HANDBOOKS FOR

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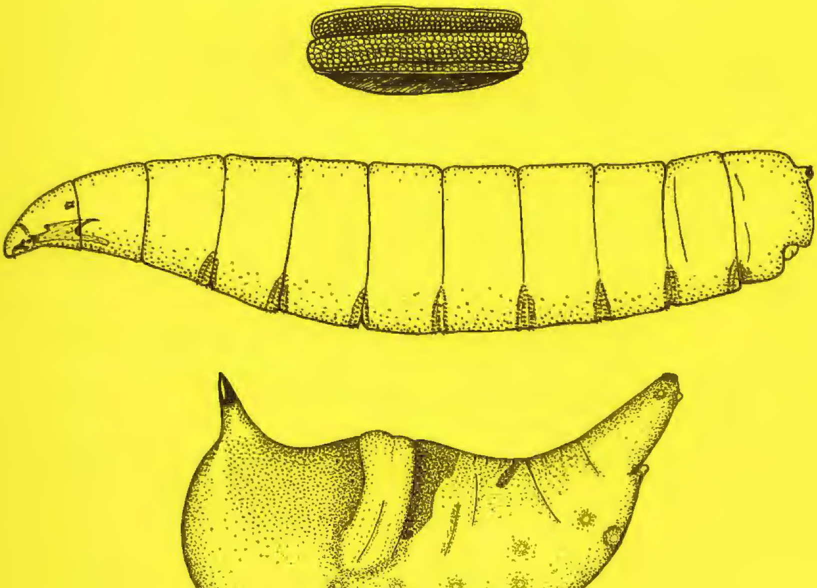
Vol. 10, Part 14

AN INTRODUCTION TO THE IMMATURE STAGES OF BRITISH FLIES

DIPTERA LARVAE, WITH NOTES ON EGGS, PUPARIA AND PUPAE

K. G. V. Smith



ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

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Identification of British Insects

Vol. 10, Part 14

Editors: W. R. Dolling & R. R. Askew

AN INTRODUCTION TO THE IMMATURE STAGES OF BRITISH FLIES

DIPTERA LARVAE, WITH NOTES ON EGGS, PUPARIA AND PUPAE

By

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1989
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The aim of the *Handbooks* is to provide illustrated identification keys to the insects of Britain, together with concise morphological, biological and distributional information.

Each handbook should serve both as an introduction to a particular group of insects and as an identification manual.

Details of handbooks currently available can be obtained from Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD.

Cover illustration: egg of Muscidae; larva (lateral) of *Lonchaea* (Lonchaeidae); floating puparium of *Elgiva rufa* (Panzer) (Sciomyzidae).

To Vera, my wife,
with thanks for sharing
my interest in insects

World List abbreviation: *Handbk Ident. Br. Insects.*

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Contents

Introduction

Knowledge of the larvae of Diptera lags far behind that of the adults. Of the 130 or so families of Diptera currently recognised in the world some 20 remain undescribed in the larval stages, including the following which occur in the British Isles: Acartophthalmidae, Asteiidae, Camillidae, Chyromyidae, Stenomicridae, Tethinidae and Trixoscelidae (formerly included in the Heleomyzidae). These families are, however, included in the present handbook with suggestions as to where their larvae should be sought. Of the more than 80,000 species of Diptera known to science probably less than two per cent have been described in the immature stages while adults of further new species are continually being described.

The families known best in the larval stage are usually those of medical or economic importance (e.g. Culicidae, Tipulidae). More recently families whose larvae are of importance as ecological indicators are being systematically studied (e.g. Chironomidae). For the majority of families, however, only a few species come into these categories and description of the immature stages has remained rather casual. Fortunately work on the immature stages of a particular family that occupies a distinct ecological niche has been recognised as a valuable research topic for university students working for higher degrees. This has resulted in several valuable and comprehensive studies, e.g. Dixon (1960) and Hartley (1961) on Syrphidae; Okely (1974) and Pitkin (1988, in part) on Sphaeroceridae.

Unfortunately all families do not lend themselves to concentrated short term study and may require a long and continuous effort before a reasonably comprehensive treatment can be achieved, e.g. Brindle's work on Tipulidae (1952–1967) and the 25 years required to produce Skidmore's (1985) book on Muscidae. Some fine work has been done in Europe especially by Dušek & Laska (1967, summary) on Syrphidae, and Hennig (1943a–1956) and Schumann (1953–1974) on Cyclorrhapha.

The identification of larvae beyond family level has thus remained a difficult process requiring a knowledge of, and access to, a very widely scattered literature. In this *Handbook* keys to families and sub-families of final stage larvae are given as far as this is possible. In some families further keys and illustrations are given to facilitate identification to genera and sometimes to species. For the latter the aim has been to include species of medical and economic importance, species commonly involved in the everyday enquiries of environmental health officers or the general public (including non-British species regularly introduced in imported food, etc.) and those species most frequently encountered as larvae during ecological surveys or of special value in teaching biology at school or university level. To further these aims some bionomic keys are given at appropriate points where a limited number of species occur in a restricted habitat. In a section on ecology there are some listings of families, genera or species to be found in specific habitats which, by restricting the possibilities, should facilitate more rapid identification by reference to the figures alone. A full index provides rapid access to ecological information in the text. There are brief general comments on eggs and pupae, and illustrations showing their diversity of form.

The following comprehensive specialist works on larvae are of value in identification. Hennig (1948–1952) is well illustrated and lists the world species described as larvae up to that time with a full bibliography. Peterson (1957) treats Nearctic species but Teskey (in McAlpine *et al.*, 1981) does so in much greater detail. Séguy (1950) gives much detailed information on all aspects of fly biology arranged under subject and habitat and similar information for British species is given in Stubbs & Chandler (1978) which includes a key to families of larvae (by Brindle & Smith). Brauns (1954) deals with terrestrial Diptera larvae and pupae and is well illustrated. Teskey (1984) gives a well-illustrated key to aquatic Diptera larvae. Oldroyd & Smith (in Smith, 1973) give a key to families of larvae of medical importance. Smith (1986) deals with species of forensic importance including those found on carrion (human and animal). Köppen (1972) covers some agricultural pest species. Askew (1971) and Clausen (1940) review parasitic Diptera. References to particular families are given in each section below.

As this book goes to press a very important two volume work has appeared on the immature stages of the Cyclorrhapha (Ferrar, 1987) and also part 2 of the *Manual of Nearctic Diptera* (McAlpine *et al.*, 1987), also covering Cyclorrhapha, has been published.

Acknowledgements

In his Introductory *Handbook* to the Diptera the late Harold Oldroyd (1970b) expressed the hope that a volume dealing with the early stages of flies would eventually be produced in this series. Indeed, we had intended that we should cooperate in such a venture but his early death sadly prevented this. Nevertheless many of his ideas expressed both verbally and in his writings, especially in his unique book *The Natural History of Flies* (1964), have stimulated an interest in the biology of flies among Dipterists, including the present author.

The following colleagues working in the British Museum (Natural History) (including those on the staff of the Commonwealth Institute of Entomology) are warmly thanked for reading appropriate sections of the work and for their constructive criticism, though they must not of course be held responsible for any inaccuracies that remain: John Boorman, John E. Chainey, Dr Peter S. Cranston, Dr Roger W. Crosskey, William R. Dolling, Dr Keith M. Harris (CIE), Dr Brian R. Pitkin, Adrian C. Pont, and Dr Ian M. White (CIE). Peter Chandler kindly checked the Mycetophilidae and Platypezidae and Phil Withers checked Psychodidae.

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Adrian Pont very kindly helped me with translating the subtleties of the German and Russian languages, thus avoiding many misinterpretations from the literature.

Finally I thank my wife for her careful and critical preparation of the typescript, her painstaking proof-reading and compilation of the index, and her enthusiastic support throughout my entomological activities.

Life-histories and ecology

Flies are highly adaptive insects and their larvae develop successfully in a very wide range of media, e.g. soil, rotting wood, plant and animal tissues (including man, alive or dead), fungi, dung and sewage, water (mostly fresh, sometimes brackish, occasionally marine), hot springs and geysers (some Ephydridae, Stratiomyidae) and even in petroleum pools (*Halaeomyia*, Ephydridae). Diptera exploit most of the available ecological niches in most of the biological roles, e.g. saprophages (many), commensals (some Scatopsidae, Chironomidae and Phoridae), predators (many), parasites (many), symbionts (some Chironomidae and algae) and scavengers.

Most of the protein feeding is done in the larval stage and the adults mostly need water to replace that lost during activity, especially flight, and sugars, from nectar or honeydew, to provide their energy. Some adults also take protein, e.g. predators, blood feeders, pollen feeders.

As a rule, aquatic larvae are carnivorous or live on algae. Apart from predators, the *precise* nature of the food taken by terrestrial larvae is often inadequately known. Thus the larva of the bluebottle (*Calliphora*) is classed as a carrion feeder but in fact bacteria on the carrion are probably the main food source (Roberts, 1971a). Similarly bacteria are probably the main source of food and vitamins for housefly larvae (Levinson, 1960). Baumberger (1919) found that many supposedly saprophagous fly larvae are actually mycetophagous. Clearly there is plenty of scope for careful research here.

The ancestral type of habitat for Diptera is probably in bogs and swamps and among mosses and decaying wood on drier land. Thus aquatic and terrestrial types of larvae developed together and both are present in many families of Nematocera (e.g. Tipulidae, Ceratopogonidae) and Brachycera (Stratiomyidae, Dolichopodidae, etc.). Many more Nematocera than Brachycera became purely aquatic, the Brachycera tending towards a more terrestrial mode of life. The larvae of Nematocera and Brachycera often exhibit a wide range of adaptative forms, but in the higher Brachycera (e.g. terrestrial Empididae and Dolichopodidae) the larvae are more streamlined and nearer the maggot type of larvae typical of the Cyclorrhapha, though the Syrphidae (Cyclorrhapha Aschiza) also have a remarkably wide range of forms.

