puparium compared with those of *Eristalis tenax* L., and *Helophilus* spp. *Entomologist's Gazette*, **4**, 282-286.
- Creager, D. B. and Spruijt, F. J. 1935. The relation of certain fungi to larval development of *Eumerus tuberculatus* Rondani (Syrphidae, Diptera). *Annals Entomological Society of America*, **28**, 425-437.
- Declere, K. and Rotheray, G. E. 1990. The puparium and larval habitat of the hoverfly *Tropidia scita* (Diptera: Syrphidae). *Entomologist's Gazette*, **41**, 157-160.
- Delucchi, V., Pschorn-Walcher, H. and Zwölfer, H. 1957. *Cnemodon*-Arten (Syrphidae) als Räuber von *Dreyfusia piceae* Ratz. (Adelgidae) II. Morphologie und Biologie von *Cnemodon dreifusiae* Del. et. P.-W., nebst Beobachtungen über *C. latitarsis* Egger. *Zeitschrift für angewandte Entomologie*, **41**, 246-259.
- Dixon, T. J. 1959. Studies on oviposition behaviour of Syrphidae (Diptera). *Transactions of the Royal Entomological Society of London*, **111**, 57-80.
- Dixon, T. J. 1960. Key to and descriptions of the third instar larvae of some species of Syrphidae (Diptera) occurring in Britain. *Transactions of the Royal Entomological Society of London*, **112**, 345-379.
- Doležil, Z. 1972. Developmental stages of the tribe Eristalini (Diptera, Syrphidae). *Acta Entomologica Bohemoslovaca*, **69**, 339-350.
- Donisthorpe, H. 1927. *The guests of British Ants*. Routledge and Son, London.
- Donisthorpe, H. 1928. The bionomics of *Pocota apiformis* Schrank. *The Entomologist*, **61**, 150-151.
- Duffield, R. M. 1981. Biology of *Microdon fuscipennis*, with interpretations of the reproductive strategies of *Microdon* species North of Mexico. *Proceedings*

Entomological Society of Washington, **83**, 716-724.

- Dufour, L. 1840. Sur les métamorphoses des Diptères *Annales Science Naturelle*, **13**, 148-163.
- Dunn, J. A. 1949. The parasites and predators of potato aphids. *Bulletin Entomological Research*, **40**: 97-122.
- Dušek, J. 1962. Beiträge zur Kenntnis von Larven der Gattung *Cheilosia* Meigen (Diptera, Syrphidae). *Časopis Československé Společnosti Entomologické*, **59**, 68-73.
- Dušek, J. and Krístek, J. 1959. Poznámky k výskytu a bionomii larev přestřenek (Diptera, Syrphidae) v Hálkách topolových Dutilek. *Zoologické Listy*, **8**, 299-308.
- Dušek, J. and Láška, P. 1959. Beitrag zur Kenntnis einiger unbekannter aphidophager Syrphiden-Larven (Diptera, Syrphidae). *Acta Societatis Entomologicae Cechoslovenicae*, **56**, 279-292.
- Dušek, J. and Láška, P. 1960. Příspěvek k poznání larev přestřenek (Syrphidae, Diptera) II. *Přírodovědný Časopis Slezský*, **21**, 299-230.
- Dušek, J. and Láška, P. 1962. Beiträge zur Kenntnis einiger syrphiden Larven (Diptera, Syrphidae). *Časopis Československé Společnosti Entomologické*, **59**, 348-356.
- Dušek, J. and Láška, P. 1964. A contribution to distinguishing the European species of the subgenus *Syrphus* Fabricius (Diptera, Syrphidae) according to male genitalia and larvae. *Časopis Československé Společnosti Entomologické*, **61**, 58-70.
- Dušek, J. and Láška, P. 1967. Versuch zum Aufbau eines natürlichen Systems mitteleuropäischer Arten der Unterfamilie Syphinae (Diptera). *Acta Scientiarum Naturalium Brno*, **1**, 349-390.
- Dušek, J. and Láška, P. 1988. Saprophage Larven von *Ferdinandea cuprea* und *Brachypalpus valgus* (Diptera, Syrphidae). *Acta Entomologica Bohemoslovaca*, **85**, 307-312.
- Edmunds, J. 1974. *Defence in Animals: a survey of anti-predator defences*. Longmans, London.
- Fielding, M. 1953. *The parasites and predators of aphids infesting cabbages*. Unpublished Ph.D. thesis, *University of Liverpool*.
- Fitton, M. G. and Rotheray, G. E. 1982. A key to the European genera of diplazontine ichneumon-flies, with notes on the British fauna. *Systematic Entomology*, **7**, 311-320.
- Foster, W. A. 1990. Experimental evidence for effective and altruistic colony defence against natural predators by soldiers of the gall-forming aphid *Pemphigus spyrothecae* (Hemiptera: Pemphigidae). *Behavioural Ecology and Sociobiology*, **27**, 421-430.
- Frauenfeld, G. 1866. Zoologische Miscellen X. *Verhandlungen des Zoologisch - Botanischen Gesellschaft in Wien*, **16**, 961-982.
- Frauenfeld, G. 1868. Zoologische Miscellen XIV. *Verhandlungen des Zoologisch - Botanischen Gesellschaft in Wien*, **18**, 147-166.
- Friederichs, K., Schaefferberg, B. and Sturn, H. 1940. Über die Feinde des Kiefernspanners mit Berücksichtigung des Mischwaldes. *Zeitschrift für Angewandte Entomologie*, **27**, 621-641.
- Fryer, J. C. F. 1915. The food-plant of *Chilosia variabilis* Panzer. *Entomologist's monthly Magazine*, **51**, 193.
- Gäbler, H. 1930. Die postembryonale Entwicklung des Tracheensystems von *Eristalis tenax* L. *Zeitschrift für Morphologie und Ökologie der Tiere*, **19**, 427-492.
- Gäbler, H. 1932. Beitrag zur Kenntnis der *Eristalis*-Larven (Dipt.) *Stettiner Entomologische Zeitung*, **93**, 143-147.
- Gäbler, H. 1938. Massenaufreten von Larven der Schwebfliegenart *Syrphus torvus* O.-S. *Forslich-Naturwissenschaftliche Zeitschrift* **60**, 611-616.