Among the Cyclorrhapha, the Acalyptratae and Calyptratae have exploited most of the possible habitats arising from the decomposing 'compost' type of breeding medium through dung and carrion to living plant and animal tissues.

Some specific life histories are described under the Medical and Economic sections and under each family. Some specific ecological associations are listed here under the sections on agricultural importance and, for Diptera occupying macro- and micro-habitats, Stubbs & Chandler (1978), which complements Colyer & Hammond (1968), should be consulted. Séguy (1950) is also useful. Broader ecological issues are discussed by Oldroyd (1964). Some specific habitats occupied by Diptera in their larval stages are listed below, with an indication of those most likely to be found there.

Soil. Many families (except those with purely aquatic larvae) have some members which may occasionally be found in soil in the immature stages, usually for the purpose of pupation. However the families most likely to be encountered in sampling soil are: Tipulidae, Bibionidae, Chironomidae, Therevidae, Stratiomyidae, Tabanidae, Rhagionidae, Asilidae, Empididae, Dolichopodidae, Phoridae, Sphaeroceridae and Muscidae.

Dead wood. Over 200 species representing 42 families spend their immature stages in dead wood. The type of wood can influence the fauna, conifers supporting different species to deciduous trees. Rates of decay between tree species also vary. However, since dead wood is not readily identifiable in practice, the records are grouped here.

Keys to the larvae of wood-inhabiting Diptera are provided by Krivosheina & Mamaev (1967) and Mamaev, Krivosheina & Pototskaya (1977) key species predaceous upon tree trunk 'pests'. Teskey (1976) deals with Nearctic species associated with trees. Kitching (1971) deals specifically with the fauna of rot-holes.

Diptera most frequently encountered are Tipulidae (especially *Ctenophora*), Mycetophilidae, Sciaridae, Ceratopogonidae (especially *Forcipomyia*), Cecidomyiidae (especially Lestremiinae), Stratiomyidae, Xylomyidae, Xylophagidae, Empididae (especially Tachydromiinae, Ocydromiinae), Dolichopodidae, Syrphidae, Pallopteridae, Lonchaeidae, Clusiidae and Muscidae (especially *Phaonia*). Where bark beetles (*Scolytus*) are present, larvae of *Medetera* (Dolichopodidae) and *Odinia* (Odiniidae) may occur. In nests of Sphecidae (Hymenoptera) the larvae or puparia of Sarcophagidae or *Eustalomyia* (Anthomyiidae) may be found.

Puparia of parasitic species may also be found: Tachinidae, e.g. *Triarthria* (on earwigs), *Loewia* (on centipedes), *Admontia* (*Trichopareia*) (on tipulid larvae); Rhinophoridae (on woodlice).

Dung. Skidmore (in Stubbs & Chandler, 1978) lists the British species associated with various types of dung and notes that about five per cent of the British Diptera (*c.* 300 species) have been recorded as coprophilous, two per cent (*c.* 120 species) exclusively in the larval stage. Kumar & Lloyd (1976) provide a bibliography of arthropods associated with dung. The association of flies with dung has received considerable attention due to the possible health hazards of adults flying from excrement to foodstuffs but precise ecological studies are few.

The following papers deal with the fly faunas of different types of dung: cow (Laurence 1953b–55, Papp & Garzó, 1985); dog (Disney, 1973a, 1976a); human (Howard, 1900, Steyskal, 1957); horse and donkey (Papp, 1976); sheep (Papp, 1985).

Of the 38 families listed by Skidmore the following are most frequently encountered as larvae in dung and listed in approximately the order of abundance found in cow dung by Laurence (1954): Psychodidae, Sphaeroceridae, Sepsidae, Scathophagidae, Trichoceridae, Anisopodidae, Ceratopogonidae, Muscidae (many predaceous), Chironomidae (*Smittia*), Stratiomyidae, Scatopsidae, Empididae (? all predaceous), Cecidomyiidae, Syrphidae. The entry under dung in the index indicates references in the text to that of specific animals.

Diptera breeding in sewage include: Psychodidae, Chironomidae, Anisopodidae, Syrphidae (*Eristalis*), Ephydridae, Sphaeroceridae and Scathophagidae (Lloyd *et al.*, 1940; Green, 1970; Busvine, 1980).

Carrion. Following the death of an animal various insects and other invertebrates, but especially Diptera and Coleoptera, invade the corpse in a succession of about five distinct 'waves' of species. Each wave coincides with a particular stage of decay of the corpse and may contain not only carrion feeders but also their predators and parasites. The feeding of Diptera larvae rapidly accelerates the decomposition of the corpse. A general account of carrion fauna and succession (especially on man) is given in Smith (1986b) (see also under Medical Importance—Forensic). Detailed individual studies of succession involving Diptera on particular animals in Britain are few: snails (Beaver, R. A., 1971), rabbit (Chapman, R. F. & Sankey, 1955), voles (Lane, 1975), fox (Smith, 1975). The families important as larval carrion feeders are as follows in their approximate order of appearance on a corpse: Calliphoridae (*Calliphora, Lucilia* and later *Cynomya, Phormia, Protophormia*), Muscidae (*Musca, Muscina*), Sarcophagidae, Piophilidae, Fanniidae, Drosophilidae, Sepsidae, Syrphidae (*Eristalis*), Ephydridae (*Teichomyza*), Muscidae (*Ophyra*), Phoridae, Piophilidae (including Thyreophoridae).

Water. The distinction between truly terrestrial and truly aquatic larvae is not always a clear one. Habitats range from marshy soil, among aquatic mosses, on rock face seepages, ditches, plant axils and tree rot holes to larger bodies of standing or flowing water.

Most families of Nematocera, several families of Brachycera and a few families of Cyclorrhapha have truly aquatic immature stages. Exclusively aquatic: Chaoboridae, Culicidae, Dixidae, Ptychopteridae, Simuliidae and Thaumaleidae. Mostly aquatic: Ceratopogonidae, Chironomidae. Families with some aquatic members: Psychodidae, Tipulidae, Stratiomyidae (Stratiomyinae, Clitellariinae), Rhagionidae (*Atherix, Atrichops*, now regarded as a separate family Athericidae), Tabanidae (mostly wet soil, *Chrysops* and some *Hybomitra* truly aquatic), Empididae (Hemerodromiinae, Clinocerinae, Oreogetoninae), Dolichopodidae, Syrphidae (Eristalini and *Chrysogaster*), Ephydridae, Sciomyzidae, Scathophagidae (*Spaziphora, Hydromyza*), Muscidae (most Limnophorinae, probably some Coenosiinae, *Phaonia exoleta* Meigen in tree rot holes (see also under plants), *Graphomya maculata* Scopoli in mud in puddles).

The few marine species are dealt with in the next section.

Sea shore. Diptera of marine environments are treated in Cheng (1976). Some breed in the littoral or intertidal zone: Chironomidae (*Thalassomya, Psamathiomya, Halocladius, Clunio* and *Thalassosmittia*), Tipulidae (*Limonia* (*Geranomyia*) *unicolor* Haliday), Dolichopodidae (*Aphrosylus, Dolichopus nubilis* Meigen, *Machaerium, Hydrophorus oceanus* Macquart, *Hygrocoleuthus, Rhaphium consobrinum* Zetterstedt), Empididae (? *Chersodromia*—immature stages unknown), Syrphidae (*Eristalinus aeneus* (Scopoli)), Ephydridae (*Parydroptera*), Canacidae.

On the drift line, among seaweed (see Backlund, 1945a), larvae of the following families occur: Coelopidae, Helcomyzidae, Sepsidae (*Orygma*), Sphaeroceridae (*Thoracochaeta* spp., ? *Leptocera* (*Rachispoda*) *fuscipennis* Haliday), Scathophagidae (*Scathophaga litorea* Fallén, *S. calida* Curtis, *Ceratinostoma ostiorum* Curtis), Anthomyiidae (*Fucellia*), Fanniidae (*Fannia canicularis*).

Coastal sand dunes may be a harsh environment but Ardö (1957) found 750 species of Diptera on dunes in Sweden. However, less than 50 species were confined to dunes (stenotopic). The following Diptera are *known* to breed in the sand: Scatopsidae (*Aspistes berolinensis* Meigen), Tipulidae (*Tipula juncea* Meigen), Asilidae (*Philonicus albiceps* Meigen), Therevidae (*Thereva annulata* F.), Chamaemyiidae (larvae predaceous on coccids at base or roots of grasses), Trixoscelidae (*Trixoscelis* puparia have been found in sand under sea sandwort *Honkenya*, but the larva is undescribed and probably develops in guano), Anthomyiidae (*Delia* spp., probably on roots of grasses).

In view of the number of species associated with this habitat, and the few species reared, there is clearly scope for further research.

Predators. Many truly aquatic Nematocera larvae, many terrestrial Brachycera, but only a few Cyclorrhapha are predaceous in the larval stage. The prey usually consists of other insect larvae or small worms. Some families are specialist feeders, e.g. Syrphini on aphids, Sciomyzidae on molluscs. The family distribution of the predaceous habit in larvae is as follows: Tipulidae (Pediciini, Hexatomini), Mycetophilidae (Keroplatiinae), Cecidomyiidae (some Cecidomyiidi), Chaoboridae, Culicidae (only Toxorhynchitini), Ceratopogonidae (Ceratopogoninae), Chironomidae (Tanypodinae, some Chironominae, few Orthocladinae), Tabanidae, Rhagionidae (including Athericidae), Xylophagidae, Xylomyidae, Stratiomyidae (Pachygastrinae), Therevidae, Scenopinidae, Asilidae, Empididae, Dolichopodidae, Phoridae, Syrphidae (on aphids, etc.), Chamaemyiidae (on Homoptera), Drosophilidae (*Acletoxenus* on Homoptera), Chloropidae (*Chloropisca* on sugar beet root aphid), Sciomyzidae (molluscs), Scathophagidae, Muscidae (Limnophorinae, Coenosiinae, Phaoniinae some Mydaeinae, *Muscina, Ophyra, Hydrotaea,* etc.), Anthomyiidae (some *Delia*, etc.).

Parasites and parasitoids. Parasitic larvae are infrequent in the Nematocera and Brachycera and become more common in the Cyclorrhapha where it is the normal lifestyle for some families, e.g. Conopidae, Tachinidae. Some families have parasitic species abroad but not in Britain and others have a wider range of hosts abroad, e.g. Bombyliidae, Conopidae. The parasitic habit is distributed in British families as follows. The hosts in Britain are indicated in brackets (see also under hosts). Useful references are Clausen (1940), Askew (1971): Chironomidae (*Parachironomus, Glyptotendipes* in aquatic molluscs), Cecidomyiidae (Homoptera), Acroceridae (spiders), Bombyliidae (Hymenoptera, Orthoptera, Lepidoptera), Phoridae (*Phalacrotophora* on Coccinellidae (Coleoptera), *Borophaga incrassata* Meigen on *Bibio* (Diptera), *Pseudacteon* on ants), Pipunculidae (Homoptera), Chloropidae (*Siphonella* in spider egg sacs), Sciomyzidae (parasitoid on molluscs), Calliphoridae (*Pollenia* and *Bellardia* in earthworms; *Melinda, Eggisops*, molluscs), Rhinophoridae (woodlice), Sarcophagidae (*Senotainia*, wasps; *Sarcophaga*, spider egg cocoons, insects, etc, snails), Oestridae (sheep, deer), Hypodermatidae (cattle, horses, deer), Gasterophilidae (horses), Tachinidae (insects, including other Diptera).

Nests. The larvae of several families are specifically associated with nests of social insects, birds or mammals, as commensals, scavengers or parasites as follows.

Nests of social insects (useful reference O'Toole in Stubbs & Chandler, 1978): Ceratopogonidae, Sciaridae, Scatopsidae (ants), Bombyliidae (bees), Phoridae (e.g.

Aenigmatias on ants), Syrphidae (*Microdon*, ants; *Volucella*, wasps), Sphaeroceridae, Milichiidae (ants), Braulidae (honey-bees), Sarcophagidae (Miltogramminae, wasps and bees), Fanniidae, Muscidae.

Birds' nests (useful references: Hicks, 1959, 1963a, 1971; Woodroffe, 1953): Scatopsidae, Chironomidae (*Bryophaenocladius nitidicollis* (Goetghebuer)), Scenopinidae, Phoridae, Chyromyidae, Piophilidae (Neottiophilinae), Carnidae, Heleomyzidae, Trixoscelidae, Sphaeroceridae, Fanniidae, Muscidae (some *Helina, Hydrotaea, Muscina, Ophyra*), Anthomyiidae (*Anthomyia*), Sarcophagidae, Calliphoridae (especially *Protocalliphora, Calliphora*), Hippoboscidae.

Mammal burrows and nests (useful references: Hackman, 1967; Hutson, in Stubbs & Chandler, 1978): Heleomyzidae, Sphaeroceridae, Phoridae, Camillidae, Sciaridae.

Fuller lists of rearings of Diptera from nests are given in the references cited. Careful work is still needed on the ecology of nest-frequenting Diptera. E. B. Basden's extensive collection of Diptera from nests is available for study in the Royal Museum of Scotland (see Rotheray, 1989 for summary).

Plant feeders. The larval stages of many Diptera are described in the literature as living in and feeding on 'decaying vegetation'—a category not specifically included in this Handbook, except for dead wood. However, many terrestrial (some aquatic larvae feed on algae and mosses) species feed on the living tissues of plants in specific ways as listed below. Records marked with a ? need further investigation or confirmation. Larvae of agricultural importance are treated more fully in the section so titled.

Surface leaf feeders: Tipulidae (Cylindrotominae, mosses), Mycetophilidae (*Boletina*, liverworts; *Gnoriste*, ? mosses; *Docosia*, ? lichens), ? Rhagionidae (*Ptiolina* on mosses).

Leaf-miners: Cecidomyiidae (some Lestremiinae, liverworts; higher plants), Chironomidae, ? Sciaridae (*Phytosciara* on *Ranunculus*), Rhagionidae (*Spania nigra* Meigen, liverworts), Dolichopodidae (*Thrypticus*, in stems), Syrphidae (some *Cheilosia*), Agromyzidae, Tephritidae (some), Anthomyzidae (*Anagnota, Paranthomyza*), Lauxaniidae, Psilidae, Drosophilidae (*Scaptomyza*), Ephydridae, Scathophagidae, Anthomyiidae (especially *Pegomya*). Mines caused by Diptera (unlike other orders) show primary and secondary feeding tracks causing a characteristic herring-bone pattern and linear mines have the frass lying alternately on the two sides (Hering, 1951); this is because mining Diptera larvae feed on their sides, facing first one direction, then the other.

Gall-formers: Cecidomyiidae, Tephritidae, ? Lauxaniidae (*Calliopum*, clover and *Viola*), Chloropidae (*Lipara*, reeds; *Chlorops pumilionis* Bjerkander, barley).

Many other Diptera larvae feed in stems, roots, flowers, seeds and fruits, some of which are of economic importance (see section on Agricultural Importance). Uffen & Chandler (in Stubbs & Chandler, 1978) list the Diptera associated with the higher plants. Teskey (1976) gives an account of Diptera larvae associated with trees (in North America), including those developing in sap exudates. Kitching (1971) deals specifically with the insect fauna of tree rot-holes (see index also).

Fungi. The larval Diptera found in fungi have been the subject of some detailed studies (Buxton, 1960; Smith, 1956; Trifourkis, 1977). Chandler (in Stubbs & Chandler, 1978) lists in detail the known fungus associations of British Diptera, which involve larvae of the following families: Trichoceridae, Tipulidae, Psychodidae, Ceratopogonidae, Chironomidae, Anisopodidae, Mycetophilidae, Sciaridae, Scatopsidae, Cecidomyiidae, Scenopinidae, Empididae (as predators), Dolichopodidae, Phoridae, Platypezidae, Syrphidae (some *Cheilosia*), Platystomatidae, Dryomyzidae, Heleomyzidae, Sepsidae, Lauxaniidae, Sphaeroceridae, Lonchaeidae, Piophilidae, Odiniidae, Asteiidae, Drosophilidae, Chloropidae, Tachinidae (as parasites of Lepidoptera (Tineidae)), Anthomyiidae, Fanniidae, Muscidae (as predators).

Only six cases of Diptera inducing galls in fungi are known: *Myocecis ovalis* Edwards (Cecidomyiidae) on *Hypochnus; Agathomyia wankowiczi* (Schnabl) (Platypezidae) on *Ganoderma applanatum* (Pers.) Pat.; *Drosophila phalerata* Meigen (Drosophilidae) on *Psathyra; Mycetophila blanda* Winnertz (Mycetophilidae) on *Lactarius deliciosus* L. ex Fries and an undescribed dipteran on *Daedalea quercina* L. and *Conocybe* (Harris & Evans, 1979).

Families recorded only as visiting adults are not included.

Caves. *Speolepta leptogaster* (Winnertz) (Mycetophilidae) is the only British fly that is almost an exclusive cave-dweller (troglobite, troglobiont, troglobie). This species breeds in caves, the larva living in a slime tube attached by lateral strands to the damp cave walls and ceiling. The larva forages from the tube to feed on algae and fungi. The head capsule is pale, which gives it the superficial appearance of a nematode. Mycetophilidae of the genus *Macrocera* may also breed in caves.

Frequent cave dwellers that also occur outside caves (troglophiles) are *Trichocera maculipennis* Meigen (Trichoceridae), *Triphleba antricola* (Schmitz) (Phoridae), and *Terrilimosina racovitzai* (Bezzi) (Sphaeroceridae).

Heleomyza serrata (L.) and *Scoliocentra villosa* (Meigen) (Heleomyzidae) occur frequently in caves but are equally common outside. *Chyromya* species (Chyromyidae) also occur in caves. The dung of bats (or other mammals), fungi, other vegetation, or the presence of water may all serve as attractive breeding media to Diptera. The phorid *Megaselia melanocephala* parasitizes eggs of the common cave spider *Meta menardi* Latreille.

Many adult Diptera may shelter or hibernate in caves (see Hutson in Stubbs & Chandler, 1978). Matile (1970) reviews the Diptera fauna of caves worldwide.

Agricultural and economic importance

The larvae of a few Diptera *regularly* attack food crops and farm animals or important horticultural plants and may be regarded as pests. These are listed below and the more significant species are also included in the notes, illustrations and some keys under the appropriate family. *Occasional* pest species are mentioned under the appropriate family.

The common names used follow Seymour (1979) and useful general texts are Edwards, C. A. & Heath (1964) and Buczacki & Harris (1981).