- Gäbler, H. 1939. Die Bedeutung der Larven von *Syrphus tricinctus* Fall. für die Vernichtung von Raupen und Afterraupen. *Tharandter forstliches Jahrbuch*, **90**, 69-74.
- Garnett, W. B., Akre, R. D. and Sehlke, E. 1985. Cocoon mimicry and predation by myremecophilous Diptera (Diptera: Syrphidae). *Florida Entomologist*, **68**, 615-621.
- Girschner, E. 1884. Ueber einige Syrphiden. *Wiener Entomologische Zeitung*, **3**, 197-200.
- Goeldlin de Tienfenau, P. 1974. Contribution à l'étude systématique et écologique des Syrphidae (Dipt.) de la Suisse occidentale. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **47**, 151-252.
- Goot, V. S. van der. 1989. *Zweefvliegen*. Veldgids 1, Amsterdam.
- Graham, M. W. R. 1991. A reclassification of the European Tetrastichinae (Hymenoptera: Eulophidae): revision of the remaining genera. *Memoirs of the American Entomological Institute*, No. **49**. Gainesville, Florida.
- Greig, C. 1989. Overwintering behaviour of the larva of *Myiathropa florea* L. (Diptera: Syrphidae). *Dipterists Digest*, No. **2**, 11-16.
- Hackman, W. and Meinander, M. 1979. Diptera feeding as larvae on macrofungi in Finland. *Annales Zoologica Fennici*, **16**, 50-83.
- Hammer, O. 1942. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn*, **105**, 141-393.
- Hardy, G. H. 1872. Memoirs on Scottish Diptera. *Scottish Naturalist*, **1871-2**, 177-180.
- Hartley, J. C. 1958. The root-piercing spiracles of the larva of *Chrysogaster hirtella* Loew (Diptera: Syrphidae). *Proceedings Royal Entomological Society of London (A)*, **33**, 81-87.
- Hartley, J. C. 1961. A taxonomic account of the larvae of some British Syrphidae. *Proceedings of the Zoological Society of London*, **136**, 505-573.
- Heeger, E. 1858. Neue Metamorphosen einiger Dipteren. *S. B. Akademie für Wissenschaft Wien*, **31**, 295-309.
- Heiss, E. M. 1938. A classification of the larvae and puparia of the Syrphidae of Illinois exclusive of aquatic forms. *Illinois Biological Monographs*, **36**, 1-142.
- Hellrigl, K. 1992. die Fichtenharzfliege *cheilosia morio* Zett. (Dipt., Syrphidae) als physiologischer Schädling an Fichten in Sütirol. *Anzeiger Schädlingkde., Pflanzenschutz, Umweltschutz*, **65**, 33-36.
- Heqvist, K. J. 1957. Über die Larve von *Temnostoma apiforme* Fabr. (Diptera, Syrphidae). *Tijdschrift voor Entomologie*, **78**, 29-31.
- Hering, E. M. 1957. *Bestimmungstabellen der Blatminen von Europa*. 's Gravenhage, W. Junk.
- Hodson, W. E. H. 1927. The bionomics of the lesser bulb flies, *Eumerus tuberculatus*, Rond., in south-west England. *Bulletin Entomological Research*, **17**, 373-384.
- Hodson, W. E. H. 1931. A comparison of the immature stages of *Eumerus tuberculatus* Rond., and *Syrirta pipiens*, Linn. (Syrphidae). *Bulletin Entomological Research*, **22**, 55-58.
- Hodson, W. E. H. 1932. A comparison of the larvae of *Eumerus strigatus*, Fln., and *Eumerus tuberculatus* Rond. (Syrphidae). *Bulletin Entomological Research*, **23**, 247-249.
- Hodson, W. E. H. 1932a. The large narcissus fly, *Merodon equestris*, Fab. (Syrphidae). *Bulletin Entomological Research*, **23**, 429-448.
- Hölldobler, K. 1929. Über die Entwicklung der Schwierfliege *Xanthogramma citrofasciatum* im Neste von *Lasius alienus* und *niger*. *Zoologischer Anzeiger*, **82**, 171-176.

- Hövmeyer, K. 1987. The population dynamics of *Cheilosia fasciata* (Diptera, Syrphidae): significance of environmental factors and behavioural adaptations in a phytophagous insect. *Oecologica*, **73**, 537-542.
- Hövmeyer, K. 1993. Population studies of *Cheilosia fasciata* (Diptera: Syrphidae), a leaf miner of *Allium ursinum*. *Ecological Entomology*, **17**, 331-337.
- Kaltenbach, J. H. 1874. *Die Pflanzenfeinde aus der Klasse der Insekten*. Stuttgart.
- Kanervo, V. 1942. Die Unterscheidung der Larven und Puppen von *Eumerus tuberculatus* Rond. und *E. strigatus* Fall. (Dipt., Syrphidae). *Annales Entomologica Fennica*, **8**, 227-233.
- Kanervo, V. 1946. Studien über die natürlichen Feinde des Erlenblattkäfes *Melasoma aenea* L. *Annales Zoologici Societatis Zoologicae Botanicae Fennicae*, **12**, 1-206.
- Keller, C. 1917. Zur Biologie und Morphologie von *Chrysomela aenea* L. und *Coleophora fuscedinella* Zell. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich*, **62**, 103-124.
- Klein-Krauthelm, F. 1936. Beitrag zur Kenntnis der Eristalinen-Larven und Puppen (Syrphidae, Diptera). *Stettiner Entomologische Zeitung*, **97**, 259-270.
- Krivosheina, N. P. and Mamaev, B. M. 1962. Larvae of the European species of the genus *Temnostoma* (Diptera, Syrphidae). *Entomological Reviews*, **41**, 570-575.
- Krivosheina, N. P. and Mamaev, B. M. 1967. Identification of larvae of dipterous insects inhabiting forests. "Nauka", 362pp [in Russian].
- Krüger, F. 1926. Biologie und Morphologie einiger Syrphidenlarven. *Zeitschrift für Morphologie und Ökologie der Tiere*, **6**, 83-149.
- Kula, E. 1983. The larva and puparium of *Eriozonea syrphoides* (Fallén) (Diptera, Syrphidae). *Acta Entomologica Bohemoslovaca*, **80**, 71-73.
- Künckel d'Herculeis, J. 1875. *Réserches sur l'organisation et le développement des Volucelles, Insectes Diptères de la famille des Syrphides. Part 1*. Paris.
- Kurir, A. 1963. Zur Biologie zweier aphidophager Schwebfliegen (Dipt. Syrphidae): *Heringia heringi* Zetterstedt und *Pipiza festiva* Meigen in den Gallen der späten Blattstieldrehgallen-Pappelblattlaus (*Pemphigus spirothecae* Passerini) auf der Pyramidenpappel (*Populus nigra* var. *pyramidalis*). *Zeitschrift für angewandte Entomologie*, **52**, 61-83.
- Lardé, G. 1989. Investigation on Some Factors Affecting Larval Growth in a Coffee-Pulp Bed. *Biological Wastes*, **30**, 11-19.
- Leclercq, M. 1944. Notes sur des Diptères des environs de Liège. *Bulletin de la Société royale de Liège 13 année*, **1**, 34-44.
- Lucchese, E. 1942. Contributi alla conoscenza dei Lepidotteri del melo: *Acrolita naevana* H. B. *Bollettino del Laboratorio di Entomologia e Agraria della Facoltà Agraria in Portici*, **5**, 1-120 and 157-174.
- Lundbeck, W. 1916. *Diptera Danica 5. (Lonchopteridae, Syrphidae)*. G. E. C. Gad, Copenhagen.
- Lyons, J. P. 1968. Contribution à l'étude biologique de *Xanthandrus comtus* Harr. (Diptera, Syrphidae). *Annales des Epiphyties*, **19**, 683-693.
- Maibach, A. and Goeldlin de Tienfenau, P. 1989. *Mallota cimbiciformis* (Fallén) nouvelle pour la faune de Suisse: morphologie du dernier stade larvaire, de la puppe et notes biologiques (Diptera, Syrphidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **62**, 67-78.