TIPULIDAE	
Tipula oleracea Linnaeus (crane fly, leatherjacket)	Oats, wheat, turnip, mangold, potato. Worst damage in spring, especially on newly ploughed land
**T. paludosa* Meigen (crane fly, leatherjacket)	Ditto
Nephrotoma appendiculata (Pierre) (crane fly, leatherjacket)	Ditto, more frequently in gardens
BIBIONIDAE	
Bibio marci (Linnaeus) (St. Mark's fly)	Celery, lettuce, asparagus, grass, *Polyanthus, Saxifraga*
Bibio, other spp. (March flies)	Winter wheat, grass, celery, sugarbeet, etc. (see Freeman & Lane, 1985)
Dilophus febrilis (Linnaeus) (fever fly)	Spring barley, grass, maize, sugarbeet, potato, lettuce, hops, tomato, chrysanthemum
CHIRONOMIDAE	
Bryophaenocladius	Roots of greenhouse plants
Smittia	Barley, winter corn, winter wheat

SCIARIDAE	
**Bradysia brunnipes* (Meigen) (mushroom Sciarid)	Mushroom
**Lycoriella auripila* (Winnertz) (mushroom Sciarid)	Ditto, also cucumber in greenhouses
**L. solani* (Winnertz) (mushroom Sciarid)	Ditto
Plastosciara perniciosa (Edwards)	Cucumber seedlings in greenhouses
Pnyxia scabei (Hopkins)	Potato; tomato and cucumber seedlings in greenhouses
CECIDOMYIIDAE	
Campylomyza ormerodi (Kieffer) (red clover gall gnat)	Red clover
Contarinia humuli (Theobald) (hop strig maggot)	Hops
C. nasturtii (Kieffer) (swede midge)	Swede, cabbage, cauliflower, rape, kale, turnip, radish
C. pisi (Winnertz) (pea midge)	Peas (pod & pea)
C. pyrivora (Riley) (pear midge)	Pear
C. tritici (Kirby) (wheat midge)	Wheat; rye, barley
Dasineura brassicae (Winnertz) (brassica pod midge)	Rape, cabbage, turnip, radish, mustard, swede, beet
D. leguminicola (Lintner) (clover seed midge)	Red and white clover flowers
D. tetensi (Rübsaamen) (blackcurrant leaf midge)	Blackcurrant
D. trifolii (Löw, F.) (clover leaf midge)	White clover leaves
Halodiplosis marginata (Von Roser) (saddle gall midge)	Wheat, barley
Henria psalliotae Wyatt (mushroom cecid)	Mushrooms
Heteropeza pygmaea Winnertz (mushroom cecid)	Ditto
Lestremia cinerea Macquart (mushroom midge)	Ditto
Mycophila barnesi Edwards (mushroom cecid/midge)	Ditto
M. speyeri (Barnes) (mushroom cecid/midge)	Ditto
Mayetiola avenae (Marchal) (oat stem midge)	Oats
M. destructor (Say) (Hessian fly)	Wheat; barley, rye
Resseliella theobaldi (Barnes) (raspberry cane midge)	Raspberry
**Rhopalomyia chrysanthemi* (Ahlberg) (Chrysanthemum midge)	Chrysanthemum
Sitodiplosis mosellana (Géhin) (wheat midge)	Rye, oats or barley
PHORIDAE	
**Megaselia bovista* (Gimmerthal) (mushroom flies)	Mushroom
**M. halterata* (Wood) (mushroom flies)	Ditto

PHORIDAE *(cont.)*	
**M. nigra* (Meigen) (mushroom flies)	Ditto
SYRPHIDAE	
**Eumerus strigatus* (Fallén) (lesser bulb/narcissus fly)	Bulbs of *Narcissus, Amaryllis*, snowdrops, etc., occasionally onion, parsnip, potato
**E. tuberculatus* Rondani (lesser bulb/narcissus fly)	Ditto
Merodon equestris (Fabricius) (large bulb/narcissus fly)	Ditto
TEPHRITIDAE	
Euleia (= *Acidia*) *heracleii* (Linnaeus) (celery fly)	Celery, parsnip
Platyparea poeciloptera (Schrank) (asparagus fly)	Asparagus (no recent records)
PSILIDAE	
Psila nigricornis Meigen (Chrysanthemum stool miner)	Chrysanthemum; carrot, lettuce
**Ps. rosae* (Fabricius) (carrot fly)	Carrot, also parsnip, celery, parsley, turnip
OPOMYZIDAE	
Geomyza tripunctata Fallén (grass & cereal fly)	Grasses; occasionally wheat
Opomyza florum (Fabricius) (grass & cereal fly)	Grasses; cereals, especially wheat
EPHYDRIDAE	
Hydrellia griseola (Fallén) & spp. (cereal leaf-miners)	Grasses; cereals (see Deonier, 1971: 106)
H. nasturtii Collin (watercress stem miner)	Watercress
DROSOPHILIDAE	
Scaptomyza apicalis Hardy	Broccoli, sprouts, cauliflower, turnip, radish & watercress; occasionally damages swede, rape, kale, mustard
AGROMYZIDAE	
Agromyza nigrella Rondani (cereal leaf miner)	Winter wheat
A. rondensis Strobl (cereal leaf miner)	Ditto
Liriomyza bryoniae (Kaltenbach) (tomato leaf miner)	Glasshouse tomato, cucumber
L. congesta (Becker) (pea leaf miner)	Pea and bean
L. pisivora Hering (pea leaf miner)	Pea
Ophiomyia simplex (Loew)	Asparagus
Phytobia cerasiferae (Kangas)	Plum trees
Phytomyza horticola Goureau	Pea and bean
P. rufipes Meigen	Cauliflower, cabbage, broccoli, rape
P. syngenesiae (Hardy)	Chrysanthemum

CHLOROPIDAE

Chlorops pumilionis (Bjerkander) (= *taeniopus* Meigen) (gout fly)	Barley; wheat, rye
Meromyza saltatrix (Linnaeus) (grass fly)	Grasses; wheat, barley, rye
**Oscinella frit* (Linnaeus) (frit fly)	Oats; sweetcorn, barley, wheat, rye, maize, rye-grass, meadow fescue

HYPODERMATIDAE

**Hypoderma bovis* (Linnaeus) (warble fly)	Cattle, occasionally horses
H. diana Brauer (deer warble fly)	Deer
H. lineatum (Villers) (lesser warble fly)	Cattle, occasionally horses

OESTRIDAE

Oestrus ovis Linnaeus (sheep nostril fly)	Sheep, goats

GASTEROPHILIDAE

Gasterophilus haemorrhoidalis (Linnaeus) (nose bot fly)	Horse, donkey
G. intestinalis (Degeer) (horse bot fly)	Ditto
G. nasalis (Linnaeus) (throat bot fly)	Ditto
G. pecorum (Fabricius)	Ditto

CALLIPHORIDAE

**Calliphora vicina* Robineau-Desvoidy (bluebottle)	Sheep (secondary)
C. vomitoria (Linnaeus) (bluebottle)	Ditto
Lucilia caesar (Linnaeus) (greenbottle)	Sheep (occasional)
**L. sericata* (Meigen) (sheep maggot fly)	Sheep

SCATHOPHAGIDAE

Nanna (= *Amaurosoma*) spp. (timothy flies)	Timothy grass; winter rye
Norellia spinipes (Meigen)	*Narcissus* (daffodils)

ANTHOMYIIDAE

**Delia antiqua* (Meigen) (onion fly)	Onion, leek, shallot, tulip
**D. radicum* (L.) (= *brassicae*) (Wiedemann) (cabbage root fly)	Cabbage, cauliflower, sprouts, kale, radish, turnip, swede, mustard, beet, celery & stocks
D. cardui (Meigen) (carnation fly)	Carnation
**D. coarctata* (Fallén) (wheat bulb fly)	Wheat, rye, barley
D. echinata (Séguy) (spinach stem fly)	Spinach
D. floralis (Fallén) (turnip root fly)	Turnip, swede

ANTHOMYIIDAE *(cont.)*	
D. platura (Meigen) (bean seed fly)	Bean, turnip, beet, radish, swede, potato, onion, pea, cabbage, sprouts, cauliflower, lettuce, rye, clover, oats, wheat
Pegohylemyia gnava (Meigen) (lettuce seed fly)	Lettuce
**Pegomya hyoscami* (Panzer) (beet leaf miner)	Mangold, beet, sugarbeet, spinach
P. rubivora (Coquillett) (loganberry cane fly)	Loganberry, raspberry, blackberry
Phorbia securis (Tiensuu) (late wheat shoot fly)	Wheat
P. sepia (Meigen) (late wheat shoot fly)	Wheat, oats

Advisory leaflets on the more important species (marked * above) and some under crops (e.g. *Brassica*, mushrooms) are available from the Ministry of Agriculture, Fisheries and Food (Publications), Tolcarne Drive, Pinner, Middlesex HA5 2DT.

In addition to the species whose larvae attack food crops listed above several Cecidomyiidae are occasional pests of grasses, trees and shrubs (especially willows, used for cricket bats and basket making) and ornamental plants (see Barnes, H. F., 1946–1956); several other Agromyzidae also attack garden plants (see Spencer, 1973b).

Diptera larvae may be found in buildings associated with food production. Several flies breed in poultry houses and the most troublesome is *Fannia canicularis* Linnaeus (Fanniidae) though Muscidae (*Musca domestica* Linnaeus, *Muscina stabulans* (Fallén) and *Ophyra* spp.) also occur. Slaughterhouses are frequented by the carrion flies *Lucilia, Calliphora* and *Sarcophaga*. Kühlhorn (1964) found 330 species of flies in 47 families associated with stables. Mushroom houses yield Sciaridae and Phoridae. Maggots (gentles) bred commercially for use by fishermen include *Calliphora* and *Protophormia*.

Species specifically associated with excrement are discussed under life-histories and ecology.

Other families of Diptera are of some agricultural (including veterinary) and economic importance, but not as larvae, e.g. Ceratopogonidae, Tabanidae, Muscidae, Hippoboscidae.

Medical, environmental health and veterinary importance

The larvae of species which suck blood or transmit disease as adults can be of indirect medical or veterinary importance, e.g. Ceratopogonidae, Culicidae, Simuliidae and Tabanidae. In these groups (especially abroad) it is often more effective to direct control measures against the larvae (mostly aquatic) rather than the adults. Because of this the immature stages have been intensively studied and their taxonomy and ecology are better known than in other families (see Smith, 1973). The larvae of other families may be more directly involved with man.

Myiasis

Diptera larvae sometimes feed on or in living animals including man and this condition is called myiasis, a term proposed by Hope (1840) in his early treatise on the subject. Zumpt (1965) fully covers the subject for the Old World, James (1947) for the New World and Smith (1973, world) is useful. Only the (much rarer) British cases involving man are cited in detail here though all the families involved are listed. No doubt many more cases occur than are diagnosed and recorded. Where myiasis is a normal way of life for fly larvae in animals this is described under the particular Diptera family concerned. The types of myiasis can be further classified as follows.

1. Blood-sucking maggots. E.g. Calliphoridae (*Auchmeromyia senegalensis* Macquart(=*luteola* Fabricius), the Congo floor-maggot (Afro-tropical)); Tabanidae (in paddy fields in Japan); Therevidae (fig. 161, Smith, 1979a, 1986a, British cases); *Protocalliphora* on birds.