- Maibach, A. and Goeldlin de Tienfenau, P. 1991. *Platycheirus perpallidus* Verrall (Diptera, Syrphidae) nouveau pour la faune de Suisse: morphologie des stades immatures et description du cycle de développement. *Bulletin Société vandoise des Sciences naturelles*, **80**, 341-356.
- Maibach, A. and Goeldlin de Tienfenau, P. 1991a. Note biologique et description des larve et puppe d'*Eristalis (Eoseristalis) rupium* F. (Diptera, Syrphidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **64**, 321-330.
- Maibach, A. and Goeldlin de Tienfenau, P. 1992. Staining technique for the Integument of Dead and Living Aquatic Larvae (Diptera: Syrphidae). *Entomologica Generalis*, **17**, 69-71.
- Maibach, A. and Goeldlin de Tienfenau, P. 1992a. Description de la puppe de *Chalcosyrphus (Xylotodes) eunotus* (Loew) et synthèse caractéristiques morphologiques des stades immatures de plusieurs genres de la tribu des Xylotini (Diptera, Syrphidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **65**, 165-175.
- Maier, C. T. 1982. Larval habitats and mate-seeking sites of flowerflies (Diptera: Syrphidae, Eristalinae). *Proceedings Entomological Society Washington*, **84**, 603-609.
- McLean, I. F. G. and Stubbs, A. E. 1990. The Breeding site of *Brachyopa pilosa* (Diptera; Syrphidae). *Dipterists Digest*, **No 3**, 40.
- Meijere, J. C. H. de 1895. Ueber zusammengesetzte stigmen bei Dipteran-larven nebst einem Beitrag zur Metamorphose von *Hydromyza livens*. *Entomologisk Tidskrift*, **38**, 65-100.
- Meijere, J. C. H. de 1916. Beiträge zur Kenntnis der Dipteren-larven und-Puppen. *Zoologische Jahrbücher (Abt. 1)*, **40**, 177-322.
- Metcalf, C. L. 1913. The Syrphidae of Ohio. *Bulletin Ohio Biological Survey*, **1**, 1-317.
- Metcalf, C. L. 1916. Syrphidae of Maine. *Bulletin Maine Agricultural Experimental Station*, **No 253**, 1-264.
- Nielsen, T. R. 1979. Hoverflies (Diptera, Syrphidae) associated with Ramson *Allium ursinum* L. *Fauna Norvegica (B)*, **26**, 21-23.
- Notton, D. G. 1991. Some Diptera host records for species of *Basalys* and *Trichopria* (Hym., Diapriidae). *Entomologist's monthly Magazine*, **127**, 123-126.
- Nurse, C. G. 1910. Notes regarding the breeding of *Cheilosia grossa*. *The Entomologist*, **43**, 313-314.
- Osten Sacken C. R. 1894. *On the Oxen-born Bees of the Ancients*. Heidelberg.
- Peace, T. R. 1962. *Pathology of Trees and Shrubs*. Oxford University Press, Oxford.
- Pontin, A. J. 1962. Some improved methods of keeping ant nests in the laboratory. *Entomologist's monthly Magazine*, **98**, 64-65.
- Rizza, A., Campobasso, G., Dunn, P. H. and Stazi, M. 1988. *Cheilosia corydon* (Dipt.: Syrphidae), a candidate for the Biological control of musk thistle in North America. *Annals Entomological Society of America*, **81**, 225-232.
- Roberts, M. J. 1970. The structure of the mouthparts of syrphid larvae (Dipt.) in relation to feeding habits. *Acta Zoologica*, **51**, 43-65.
- Rossi, F. 1848. *Systematisches Verzeichnis der Zweiflügelichten Insekten (Diptera) des Erzherzogthumes Osterreich*. Wien.
- Rotheray, G. E. 1979. The biology and host searching behaviour of a Cynipoid parasite of aphidophagous syrphid larvae. *Ecological Entomology*, **4**, 75-82.
- Rotheray, G. E. 1981. Host searching and oviposition behaviour of some parasitoids of aphidophagous Syrphidae. *Ecological Entomology*, **6**, 79-87.
- Rotheray, G. E. 1984. Host relations, life cycles and multiparasitism in some parasitoids of aphidophagous Syrphidae (Diptera). *Ecological Entomology*, **9**, 303-310.

- Rotheray, G. E. 1985. Arrested development of *Syrphus ribesii* (L.) larvae (Diptera: Syrphidae) caused by the encyrtid *Bothriothorax clavicornis* (Dalman) (Hymenoptera). *Entomologist's Gazette*, **36**, 51-53.
- Rotheray, G. E. 1986. Colour, shape and defence in aphidophagous syrphid larvae (Diptera). *Zoological Journal of the Linnean Society*, **88**, 201-216.
- Rotheray, G. E. 1986a. The larva and puparium of *Epistrophe grossulariae* (Meigen) with a note on overwintering behaviour. *Entomologist's monthly Magazine*, **122**, 215-218.
- Rotheray, G. E. 1987. The larvae and puparia of five species of aphidophagous Syrphidae (Diptera). *Entomologist's monthly Magazine*, **123**, 121-125.
- Rotheray, G. E. 1988. Morphology and feeding behaviour of the leaf-mining larva of *Cheilosia semifasciata* (Diptera: Syrphidae). *Journal of Natural History*, **22**, 865-873.
- Rotheray, G. E. 1988a. 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.
- Rotheray, G. E. 1988b. Third stage larvae of six species of aphidophagous Syrphidae (Diptera). *Entomologist's Gazette*, **39**, 153-159.
- Rotheray, G. E. 1989. *Aphid Predators. Naturalists' Handbook 11*. The Richmond Publishing Co. Ltd, Slough.
- Rotheray, G. E. 1990. Larval and puparial records of some hoverflies associated with dead wood (Diptera, Syrphidae). *Dipterists Digest*, **No 7**, 2-7.
- Rotheray, G. E. 1990a. The relationships between feeding mode and morphology in *Cheilosia* larvae (Diptera, Syrphidae). *Journal of Natural History*, **24**, 7-19.
- Rotheray, G. E. 1990b. A new species of *Bioblapsis* (Hymenoptera: Ichneumonidae) from Scotland parasitising a mycophagous hoverfly, *Cheilosia longula* (Diptera: Syrphidae). *Entomologica Scandinavica*, **21**, 277-280.
- Rotheray, G. E. 1991. Larval stages of 17 rare and poorly known British hoverflies (Diptera: Syrphidae). *Journal of Natural History*, **25**, 945-969.
- Rotheray, G. E. and Dobson, J. 1987. Aphidophagy and the larval and pupal stages of the syrphid *Platycheirus fulviventris* (Macquart). *Entomologist's Gazette*, **38**, 245-251.
- Rotheray, G. E. and Gilbert, F. S. 1989. The phylogeny and systematics of European predacious Syrphidae (Diptera) based on larval and puparial stages. *Zoological Journal of the Linnean Society*, **95**, 29-70.
- Rotheray, G. E. and MacGowan, I. 1990. Re-evaluation of the status of *Callicera rufa* Schummel (Diptera: Syrphidae) in the British Isles. *The Entomologist*, **109**, 35-42.
- Rotheray, G. E. and Bland, K. P. 1992. *Xanthandrus comtus* (Harris) (Dipt., Syrphidae) breeding in Scotland. *Entomologist's monthly Magazine*, **128**, 57-58.
- Rupp, L. 1989. The mid-European species of *Volucella* as commensals and parasitoids in the nests of bees and social wasps: studies on host finding, larval biology and mimicry. Unpublished thesis, Albert Ludwigs Universität, Freiburg. Germany.
- Schneider, F. 1953. *Syrphus nigratarsis* Zett., ein Ei- und Larven-räuber von *Melasoma* (Chrysom., Col.). *Tijdschrift over plantenziekten*, **59**, 192-194.
- Schuhmacher, H. 1968. Die Schwebfliegen im Raum Heidelberg. *Beitrage Naturkundlichen Forschung Sudwestdeutschland*, **27**, 101-108.
- Scott, E. I. 1939. An account of the development stages of some aphidophagous Syrphidae (Dipt.) and their parasites (Hymenopt.). *Annals Applied Biology*, **26**, 509-532.
- Sedlag, U. 1967. *Triglyphus primus*, eine weitgehend übersehene Syrphide (Dipt. Syrphidae). *Entomologische Berichten*, **1966**, 88-90.