2. Dermal and subdermal myiasis. Larvae penetrate unbroken skin or enter wounds or form boils or other lesions, either at the site of entry or elsewhere, e.g. Calliphoridae, Gasterophilidae, Hypodermatidae, Muscidae and Sarcophagidae.

Oldroyd (1964) reports 'I have known a female *Sarcophaga* to fly to a coat, the sleeve of which had been soiled with blood from a shot pheasant and immediately lay a batch of young larvae upon it'. *Lucilia sericata* (Meigen), a common greenbottle, is also the sheep maggot fly (fig. 809), the causal agent of sheep strike. Larvae of *Lucilia* and *Calliphora* may occur in cases of wound myiasis in man and animals. Calliphorid larvae (*Lucilia sericata, L. caesar* (Linnaeus) and *Phormia regina* (Meigen) have been used to clean wounds of necrotic tissue on the battlefield (Hinman, 1933, Imms, 1939, Greenberg, 1973) and may even exude an antibiotic (Pavillard & Wright, 1957). Osteomyelitis and other kinds of non-healing wounds have also been treated in this manner, e.g. heat burns, X-ray burns, varicose and diabetic ulcers, etc. (see also below under *Musca domestica*).

First instar larvae of *Gasterophilus* can cause a creeping myiasis in man, usually on the face and buttocks (Zumpt, 1965) but I know of no British cases. *Hypoderma* may also be incriminated in this category (Smart, 1939) but is usually involved in nasopharyngeal myiasis (see below).

Musca domestica larvae may occur in cases of human myiasis where urine is involved: e.g. in neglected cots or napkins of infants (Mumford, 1926, Chapman, R. K., 1944); in the feet and footwear of incontinent geriatric patients (see also urogenital myiasis). *M. domestica* has also been used to clean gangrenous wounds as the larvae do not attack healthy tissue (as other genera will—see above). Healing can commence 48 hours after treatment begins (Imms, 1939).

3. Nasopharyngeal myiasis. This includes invasion of the nasal fossae, frontal sinuses, pharyngeal cavities, eyeballs, eye-sockets and (aural myiasis) ears, e.g. Calliphoridae, Cuterebridae (non-British), Gasterophilidae, Hypodermatidae, Mycetophilidae, Oestridae, Phoridae, Psychodidae, Sarcophagidae and Scenopinidae.

Lucilia has been involved in a case of human aural myiasis in the U.K. (Smart, 1936) and several other cases are known from Europe and North America. Occasionally first instar larvae (fig. 693) of *Hypoderma* (mostly *lineatum* Villers) (warble flies of cattle) have been found in the orbit or eyeball of man, which they will completely destroy if they are not extracted quickly. I know of only two British cases involving *H. lineatum*, one in Devon (Style, 1924) and the other in the Hope Valley of Derbyshire in 1945 when this locality suffered 'the worst "gadfly" epidemic for many years' (Smith, A. & Greaves, 1946) (the term 'gadding' of cattle is properly used in connection with their response to the attention of the blood-sucking adult Tabanidae). The larvae of *Oestrus ovis* Linnaeus (the sheep nasal bot fly, fig. 684) may also occur in the human eye, but are far less serious than *Hypoderma* since they do not survive beyond the first instar. Anderson (1935) found a dead first instar larva of *Gasterophilus intestinalis* (De Geer) in the eye of a patient (in the U.S.A.). It is possible that an egg was transferred by wiping the back of the hand across the eye. Zumpt (1965) records (in Africa) seeing *G. intestinalis* repeatedly ovipositing on the backs of human hands when held with the palms over horses' lips.

Hurd (1954) records an unique case of 13 larvae of *Boletina* (Mycetophilidae) and several other insects being passed alive from the left atrum of his sinus following prolonged use of the aspirator or 'pooter' for insect collecting.

The occurrence of Psychodidae in nasopharyngeal myiasis involves the non-British *Clogmia* (= *Telmatoscopus*) *albipunctatus* Williston (Mohammed & Smith, 1976) but British species occurring in similar habitats (outdoor washtubs, etc.) could be similarly incriminated (e.g. *Psychoda alternata* Say, *Ps. albipennis* Zetterstedt) already recorded in case of intestinal and urogenital myiasis. The accidental inhaling of gravid females of these small flies through the mouth or nostrils could have given rise to some of these cases and is the probable explanation for the unique case of lung myiasis produced by Phoridae reported in a Japanese student and runner (Komori *et al.*, 1978).

Larvae of *Lucilia, Fannia, Sarcophaga* and *Oestrus* have been recorded in (rare) cases of aural miasis.

4. Intestinal (enteric) myiasis. This category includes larvae adapted to living as obligatory parasites in the intestines, e.g. Gasterophilidae (horse bot-flies, see under that family) and those that may be accidentally swallowed in food and be passed in the faeces and some which may invade the intestine via the rectum as facultative parasites, e.g. Anisopodidae, Calliphoridae, Drosophilidae, Ephydridae, Fanniidae, Micropezidae, Muscidae, Phoridae, Piophilidae, Psychodidae, Sarcophagidae, Sepsidae, Sphaeroceridae, Stratiomyidae, Syrphidae, Therevidae, Tipulidae.

It is improbable that the majority of ingested fly larvae can survive in the digestive tract when this is in a normal state. However, the ingestion of larvae often causes diarrhoea and the larvae are then passed out alive in the faeces. Some larvae seem especially able to survive such conditions (e.g. Piophilidae, Phoridae). True rectal myiasis may occur when flies are attracted to excreta and lay eggs on or near the anus. Subsequently larvae may penetrate the posterior part of the rectum and obtain oxygen by placing their posterior spiracles in the anal region (causing irritation there). Larvae of *Eristalis* are well adapted to this mode of life and there are many records of their involvement in myiasis including Britain (Mumford, 1926; Cookson & Oldroyd, 1937). *Fannia canicularis* (Linnaeus) and *F. scalaris* (Fabricius) have also been involved in rectal myiasis. The larvae of *Sarcophaga* may cause true rectal myiasis and Zumpt (1965) records larvae of *S. cruentata* Meigen (= *haemorrhoidalis* (Fallén)) seen leaving and re-entering the anus of a child (in Sydney).

5. Urogenital myiasis. There are no obligatory dipterous parasites in the urogenital system; all are casual invaders (facultative parasites), e.g. Anisopodidae, Calliphoridae, Ephydridae, Fanniidae, Muscidae, Phoridae, Psychodidae, Sarcophagidae, Syrphidae, Scenopinidae.

Sylvicola (= *Anisopus*) *fenestralis* (Linnaeus) larvae have been recorded from the urinary tract of female (Smith & Taylor, 1966) and male (Morris, R. F., 1968) patients. Thompson J. H. *et al.* (1970) record a larva of *Scenopinus* from the urine of a woman in the U.S.A. James (1947) says of *Teichomyza fusca* Macquart (Ephydridae) that 'numerous cases of urinary myiasis have been recorded'; some of these are European but I know of no British cases (see Fossil section, archaeological sites). *Musca domestica* has been involved in cases of urogenital myiasis and a fascinating account is given by Leon (1921) in which a male student in Romania actually ejaculated maggots (also summarized in Zumpt, 1965: 34).

With their predilection for urine, it is not surprising that *Fannia canicularis* and *F. scalaris* have frequently been involved in this type of myiasis in humans (Haddow & Lumsden, 1935). Larvae of *Psychoda albipennis, Ps. alternata, Megaselia* sp., *Calliphora vicina* and *Sarcophaga* species have also been reported as causing urogenital myiasis.

Eristalis has been recorded from the vagina of a cow (and tinned pears!).

Forensic or medico-legal importance

After death animal and human corpses are invaded by a succession of insects and other invertebrates associated with the various stages of decomposition. Not surprisingly, many of the Diptera involved are of the same families, and frequently the same species, as those involved in myiasis. The most important decomposers are blowfly (Calliphoridae) larvae of the genera *Calliphora* and *Lucilia*.

Identification of the species involved, combined with a knowledge of their rates of development and ecology, enables an estimate of time of death to be made. It may also be possible to establish if a body has been moved or concealed for part of the time. The faunal succession on carrion is dealt with in the section on life-histories and ecology and the forensic aspects are fully covered elsewhere (Smith, 1986b).

Another important medico-legal involvement with larvae is their presence on foodstuffs, drugs, etc. in domestic or commercial premises. Frequently entomologists are asked, usually by environmental health officers, not only to identify such larvae but to give additional information on the age of the larva, its country of origin and whether it could have survived refrigeration. This enables the possible source and time of infestation to be estimated and blame to be apportioned in cases involving prosecution. Busvine (1980) is particularly valuable for this type of enquiry and Oldroyd (in Smith, 1973) is useful. Such enquiries may involve larvae of non-British species and the larvae of the commonest of these are included in the present Handbook, e.g. *Ceratitis capitata* (Wiedemann) (Mediterranean fruit fly, in oranges, lemons, mangos, etc.), *Rhagoletis cerasi* (Linnaeus) (cherry fruit-fly in cherries and cherry yoghurt) (both Tephritidae); *Hermetia illucens* (Linnaeus) (Stratiomyidae, in tinned tomatoes, black peppers, root ginger, mango slices in brine, etc.) (Smith & Chainey, 1989).

Some common types of 'economic' enquiries involving native British species (plus *Hermetia illucens*) are listed below with the fly larvae involved in order of frequency of occurrence in cases I have dealt with over a period of more than 30 years.

A. Larvae in foods, drinks, etc.

1. Meat and meat products, poultry, fish, etc.: *Calliphora, Lucilia, Hermetia illucens, Sarcophaga, Hypoderma* (in venison).
2. Cheese: *Calliphora* (also butter), *Piophila, Fannia* (sometimes in wrappings of other animal protein foods, e.g. butter), *Sarcophaga*.
3. Eggs, broken and bad: *Muscina* (Muscidae), *Megaselia* (Phoridae).
4. Milk bottles (empty or full); *Spiniphora bergenstammi* (Mik) (Phoridae), *Drosophila* (especially *D. funebris* (Fabricius) and *D. busckii* Coquillett) (Drosophilidae), *Calliphora, Muscina*, Psychodidae (*Psychoda surcoufi* Tonnoir), Syrphidae (Syrphini, *Eristalis*), *Trichocera* (Trichoceridae).
5. Vegetables & vegetable products: Phoridae, Sciaridae, *Hermetia illucens*, Syrphidae, Lonchopteridae, Chironomidae (*Metriocnemus* in salads including watercress).
6. Fruit & fruit products: *Eristalis*, Tephritidae, Drosophilidae, *Hermetia illucens, Muscina stabulans* (Fallén).
7. Alcoholic & fruit drinks, vinegar, etc.: Drosophilidae larvae may still be recognisable in dehydrated food after reconstitution (see Sciaridae).

B. Larvae in domestic premises

1. Larvae emerging from soil, cracks in concrete, etc. (especially after heavy rain), in numbers on concrete surfaces or indoors: *Tipula, Lucilia*.
2. Indoors (including upstairs rooms): *Volucella* (from wasps' nests in loft), puparia of *Crataerina pallida* (from swift and house-martin nests), *Calliphora* (from nearby corpse (bird, mouse, etc. in loft, chimney, under floorboards or carpets)), *Scenopinus* (in or under carpets), *Syrphus* (from leaves of cut flowers, salads, etc.), Sciaridae in neglected houseplant pots (and Oldroyd (1964) records a bizarre case where sciarid larvae infested the mouldy peaty material used as a fire-resisting lining in an office safe).

3. In water supply: Chironomidae, Psychodidae, *Eristalis* (Syrphidae, if water is contaminated).
4. Faulty or blocked WCs: *Leptocera caenosa* (Rondani), *Fannia, Musca domestica, Eristalis*, Psychodidae.
5. In refuse in dustbins: *Calliphora, Lucilia.*

In food products where meat and vegetables (and sauces, pickles, etc.) are mixed, some transference may occur to complicate the picture on the plate or in the container (e.g. one case where jets of *Drosophila* larvae were ejected from a plastic tomato ketchup dispenser!).

Larvae of species specific to particular vegetable crops in the field may occasionally be transported alive indoors and crawl or drop off the foodplant (e.g. *Delia radicum* L. (= *brassicae*), the cabbage root-fly, or aphidophagous Syrphidae). These and others are included under species of agricultural importance.

Larvae of *Calliphora* on leaving their pabulum to search for suitable pupation sites may occur in a variety of indoor situations, e.g. bedrooms (from bird corpse in 'sealed' fireplace), in freshly delivered rolls of carpet!

Adults of several families frequently occur in numbers indoors and a consideration of their life-histories may provide clues to their source of origin.

Predators, parasites and pathogens

> "The difference between . . . a carnivore and a parasite is simply the difference between living upon capital and income."
>
> Charles Elton, 1927

Man certainly plays a large part in controlling the numbers of flies by attacking the immature stages either deliberately in controlling economic pests, as food (not intentionally in U.K.), or accidentally by his modification of the environment. However, he also provides many artificial habitats which favour the development of synanthropic Diptera. More specific enemies may be classified as predators or parasites.

Predators

Diptera larvae in the soil probably form a regular part of the diets of mammals with a subterranean life style: moles, for example, take larvae of Tipulidae, Anisopodidae, Bibionidae, Sciaridae, Stratiomyidae, Therevidae, Rhagionidae, Tabanidae, Empididae and Anthomyiidae (Godfrey & Crowcroft, 1960). Birds will take larvae near the surface, and leatherjackets, for example, are eaten by rooks, starlings, plover, gulls and pheasants (Smith, K. M., 1931). Carnivorous soil-dwelling invertebrates such as centipedes also take fly larvae as food. Some soil-dwelling beetles such as Carabidae and Staphylinidae are carnivorous as adults and larvae and feed on Diptera larvae. The staphylinid *Aloconota gregaria* Erichson may be a significant biological control agent against the wheat bulb fly *Delia coarctata* (Fallén). Predaceous Diptera larvae in the soil may prey on other Diptera larvae including each other, e.g. Empididae, Dolichopodidae (Hobby & Smith, 1961b). Many beetles, for example Staphylinidae, Silphidae and Cleridae, prey on fly eggs and larvae in carrion, fungi, etc. Wasps take Diptera larvae in exposed situations on carrion, etc.

Aquatic Diptera larvae are subject to heavy predation from fish and some water birds (e.g. dippers, ducks) as well as from the orders of insects with aquatic carnivorous larvae, such as Odonata, Plecoptera, Hemiptera and Coleoptera. Larvae of the chironomid genera *Cardiocladius* and *Eukiefferiella* will attack *Simulium*. Larvae of *Acanthocnema* (*Clinoceroides*) *glaucescens* (Loew) (Scathophagidae) feed on egg masses of *Dixa* (Dixidae) and larvae of *Phaonia exoleta* (Meigen) (Muscidae) feed on mosquito (Culicidae) larvae.

Some may also be attacked by adult Diptera, e.g. chironomid larvae are attacked by adult Dolichopodidae (*Hydrophorus, Campsicnemus, Poecilobothrus* and *Dolichopus*) (Smith & Empson, 1955). Simuliid larvae have been reported to be attacked by adult Empididae (Clinocerinae and Hemerodromiinae) and Dolichopodidae in Canada (Davies, D. M., 1981).

On plants, predaceous larvae of *Lestodiplosis* are commonly found feeding on larvae of other Cecidomyiidae (Harris, 1966).

In the U.S.A. water mites have been recorded as predators on the eggs and larvae of mosquitoes (Mullen, 1975).

Parasites

Parasites of Diptera should always be carefully preserved with all the relevant puparial fragments, etc. and data, as much remains to be discovered and many rearings in the literature are in need of careful confirmation.

The Hymenoptera provide the most important parasites of immature Diptera. A general survey is given by Shaw & Askew (in Stubbs & Chandler, 1978) and Smith (1974b). The principal parasites are as follows: Ichneumonidae (*Phygadeuon* (fig. 1321), *Mesoleptus* and related genera on fly puparia, Oxytorinae on Mycetophilidae, Orthocentrinae on Diptera near the ground, Diplazontinae on aphidophagous Syrphidae): Braconidae (Opiinae on plant feeding Schizophora, Alysiinae (figs 1319, 1320) on Cyclorrhapha); Eulophidae; Pteromalidae; some Ceraphrontoidea; Proctotrupoidea (Platygastridae on Cecidomyiidae); Diapriidae (Diapriinae on cyclorrhaphous puparia, Belytinae on Mycetophilidae), Scelionidae, Trichogrammatidae, Mymaridae (all of the last three families are egg parasites on some Cecidomyiidae, Tabanidae, Rhagionidae and Syrphidae); Cynipoidea (Eucoilidae and Figitidae on Cyclorrhapha).

In the Coleoptera some larvae of Staphylinidae, e.g. *Aleochara*, are parasites of fly puparia, mostly calypterates and especially Anthomyiidae (see Welch, 1965). The species of fly parasitised probably varies with the habitat, e.g. *Aleochara algarum* Fauvel is parasitic on seaweed flies such as *Coelopa* and *Orygma*, while *A. curtula* (Goeze) is a common parasite in the puparia of blowflies (figs 1322–1326).

Parasitism of Diptera by Diptera is not common and the few British records (see under family for details) may be summarised as follows:

Tachinidae: *Siphona* on leatherjacket larvae of Tipulidae and a *Pegomya* sp.; *Admontia* (*Trichopareia*) specialises in Tipulidae in wood, e.g. *Ctenophora, Tipula irrorata* Macquart and *T. flavolineata* Meigen.

Phoridae: *Borophaga incrassata* Meigen parasitizes larvae of *Bibio marci* L.; *Megaselia paludosa* Wood attacks leatherjackets; *M. flavicoxa* Zetterstedt parasitises larvae of *Bradysia bicolor* Meigen (Sciaridae); and *M. obscuripennis* Wood is a parasite of larvae of *Trichosia* (Sciaridae).

In the U.S.A. *Macronychia* (Sarcophagidae) has been reared from adult Tabanidae and some Tachinidae have been reared from larval and adult Tabanidae (Thompson, P. H., 1978). In Australia a tachinid has been reared from an adult *Atherigona* (Muscidae) (Smith, 1974c, Ferrar, 1977).

Parasitic fungi probably also take a steady toll of larvae, as they do of adults, though few are recorded specifically from Diptera larvae in the literature (Leatherdale, 1970). I have found the larvae of *Lonchaea palposa* Zetterstedt infested with the 'green muscardine' fungus *Metarrhizium anisopliae* (Metsch) (Smith, 1957b). D'Arcy-Burt (1987) reports the hyphomycete *Tolypocaladium cylindrosporum* Gams from the larvae of Bibionidae. Abroad, but not yet in Britain, species of *Coelomomyces* fungi have been found in the larvae of mosquitoes.

Various micro-organisms may infest dipterous larvae, e.g. viruses, bacteria, Protozoa, nematodes (fig. 1318), cestodes and trematodes. A general survey is given by Carter (in Stubbs & Chandler, 1978).

The micro-fauna and flora of dipterous larvae is a subject ripe for careful research.

Fossil larvae and pupae

Diptera larvae are sometimes, though rarely, preserved as fossils and, if carefully examined under the microscope in an oblique light, may be identified to families. Often these fossils are rather faint but details can be enhanced by moistening the surface with a thin film of water or 80% alcohol for short periods. However, great care should be taken that the rock containing the impression of the fossil is not soluble (e.g. if gypsum is present) by testing areas clear of the fossil. A useful recent reference is Whalley & Jarzembowski (1985). For fossil Diptera in general Rohdendorf (1974) and Hennig (1981) should be consulted.