- Shaw, M. R. and Askew, R. R. 1978. Hymenopterous parasites of Diptera (Hymenoptera Parasitica) p. 164-171. In A. E. Stubbs and P. J. Chandler (Eds.) *A Dipterist's Handbook* 15. The Amateur Entomologists' Society.
- Shaw, M. R. and Rotheray, G. E. 1990. *Xanthandrus comtus* (Harris) (Dipt., Syrphidae) reared. *Entomologist's monthly Magazine*, **126**, 258.
- Shillito, J. F. 1947. *Pocota personata* (Harris) (Dipt., Syrphidae) from Epping Forest. *Entomologist's monthly Magazine*, **83**, 180-181.
- Silvestri, F. 1907. La tignola dell'olivo (*Prays olcellus* Fabr.). *Bollettino del Laboratorio di Zoologia Generale e Agraria della Facoltà Agraria in Portici*, **2**, 83-184.
- Smart, J. 1948. *A handbook for the identification of insects of medical importance*. London.
- Smith, K. G. V. 1955. Notes on the egg and first instar larva of *Volucella bombylans* L. (Dipt., Syrphidae). *Entomologist's monthly Magazine*, **91**, 52-54.
- Smith, K. G. V. 1979. The larva and puparium of *Cheilosia bergenstammi* Becker (Diptera: Syrphidae) with a summary of the known biology of the genus in Europe. *Entomologist's Record and Journal of Variation*, **91**, 190-194.
- Smith, K. G. V. 1989. *An Introduction to the Immature stages of British Flies. Handbooks for the Identification of British Insects*, **10(4)**. Royal Entomological Society, London.
- Snow, W. E. 1958. Stratification of arthropods in a wet stump cavity. *Ecology*, **39**, 83-88.
- Southwood, T. R. E. 1972. The insect/plant relationship - an evolutionary perspective. *Symposium Royal Entomological Society of London*, **6**, 3-30.
- Speight, M. C. D. 1974. *Phaonia exoleta* Mg. (Diptera: Muscidae), New to Ireland. *Entomologist's Record and Journal of Variation*, **86**, 246.
- Speight, M. C. D. 1976. The puparium of *Chrysotoxum festivum* (L.) (Diptera: Syrphidae). *Entomologist's Record and Journal of Variation*, **88**, 51-52.
- Speight, M. C. D. 1986. *Portevinia maculata*: last instar larva and puparium, with notes on the relationship between this hoverfly and its larval hostplant, *Allium ursinum* (Dipt., Syrphidae). *Nouvelles revue entomologie*, **3**, 37-43.
- Speight, M. C. D. 1988. *Doros destillatorius*, espèce nouvelle pour la France, avec désignation des types des deux espèces européennes du genre *Doros*, description de leurs pupes et des détermination des adultes et des pupes. *Bulletin de la Société Entomologique de France*, **92**, 193-200.
- Speight, M. C. D. 1989. Saprophylic invertebrates and their conservation. *Nature and Environment Series*, No. **42**. (Strasbourg: Council of Europe).
- Speight, M. C. D. 1990. The puparia of *Xanthogramma festivum* and *Xanthogramma pedissequum* (Syrphidae). *Dipterists Digest*, No. **6**, 29-31.
- Stammer, H. J. 1933. Die Metamorphose der Syrphide *Temnostoma vespiforme* (L.) und die eigenartigen Anpassungen der Larve dieses Tieres an des Bohren im Holz (Dipt.). *Zeitschrift für Morphologie und Ökologie der Tiere*, **26**, 437-446.
- Strong, D. R., Lawton, J. H. and Southwood, T. R. E. 1984. *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, Oxford.
- Stubbs, A. E. 1980. The rearing of *Cheilosia paganus* and *Cheilosia fraterna* (Diptera: Syrphidae). *Entomologist's Record and Journal of Variation*, **92**, 114-117.
- Stubbs, A. E. 1982. Hoverflies as Primary Woodland Indicators with reference to Wharnccliffe Wood. *Sorby Record*, No **20**, 62-67.
- Stubbs, A. E. and Falk, S. 1983. *British Hoverflies, an illustrated identification guide*. British Entomological and Natural History Society.
- Syms, E. E. 1935. Notes on the biology of *Microdon eggeri* Mik. *Transactions Society British Entomology*, **2**, 163-165.

- Thompson, F. C. 1990. Biosystematic information: Dipterists ride the third wave, p. 179-201. In ed. M. Kosztarab and C. W. Schaefer. *Systematics of the North American Insects and Arachnids: Status and Needs*. Virginia Agricultural Experiment Station Information Series 90-1.
- Trägårdh, I. 1923. Skogsentomologiska Birdrag II. 1. Grankadflugan. *Chilosia morio* Zett. *Meddelanden fran Statens Skogsforsoksanstalt*, **20**, 401-424.
- Varley, G. C. 1935. A new Syrphid larva and some other aquatic insect larvae which obtain their oxygen from plant roots. *Proceedings Royal Entomological Society of London (A)*, **10**, 30-31.
- Varley, G. C. 1937. Aquatic insect larvae which obtain oxygen from the roots of plants. *Proceedings Royal Entomological Society of London (A)*, **12**, 55-60.
- Vimmer, A. 1925. *Larvy a kukly dvojkridleho hmyzu stredoevropskeho se zvlastnim zretelem na skudce rostlin kulturnich* (Praha), 210-266.
- Vimmer, A. 1931. Ueber die Larven Kleiner Fliegen, welche in der Tschechoslovak. Rep. durch Ausnagen von Hyponomen den pflanzen schaden. *Archiv pro Přirodovědecký Výzkem Ceckoslovakia*, **18**, 1-59.
- Vockeroth, J. R. 1969. A revision of the genera of the Syrphini (Diptera, Syrphidae). *Memoirs of the Entomological Society of Canada*, **62**, 1-176.
- Vockeroth, J. R. 1990. Revision of the Nearctic species of *Platycheirus* (Diptera, Syrphidae). *Canadian Entomologist*, **122**, 659-766.
- Vockeroth, J. R. and Thompson, F. C. 1987. Syrphidae. In, J. McAlpine, et al. (Eds.), *Manual of Nearctic Diptera*, **2**, 713-743. Quebec: Agriculture Canada.
- Waitzbauer, W. 1976. Die Insektenfauna männlicher Blütenstände von *Typha angustifolia*. *Zoologischer Anzeiger (Jena)*, **196**, 9-15.
- Weems, H. V. 1954. Natural enemies and insecticides that are detrimental to beneficial Syrphidae. *Ohio Journal of Science*, **54**, 45-54.
- Whiteley, D. 1987. Hoverflies of the Sheffield Area and North Derbyshire. *Sorby Record, Special Series, No. 6*. (Sorby Natural History Society, Sheffield).
- Zimina, L. V. 1986. A review of palaeartic hoverflies of the genus *Callicera* Panzer (Diptera, Syrphidae). *USSR Review of Entomology*, **65**, 633-638.