Many insects (often fragmented), especially Coleoptera, are found by archaeologists during their excavations. The insect fauna on such sites is usually in the region of prehistoric refuse dumps or cess pits and the immature stages of Diptera are frequently represented as follows: Tipulidae (especially larval head capsules), Chironomidae (larval head capsules), Drosophilidae (puparia), Sepsidae (puparia), Ephydridae (*Teichomyza* and *Scatella* puparia), Sphaeroceridae (puparia), Scathophagidae (puparia), Muscidae (*Musca, Muscina, Neomyia* (= *Orthellia*), *Eudasyphora* (= *Dasyphora*), puparia or parts of).

Puparia are often darkened and may be covered in debris. They should be soaked in cold 10% KOH, cleared of debris, then teased apart so that the mouthparts can be extracted from the puparial cap (see also collecting, preservation, etc.). Some useful references for identification are Phipps (1983), Skidmore (1985) and Smith (1986b).

Collecting, rearing, preservation and examination

Dipterists collecting adults usually use nets, and larvae are rarely seen. In fact Diptera larvae are more likely to be encountered by specialists in other groups of insects using entirely different collecting methods. It is therefore well worth while educating colleagues to collect alive any Diptera larvae they may find. This casual method of collection should not be spurned as it often yields Diptera larvae of considerable interest of which the adults may be only rarely seen.

The systematic collecting of larvae does present certain problems as the extent of possible habitats is so large that some form of sampling is necessary. The types of habitat occupied by fly larvae are outlined under the section on life-histories and ecology and the collecting methods employed must be dictated by the microhabitat favoured and the known, or suspected, behavioural characteristics of the groups to be collected.

Having collected larvae in a given habitat it is important to ascertain where and on what they were probably feeding. Some larvae occur in strictly defined habitats but others such as certain soil-dwelling larvae may also be found in leaf-litter, wood debris or dung. Among aquatic larvae some normally associated with running water can be found in still water and some terrestrial larvae may be found in aquatic moss. The larvae may move from one microhabitat to another during their life-history. For example, semi-aquatic larvae may move to drier habitats for the purpose of pupation, and carrion-feeding calliphorid maggots migrate from carrion for a considerable distance prior to pupation. All possibilities of this sort should be considered when examining samples and where possible the larvae should be grouped into similar types and sizes and some of each kept alive for possible rearing to adult in order to establish identity. Pupae or puparia should be kept alive.

Glass or plastic tubes or tins are suitable containers for keeping terrestrial larvae alive, together with some of the pabulum in which they were found. Aquatic larvae should be placed in suitable jars or bottles. Larvae suspected of being carnivorous should be kept singly.

Useful equipment for collecting terrestrial larvae includes a small trowel for soil sampling, a strong knife for splitting bark, wood, etc., a sieve or nest of sieves of graded mesh size, forceps, a fine paint brush (for tiny delicate larvae), a white sheet or dish for sorting, a notebook, adhesive labels and pencil. A pooter or insect aspirator could be useful in some dry situations but *must* be of the 'blow' type to avoid health hazards (see section on Medical Importance).

For aquatic species a strong metal-framed pond net is essential; a wire hook for securing weed is useful and a strong stick for turning stones and a large white tray for sorting.

A useful way of sorting soil indoors is by floatation in which the sample is immersed and broken up in a solution of magnesium sulphate (Epsom salts) at a strength of about one pound (0.488 kilo) to one gallon (4.55 litres) of water. The larvae float on the surface (puparia often around the edges) and should be picked off quickly as this solution can anaesthetise aquatic animals. An alternative solution can be made using some common salt in water. The floatation methods only work for free-living larvae and are no substitute for careful hand searching which may also yield larvae hidden in cocoons and silken tubes.

Soil-dwelling species may be sampled by using a solution of orthodichlorobenzene (Jeyes' Fluid). About half-an-ounce (14 g) of the liquid to one gallon of water is poured on cleared ground at the rate of 2 gallons (9.1 litres) of the mixture per square yard (0.83 sq. m). Any larvae should surface before half an hour or so (see Brindle & Smith, in Stubbs & Chandler, 1978).

Further information on collecting and equipment is given in Oldroyd (1970a), Brindle & Smith (in Stubbs & Chandler, 1978), Cogan & Smith (1974) and Southwood (1978).

Rearing is only of value if the larvae or puparia are segregated into suitable individual containers so that the immature stages can be linked to the subsequent adult and identification confirmed. As far as possible the conditions in which the larvae were found should be re-created in miniature, especially humidity. Humidity or moisture gradients can be achieved by tilting containers containing moss, soil and a little water so that sub-aquatic larvae can choose the level that best suits them. A range of plant (or animal) food collected in the larval habitat should be provided as possible food for the larvae, care being taken not to introduce anything likely to prey upon the larva. Close observation and care is necessary until it is clear that the conditions provided are satisfactory. Containers can vary from tins, gauze topped tubes or jars, petri dishes, etc., whichever seems best to fit the particular moisture requirement without encouraging mould.

Rearing larvae of unknown habits and identity is not easy but the interest and satisfaction of possibly establishing a new life-history and describing a hitherto unknown larva is sufficient reward for making the attempt. Wong (1972) reviews rearing techniques.

Larvae selected for preservation are best killed in hot (60–70°C) water if this is available. This also expands the larvae which can then be placed and stored in 80% alcohol with a little glycerine added to guard against drying out through evaporation. A better medium for preservation is Berlese preservative which is prepared in a similar way to Berlese mountant (see below), but without gum arabic. This is a clear fluid that does not set and specimens may be kept in it indefinitely and mounted as required. If it thickens because of evaporation it can easily be thinned with small amounts of distilled water.

Specimens preserved in alcohol may need to be softened and cleared to facilitate microscopical examination or the preparation of permanent mounts on microscope slides. The larvae should be placed in 10% caustic potash and left overnight or the process can be accelerated by placing the specimen in caustic potash in a small tube immersed in boiling water. Very small, delicate larvae should be watched carefully during this process as they may clear too quickly. The specimens should then be transferred to glacial acetic acid for 5–10 minutes and finally placed in a drop of Berlese preservative in a watch glass or on a cavity slide for examination or dissection under a low power stereoscopic microscope. It is better to attempt identification before making a permanent mount as it is often essential to manoeuvre the specimen into different positions. As one proceeds with identification it soon becomes clear from the key characters if dissection will be necessary and if a permanent mount of the whole or a part of the specimen needs to be made for more detailed study under a compound microscope.

Permanent slide mounts can be made by transferring the specimen from glacial acetic acid into clove oil and then into Canada balsam. However the refractive index of Canada balsam is such that fine structures may be difficult to see and a far superior medium for temporary slides is Swan's Berlese Mountant which is made as follows (formula after Dr K. M. Harris):

Gum arabic	12 g
Chloral hydrate	20 g
Glacial acetic acid	5 ml
50% w/w glucose syrup	5 ml
Distilled water	30–40 ml

Measure ingredients into a beaker or wide-mouthed bottle (the glucose syrup is made by dissolving a given weight of glucose in an equal weight of distilled water). Place in gentle heat (slide-oven at 35°C) for 24 hours or more, stirring occasionally until ingredients dissolve. Leave for a few days until debris from the gum arabic settles and then decant clear fluid into a clean screw-top bottle. If necessary, evaporate water by leaving the open container in a slide-oven for a few days, until drops of mountant retain their shape on a slide rather than spreading over the surface.

It is usually necessary to examine the slides from time to time, topping up with mountant to compensate for evaporation. After the slides have dried for a few months (minimum of 3 weeks at 35°C) they should be ringed to prevent further evaporation. Unfortunately most ringing reagents react with the mountant and crystallization still occurs so that permanent slides should be made with Euparal, mounting direct from 95% alcohol or propanol.

If only empty puparia are available they can be treated in the same way as larvae, but it should be remembered that puparial caps may become detached and these are important since they contain the mouthparts of the last instar larva which can be used in identification. The spiracles of the final instar larvae are also present on the puparium.

A useful ruse for the rapid examination of the posterior spiracles of dead large firm larvae or puparia (alive or dead) is to plunge them head down in some 1/4" depth of fine sand in a watch glass which holds them in position under the microscope.

Users of this Handbook are hardly likely to need the use of the scanning electron microscope. Nevertheless, for the clarification of minute structures at the limit of the light microscope the instrument opens up new dimensions in larval study. The SEM has transformed our understanding of the functional morphology of egg and larval structures (e.g. Hinton, 1981). The techniques of preparation of larval material for SEM examination are described by Grodowitz *et al.* (1982).

Biology and morphology of the immature stages

Diptera are holometabolous insects with a complete metamorphosis of four stages: egg, larva, pupa and adult.

During growth the larvae of most Diptera pass through a series of moults, the period between the moults being called *instars*. Moults that take place soon after hatching and just prior to pupation are easily overlooked but those that take place during the active feeding period are easily observed.

Nematocera usually have the largest number of moults, e.g. four instars in Culicidae and six or seven in Simuliidae. Among Brachycera, some Tabanidae have up to nine instars and may take up to two years to complete their development. The maggots of Cyclorrhapha usually have three instars and most feeding and growing is done in the third instar.

Some larvae of Cecidomyiidae reproduce by *paedogenesis*, i.e. reproduction by an animal that becomes sexually mature before reaching the adult form. In this method of reproduction a few (up to about 35) large eggs are produced which can be seen through the larval cuticle. These become larvae and feed on their parent larva from inside (fig. 118). This condition can continue for several generations without the appearance of an adult. These midges (e.g. *Miastor*) thus reproduce like aphids and remain in their birthplace producing a great mass of larvae which may be found under the bark of logs. Eventually the daughter larvae will cease to produce eggs and pupate normally. Both sexes are produced in this way though of course all offspring of one larva are of the same sex as the parent larva. These paedogenetic larvae do not develop a sternal spatula but it reappears when pupation is imminent which confirms the function of this structure as a prerequisite to pupation. Pupal paedogenesis is also known in the British species *Henria psalliotae* Wyatt, a pest of mushrooms. This reproductive pupa is called a *hemipupa* (Wyatt, I. J., 1961).