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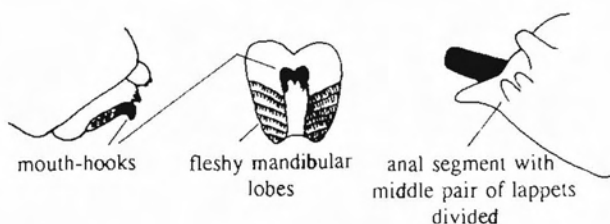
<i>Anasimyia</i>	64.	<i>Melanostoma</i>	78.
<i>Baccha</i>	64.	<i>Meligramma</i>	78.
<i>Brachyopa</i>	64.	<i>Meliscaeva</i>	79.
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<i>Brachypalpus</i>	65.	<i>Merodon</i>	79.
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<i>Epistrophe</i>	71.	<i>Pocota</i>	85.
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<i>Episyrphus</i>	72.	<i>Rhingia</i>	86.
<i>Eriozona</i>	72.	<i>Scaeva</i>	87.
<i>Eristalinus</i>	73.	<i>Sericomyia</i>	87.
<i>Eristalis</i>	73.	<i>Sphaerophoria</i>	87.
<i>Eumerus</i>	74.	<i>Sphegina</i>	88.
<i>Eupeodes</i>	74.	<i>Spilomyia</i>	88.
<i>Fagisyrrhus</i>	77.	<i>Syritta</i>	89.
<i>Ferdinandea</i>	75.	<i>Syrphus</i>	89.
<i>Hammerschmidtia</i>	75.	<i>Temnostoma</i>	90.
<i>Helophilus</i>	76.	<i>Trichopsomyia</i>	90.
<i>Heringia</i>	76.	<i>Tropidia</i>	90.
<i>Lejogaster</i>	69.	<i>Volucella</i>	91.
<i>Leucozona</i>	77.	<i>Xanthandrus</i>	91.
<i>Mallota</i>	77.	<i>Xanthogramma</i>	92.
<i>Megasyrphus</i>	71.	<i>Xylota</i>	92.
<i>Melangyna</i>	77.		

COLOUR PLATES

Quick Identification of British Hoverfly Larvae

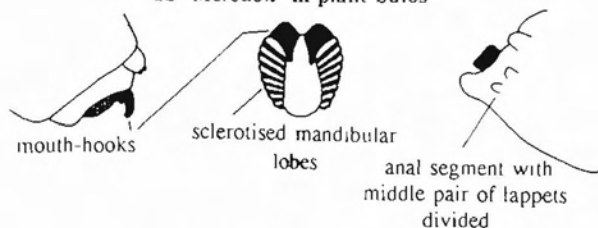
Most hoverfly larvae can be quickly identified to genus using the colour plates and characters listed below. Use the colour plates to see which picture resembles the larva to be identified and, on the opposite page, confirm with the characters given for that taxon. Ignore differences in colour, except for predatory larvae. The order of presentation in the colour plates follows approximately Appendix 2.

1a *Eumerus* wet, fungal decay in plant bulbs

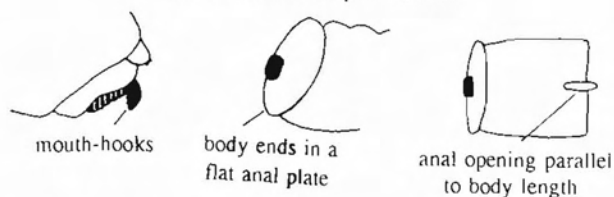


Cheilosia not photographed, fungal decay of plant roots similar to *Eumerus* (1a) except anal segment with 3 pairs of lappets

1b *Merodon* in plant bulbs



1c *Portevinia* in plant bulbs



1e-f *Cheilosia* tunnelling in roots and stems

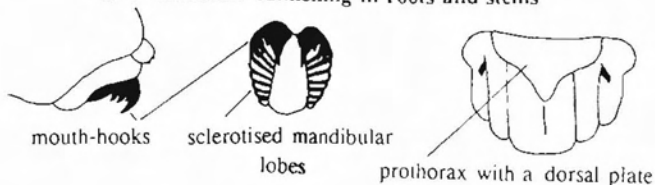


PLATE 1



1a *Eumerus tuberculatus*



1b *Merodon equestris*



1c *Portevinia maculata*



1d *P. maculata* in bulb of *Allium ursinum*

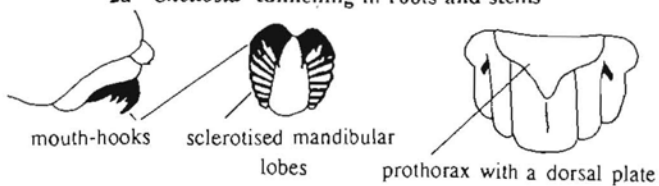


1e *Cheilosia albitarsis*

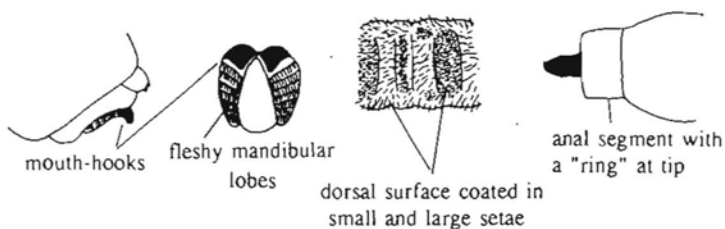


1f *Cheilosia antiqua*

2a *Cheilosis* tunnelling in roots and stems



2c-d *Cheilosis* in fruiting bodies of fungi



2e-f *Cheilosis* leaf-miners

distinguished from other *Cheilosis* by the six-toothed mouth-hooks



PLATE 2



2a *Cheilosia grossa*



2b *Cirsium palustre* infested with *C. grossa*



2c *Cheilosia longula*



2d *C. longula* myophagous in *Boletus* fungi



2e *Cheilosia semifasciata*



2f *Cheilosia semifasciata*, non-mined and mined leaves of *Umbilicus rupestris*.

3a *Rhingia* dung, particularly cow-pats

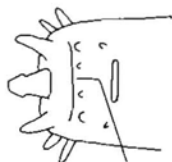


anal segment with one transverse fold between anal opening and the tip

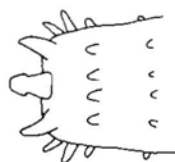


posterior end of body with black stick-like projections

3b *Ferdinanda* sap-runs on deciduous trees



anal segment with one transverse fold between anal opening and the tip



posterior end of body with fleshy stump-like projections

3c-e *Microdon* in and around ant nests

The domed, hemispherical shape in cross-section and the marginal band of setae distinguish *Microdon*



3f *Volucella* (in part) in bee and wasp nests



thorax narrow with a few large spicules on the anterior fold



prolegs with a transverse row of 3-4 long crochets

V. inflata not photographed, is similar to 3f but apparently occurs in sap-runs.

PLATE 3



3a *Rhingia campestris*



3b *Ferdinandea cuprea*



3c *Microdon eggeri*



3d *Microdon devius*



3e *Microdon mutabilis*



3f *Volucella pellucens*

4a *Volucella* wasp nests



thorax narrow with a few large spicules on the anterior fold



prolegs with a transverse row of 6-8 crochets

4b *Xanthandrus* on trees and shrubs feeding on gregarious lepidopteran caterpillars



tip of prp with posterior projections

Melanostoma not photographed, feeding in leaf litter and some ground layer aphids

Similar to 4b with less white fat showing. Distinguished from *Xanthandrus* and other green larvae by the prp which is about as broad as long with 3 pairs of oval-shaped spiracular openings and no posterior projections.

4c-f *Platycheirus* feeding in leaf litter and ground layer aphids, rarely on trees



prp generally broader than long without dorsal spurs



body with upper and lower lateral stripes of fat, sometimes indistinct



dorsal surface with chevrons, sometimes indistinct eg 4c

PLATE 4



4a *Volucella inanis*



4b *Xanthandrus comtus* and *Calopitilia syringella*



4c *Platycheirus fulviventris*



4d *Platycheirus peltatus*

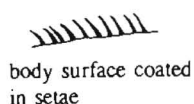
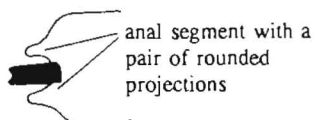


4e *Platycheirus scutatus*



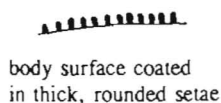
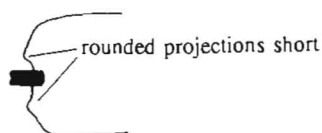
4f *Platycheirus podagratus*

5a-b *Pipiza* flocculent (covered in white powdery strands) aphids, aphids on ground layer plants and aphids in galls

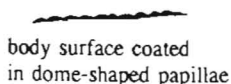
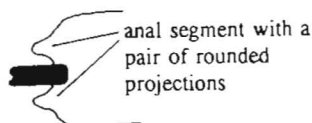


Pipizella not photographed, root aphids in ant nests

Similar to 5b except larva flattened from above and:



5c *Heringia* flocculent and gall-inducing aphids on trees



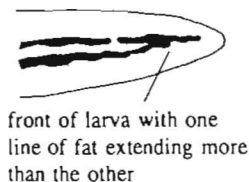
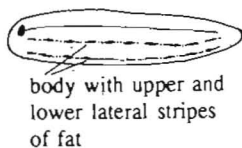
Trichopsomyia not photographed, in psyllid galls on rushes

Similar to 5c except cream-coloured.

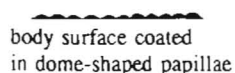
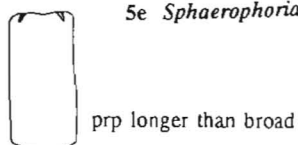
Meligramma guttata not photographed, aphids on trees

Similar to 5c except anal segment lacking projections and larva with slight mid-dorsal projections along the body.

5d *Baccha* ground layer aphids



5e *Sphaerophoria* ground layer aphids



5f *Episyrrhus* see overleaf

PLATE 5



5a *Pipiza austriaca*



5b *Pipiza luteitarsis*



5c *Pipiza noctiluca*



5d *Baccha* sp.



5e *Sphaerophoria menthastri*



5f *Epsyrphus balteatus*

5f *Episyrrhus* wide range of aphids



spiracular openings
black lined

prp lacks dorsal
spurs & a basal rim



body coated in
dome-shaped papillae

Meliscaeva not photographed, aphids on shrubs and trees

similar to 5f except *M. cincella* yellowish-brown



prp with a basal rim
(*M. auricollis*)



prp sloping away behind
(*M. cincella*)

6a-c *Syrphus* wide range of aphids

The 3 colour forms shown are in approximate order of frequency.



spiracular openings extending
over the sides of the prp

prp broader than long or
about as long as broad

6d-f, 7a-b *Melangyna* mostly arboreal aphids

Species-specific colour patterns are evident in this genus. refer to plates.



shiny bulbous tip

matt at base

prp usually longer than broad

PLATE 6



6a *Syrphus ribesii* - white colour form



6b *Syrphus ribesii* - red colour form



6c *Syrphus ribesii* - brown colour form



6d *Melangyna arctica*



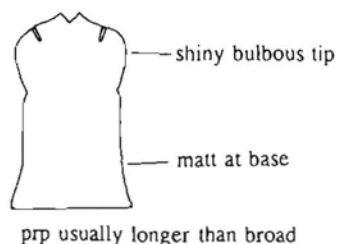
6e *Melangyna cincta*



6f *Melangyna lasiophthalma*

7a-b, 6c-f *Melangyna* mostly arboreal aphids

Species-specific colour patterns are evident in this genus, refer to plates.



7c *Parasyrphus nigritarsis* leaf-beetle eggs, larvae & puparia on *Alnus* & *Salix*

Species-specific colour pattern, refer to plate. Note that specimen photographed was overwintering and orange spots are yellow in an actively feeding larva.

7d-e *Parasyrphus* aphids on shrubs and trees

Larva with narrow body and longitudinal stripes.



body hemispherical in cross-section

7f *Epistrophe* aphids on shrubs and trees



body flattened from above

PLATE 7



7a *Melangyna quadrimaculata*



7b *Melangyna umbellatarum*



7c *Parasyrphus nigratarsis*



7d *Parasyrphus punctulatus*



7e *Parasyrphus vittiger*



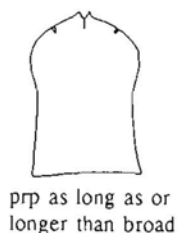
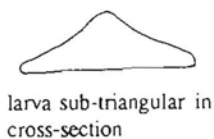
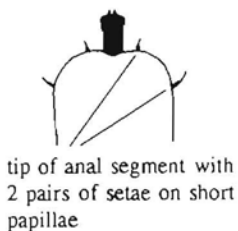
7f *Epistrophe eligans*

8a *Epistrophe* see 7f

8b *Meligramma* aphids on shrubs and trees

Species-specific colour patterns are evident in this genus. *Meligramma triangulifera* is like a bird dropping (8b); *M. gutata* (not photographed) is dark brown, like 5c & 9e, and *M. euchroma* (not photographed) is mottled orange and white.

8c-d *Leucozona* aphids on shrubs and trees



Chrysotoxum not photographed, in and around ant nests feeding on root aphids

Larva similar to 8c-d, except with 3 pairs of setae on short papillae at the tip of the anal segment and the colour pattern is more diffuse without chevrons.

8e-f *Dasysyrphus* aphids on shrubs and trees

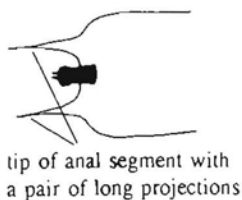


PLATE 8



8a *Epistrophe grossulariae* and aphid



8b *Meligramma triangulifera*



8c *Leucozonia lucorum*



8d *Leucozonia (l.) lateraria*



8e *Dasysyrphus tricinctus*

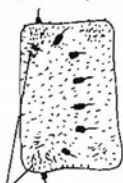


8f *Dasysyrphus venustus*

9a-c *Eupeodes* aphids mostly on trees, particularly conifers, but some species very common on ground layer aphids (*E. corollae*, *E. luniger*)



prp with spiracular openings nearly reaching base



dorsal surface with some aggregated spicules



posterior locomotory organs tri-lobed

Doros, *Xanthogramma* not photographed, associated with ants

Similar probably to 9a but paler.



prp dome-shaped



spiracular openings straight (*Doros*)



spiracular openings wavy (*Xanthogramma*)

9d *Scaeva* aphids on trees, particularly conifers but *S. pyrastris* very common on ground layer aphids

Similar to *Eupeodes* except for colour pattern and dorsal spicules evenly spread, not aggregated in clumps.

9e *Paragus* aphids on ground layer plants

The specimen photographed is preserved. In life the colour pattern is similar to 9a.



tip of anal segment with a row of 4 setae

Meligramma gutata is dark in colour, like 9e, but lacks a row of setae on the anal segment.

9f *Didea* aphids on shrubs and trees



prp with inwardly sloping spiracular plates



body coated in stiff upright setae

PLATE 9



9a *Eupeodes luniger*



9b *E. luniger* showing anal grasping organ



9c *Eupeodes nielseni*



9d *Scaeva pyrastris*



9e *Paragus haemorrhous* preserved specimen



9f *Didea fasciata* preserved specimen

10a *Eriozona* aphids on conifers



body coated in thick
black triangular-shaped
spicules

10b-d *Brachyopa* in sap-runs, under loose bark



underside of anal segment
with 4 pairs of sensilla



larva with transverse
rows of setae, or -



coated in blotches
(*B. insensilis*)

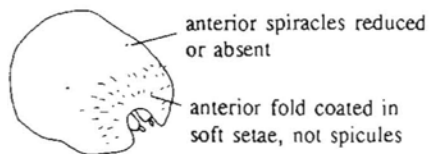
10e *Hammerschmidtia* under bark of *Populus*

Similar to *Brachyopa* except body evenly coated in setae, not rows.

10f *Chrysogaster*, *Lejogaster*, *Orthonevra* decaying vegetation in ponds, streams etc



larva with lower
lateral ridge



tip of prp pointed



PLATE 11



11a *Lejogaster splendida*



11b *Orthonevra brevicornis*



11c *Neoascia podagrica*



11d *Sphegina clunipes*



11e *Syritta pipiens*

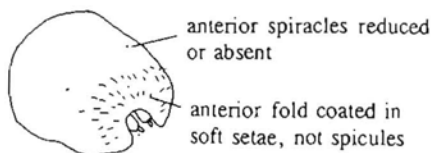


11f *Xylota segnis*

11a-b *Chrysogaster*, *Lejogaster*, *Orthonevra* decaying vegetation in ponds, streams etc



larva with lower lateral ridge



anterior spiracles reduced or absent
anterior fold coated in soft setae, not spicules



tip of prp pointed

11c *Neosasia* in ponds, marshes, wet manure etc



1st pair of lappets divided at tip



anterior margin of prothorax with a pair of hooks

11d *Sphegina* under bark, in sap-runs

Similar to 11c but lacking hooks and flattened from above.

11e *Syritta* wet compost and manure



anal segment short with 3 pairs of lappets



prolegs elongate with a transverse row of crochets

11f *Xylota* see overleaf

PLATE 11



11a *Lejogaster splendida*



11b *Orthonevra brevicornis*



11c *Neoascia podagrica*



11d *Sphegina clunipes*

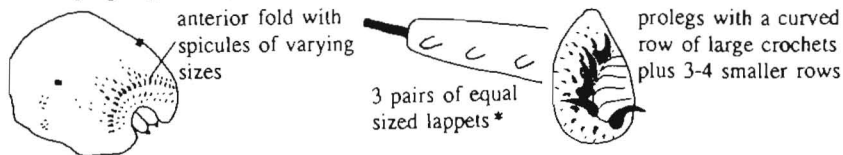


11e *Syrirta pipiens*



11f *Xylota segnis*

12a-b; 11f *Xylota* in sap-runs, under bark and in decaying heartwood (also *X. segnis* in decaying vegetation)

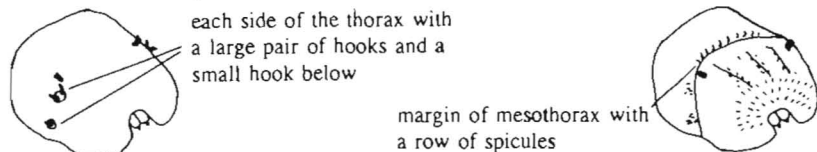


Chalcosyrphus not photographed, under bark

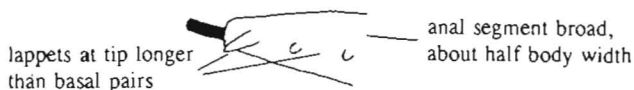
Tropidia not photographed, decaying vegetation in ponds and ditches

Similar to 11f except for hooks on the thorax.

Similar to 11f except mesothorax.



12c *Pocota* rot-holes in deciduous trees

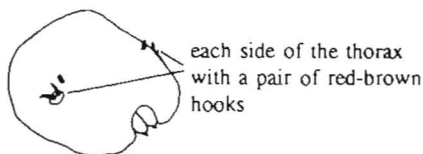


12d *Brachypalpus* rot-holes in deciduous trees



Brachypalpoides not photographed, decaying heartwood

Similar to 12d except for arrangement and colour of hooks.



12e-f *Criorhina* decaying heartwood

Thorax with a very distinctive arrangement of hooks, see 12f.

* late addition, *Psilota* sap-runs, like 11f but anal segment with 1 pair of lappets

PLATE 12



12a *Xylota sylvarum*



12b *Xylota tarda*



12c *Pocota personata*



12d *Brachypalpus laphriformis*



12e *Criorhina floccosa*



12f *Criorhina floccosa*, head and thorax

13a *Milesia* not British but similar to *Brachypalpus* and *Brachypalpoides*, see Plate 12

13b *Caliprobola* decaying heartwood in roots of deciduous trees and stumps



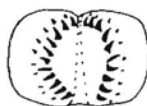
anal segment with longest section between 2nd and 3rd pair of lappets

13c-d *Temnostoma* not British

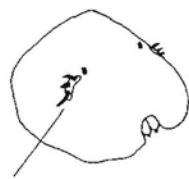
13e *Callicera* rot-holes



anal segment with 1st two pairs of lappets reduced

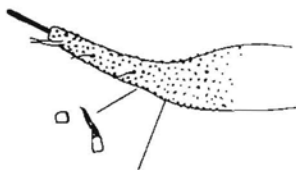


prolegs fused medially forming single structures, not pairs



each side of the thorax with 3-4 hooks

13f *Myolepta* rot-holes



posterior end of body coated in papillae, most with tufts of setae

PLATE 13



13a *Milesia virginiensis*, from the U.S.A.



13b *Caliprobola speciosa*



13c *Temnostoma vespiforme*



13d *T. vespiforme*, head and thorax

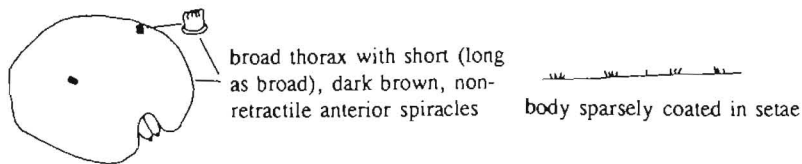


13e *Callicera rufa*

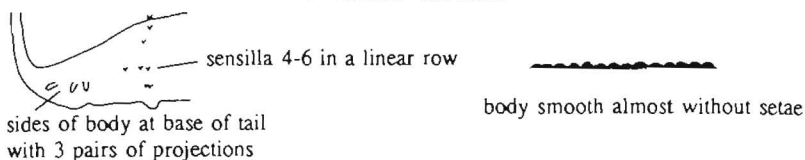


13f *Myolepta luteola*

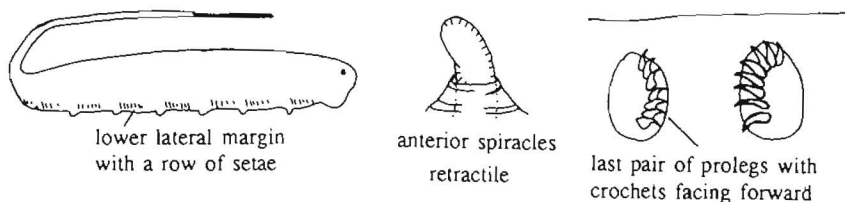
14a *Sericomyia* moorland pools



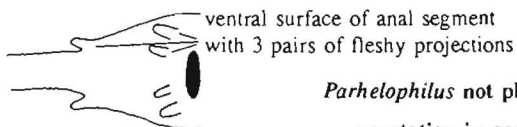
14b *Mallota* rot-holes



14c *Anasimya* decaying vegetation in ponds and marshes



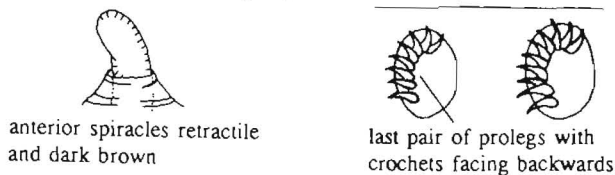
14d *Helophilus* decaying vegetation in ponds, also wet manure and silage



Parhelophilus not photographed, decaying vegetation in ponds and marshes

Similar to 14d but lacking fleshy projections on the anal segment.

14e *Eristalis/Eoseristalis* decaying organic material in ponds, mud, farmyards etc



Eristalinus not photographed, marshes ponds and seaside pools

Similar to 14e except a row of spicules just in front, not between, last pair of prolegs.

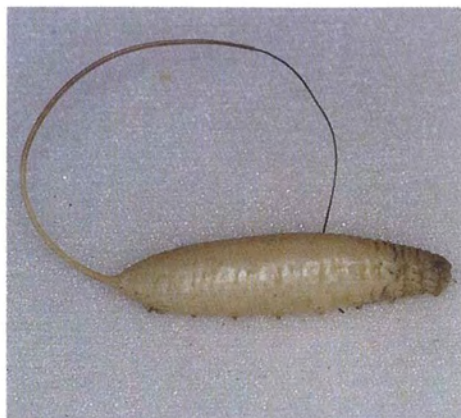
14f *Myathropa* rot-holes, decaying heartwood, sap-runs, under bark

Similar to 14e except anterior spiracles pale, not dark, brown.

PLATE 14



14a *Sericomyia lappona*



14b *Mallota cimbiciformis*



14c *Anasimyia lineata*



14d *Helophilus pendulus*

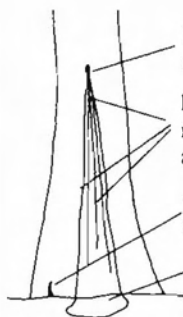


14e *Eristalis tenax*



14f *Myathropa florea*

15a-b Examining sap-runs



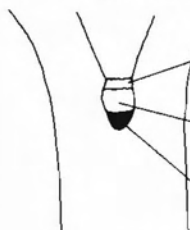
larvae may be in more extensive amounts of sap hidden under the bark

larvae may be found anywhere in the sap-run, in the wet material or at the drier margins and particularly under loose pieces of bark

examine cracks in the bark for sap-runs, they can be underground

larvae also occur in sap-soaked soil at the base of the sap-run

15c Examining rot-holes between diverging branches



a "plug" of dry material may need removing before wet conditions are found; search the "plug" for puparia

if necessary, stir up the contents with a stick to dislodge larvae to the surface

larvae often aggregate at the bottom of the rot-hole

15d Examining rot-holes in decaying heartwood



check these areas for puparia

if necessary, remove plug of dry material

seams of decay at the bottom of the rot-hole, larvae often aggregate in these seams and can be time-consuming to extract

15e-f Examining fallen branches and trees

shaded branches are often richest in larvae
search under loose bark, particularly at exposed ends



most larvae occur low down where decaying sap accumulates

PLATE 15



15a Sap run on *Fagus*



15b Sap run on *Fagus*, close up



15c Twin trunk rot-hole in *Acer*



15d Rot-hole in trunk of *Acer*

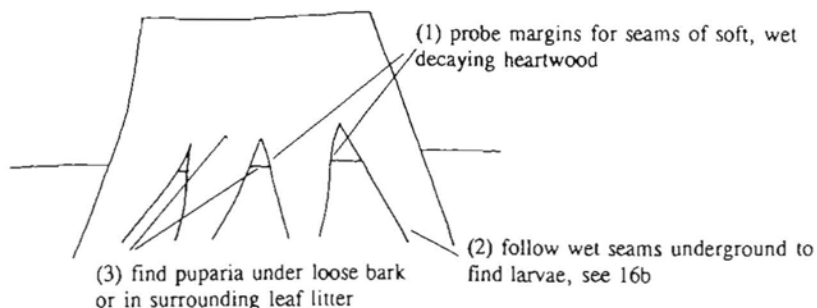


15e Fallen *Ulmus* branch in stream

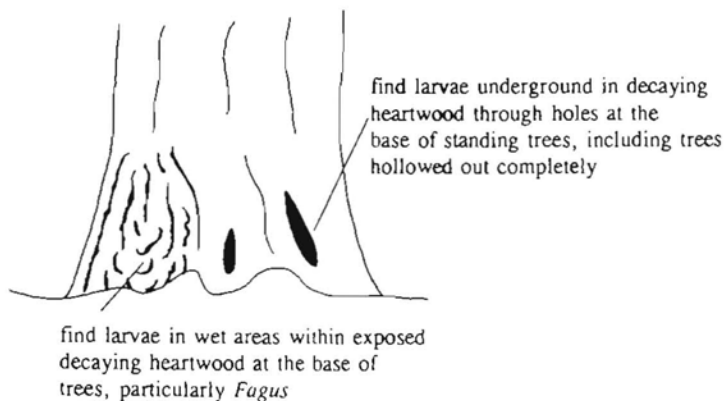


15f Fallen trunk of *Populus tremula*

16a-b Examining stumps



16c Examining old trees



16d Examining compost and silage

Search wet areas including pools and standing water; most larvae are a few cms under the surface. Use a knife or sieve.

16e-f Examining ponds and marshes

Search among the roots of emergent vegetation, accumulations of decaying leaves and other vegetation and exposed mud at the margins. Use a knife or sieve.

PLATE 16



16a Fagus stump



16b Fagus stump, wet decaying wood with larva of *Xylota syvarum*



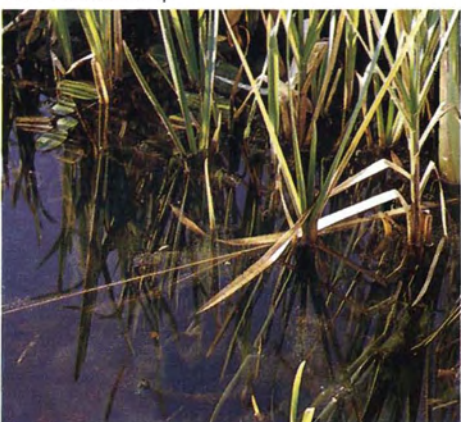
16c Holes at base of *Acer*



16d Manure heap



16e Vegetation-filled pond



16f Close-up, pondside vegetation



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Photos

Front Cover: *Criorhina floccosa*

Above: *Xanthandrus comtus* feeding on lilac leaf-miner caterpillar

Photographs by Graham E. Rotheray

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