Some Chironomidae appear to be paedogenetic but actually the adult female lays her eggs while she is still inside the pupal skin and is thus a *pharate adult*.

In most Nematocera and Brachycera the fully fed larvae form pupae but in Cyclorrhapha the last (third) instar larva forms a puparium from the last larval skin inside which it pupates. Stratiomyidae are exceptional in the Brachycera in not shedding the last larval skin when they pupate but this appears to be a protective device unrelated to the cyclorrhaphous puparium. Some Nematocera also pupate inside the last larval skin, e.g. *Mayetiola* and *Chortomyia* (Cecidomyiidae), some Scatopsidae, *Penthetria holosericea* Meigen (non-British—Bibionidae) and the non-British Perissomatidae.

Eggs

The eggs of flies are generally oval or spindle-shaped, white or pale yellow and relatively featureless to the naked eye. Under the microscope many are seen to have a sculptured surface and some also have horns, stalks or a raised network of ridges. These surface features are largely respiratory adaptations to prevent the eggs from drowning after rain and function as a respiratory plastron which holds a thin film of air, as in many aquatic beetles and bugs (Hinton, 1961). The ornamentation of an egg increases surface tension and may cause it to float, and the eggs of aquatic species may have more elaborate floatation devices (e.g. mosquitoes, figs 976–978). At the head end of the egg is the micropyle (fig. 1023), an opening for the admission of sperm.

The largest number of eggs (*c.* 2,000) is produced by some aquatic flies whose larvae suffer enormous mortality from predation (e.g. *Chironomus plumosus* L.). Female blow-flies (*Calliphora*) lay about 300 eggs, usually in several small batches. The female housefly (*Musca domestica* L.) lays eggs singly in small or large batches at the rate of 100–150 per day up to 1,000. At the other extreme, Hippoboscidae and other Pupipara mature only one egg at a time, nurture it internally and eventually deposit a fully grown larva. Some families (e.g. Sarcophagidae) are normally viviparous and produce living first stage larvae, but when food is scarce even the bluebottle (*Calliphora*, Calliphoridae) will retain its eggs and produce living first stage larvae.

Probably the eggs of the majority of Diptera are dropped in flight and roll into crevices in the ground but some are placed more deliberately and individually on a suitable medium in which the larvae can develop and this is especially so with parasitic species.

Hinton (1981) does not include Diptera in his tabulation of parental care in insects but *Atherix* (Athericidae) exhibits something approaching this. The females practise communal egg-laying on leaves overhanging streams where they then die in masses like swarms of bees. The larvae hatch in the midst of the dead and dying females and drop into the water. Females of the Nearctic tabanid *Goniops chrysocoma* Osten Sacken stay with their eggs until they hatch.

There is no general work on the identification of the eggs of Diptera but illustrations of a wide range of eggs are given in this *Handbook* (figs 968–1108). The major work of Hinton (1981) on insect eggs will be found useful, especially on microstructure (see also Salkeld, 1980).

Since the egg is so neglected in descriptions it is worth remembering that this stage can often be obtained from live female adults whose identity can usually be established with certainty. Eggs may also be recovered from dry museum specimens when the ovipositor and abdomen are being macerated prior to dissection and study. The precise site of capture of the female, coupled with the structure of the egg and ovipositor may also yield clues as to possible oviposition media in which development may take place (Smith, in Stubbs & Chandler, 1978: 247).

Larvae

The larvae of Diptera are very variable in appearance but may be distinguished from most other insect larvae by the lack of jointed thoracic legs, a rather slender form and usually active directional movement. A general study of larval morphology is provided by Teskey (in McAlpine *et al.* 1981) which has proved invaluable in the preparation of the following brief account. Some detailed studies of particular larval structures are cited in the appropriate sections below.

Head

The structure of the head varies considerably but three types may be recognised: *eucephalic*—with a well-developed head capsule and distinct, toothed mandibles which move against each other in a horizontal or oblique plane (most Nematocera, figs 2–4); *hemicephalic*—with the head capsule incomplete, partly retractile, and sickle-shaped mandibles which move in a vertical plane (Orthorrhapha—Brachycera, figs 166–167, 170, 185); *acephalic*—the head capsule is further reduced and retracted into the thorax and forms, with the mouthparts, a *cephalopharyngeal skeleton* (Cyclorrhapha, fig. 788).

In the Cecidomyiidae the head capsule is almost absent except for the *sternal spatula* (sometimes referred to as the 'breastbone'), a peculiar ventral structure which is regarded as characteristic of the family though even this is absent in some species (figs. 105–116). It is present only in the third instar (but not in paedogenetic forms) and is used for tunnelling in the soil.

Some aquatic nematocerous larvae (e.g. Simuliidae, Culicidae, some Chironomidae), in addition to the mandibles, have the labrum modified into mouthbrushes (figs 43–44, br) which are used to sweep microplankton towards the mouth opening. In some aquatic non-predaceous Nematocera (e.g. Anisopodidae, Culicidae, Psychodidae, Ptychopteridae, Scatopsidae, Trichoceridae and some Tipulidae) the pharynx has a complex filtering apparatus for straining food particles from the water. Except for some aquatic larval Stratiomyidae this structure is absent in larvae of the

Orthorrhapha—Brachycera which are mostly predaceous. In these Brachycera the pharynx is sclerotized and in some families (e.g. Dolichopodidae, Empididae, Stratiomyidae) may also be fused with the internal skeleton of the head. In the Cyclorrhapha the head consists of an outer membranous segment and the internal cephalopharyngeal skeleton, a characteristic feature of the familiar maggot type of larva. The cephalopharyngeal skeleton is normally divisible into three main parts: the basal or pharyngeal sclerite (ps); the intermediate or hypopharyngeal sclerite (hs) (tentoropharyngeal) and the mouth hooks or mandibles (m) (fig. 788). The pharyngeal sclerite consists of a pair of roughly U-shaped sclerites on either side of the pharynx. The two arms of each of these sclerites are called the dorsal (dc) and ventral cornua (vc) (singular cornu) or 'wings' and the latter are fused to the pharynx on each side. The pharyngeal sclerites may be joined by a bridge anterodorsally and a pair of slender parastomal bars may project from the anterior margin above the hypostomal sclerite (fig. 788, p). Below the basal part of the mandible there may be a dental sclerite (ds) and beneath (Muscidae, fig. 911, ob, ar) or between (Calliphoridae, fig. 788) the apices of the mandibles other accessory oral sclerites (os) may be present. Papers by Roberts (1969–1971a) should be consulted for a detailed discussion of the mouthparts of larval Diptera in relation to feeding habits. A knowledge of the functional morphology of mouthparts may provide important clues as to whether or not an unidentified larva is the cause of primary damage to its host.

The *antennae* (fig. 2) are usually close to the anterior mandibular articulations near the anterodorsal corners of the genae (cheeks). They may be very small (e.g. Anisopodidae, Bibionidae, Ptychopteridae, some Psychodidae, many Mycetophilidae) and are normally subdivided into three divisions (though in some Chironomidae seven may be evident). In Chaoboridae the antennae have evolved into prehensile structures with apical spines used for capturing prey (fig. 45, an).

The *eyes* are also located on the genae. In the Nematocera and orthorrhaphous Brachycera the eyes are usually simple (double in many Chironomidae) but in some Culicidae and Chaoboridae a compound eye is present, in front of the simple eye (ocellus). Little work has been done on the eyes of larval Diptera but Roberts (1970b) is useful. An egg-burster or hatching spine may be present on the head of the first instar larva of some Diptera (fig. 984) (see Edwards, F. W., 1919; Madwar, 1934; Hinton, 1981). Egg-bursters in Diptera require further investigation (see Smith, 1955a).

Body

This is very variable in shape. Most Nematocera and some Brachycera are slender and subcylindrical; Therevidae, Scenopinidae and some Ephydridae and Canacidae are spindle-shaped (fusiform); Cyclorrhapha and Xylophagidae are markedly narrowed anteriorly; Fanniidae, Lonchopteridae, Platypezidae, Stratiomyidae and Xylomyidae are dorsoventrally flattened; Chaoboridae and Culicidae have a swollen thorax; Simuliidae are swollen posteriorly while some Syrphidae and parasitic groups are generally stout; Conopidae are pear shaped and *Microdon* (Syrphidae) species are hemispherical.

Nematocera usually have 12 body segments, other Diptera 11. Three of these segments comprise the thorax and the remainder the abdomen. Variation in the numbers of abdominal segments nearly always involves a decrease in Nematocera and an increase in other Diptera.

In the Chaoboridae, Culicidae and Simuliidae the three thoracic segments are fused. In the Anisopodidae and Psychodidae subdivision of the segments, or pseudosegmentation, occurs (figs 40, 70, 71). The Therevidae and Scenopinidae have 20 segmental divisions.

The *cuticle* of Diptera larvae is usually only weakly sclerotized and non-pigmented, a condition probably explained by their mainly concealed mode of life in a humid terrestrial atmosphere or by the adoption of an aquatic or semi-aquatic environment. Larvae living in a drier pabulum have a tougher cuticle to protect them from abrasion and water loss (e.g. Asilidae, Xylophagidae). The larvae of Stratiomyidae and Xylomyidae have a tough cuticle of a shagreened appearance caused by the deposition of calcium carbonate, apparently an adaptation to either periodic drought in normally moist terrestrial or temporary aquatic habitats (Hinton, 1953), or for survival in acid conditions which cannot be tolerated by the larvae of other species not having this characteristic (McFadden, 1967). The larvae of some *Pericoma* species (Psychodidae) are covered in a layer of mud trapped by curved hairs on the dorsal surface.

In *colour* the larvae of most Diptera are yellowish or whitish, probably reflecting their habit of usually living in concealment (e.g. in soil, dung, stems, wood, leaf mines, etc.). Larvae that live on the surface of plants may be greenish, especially if they feed on the plants (e.g. Tipulidae, subfamily Cylindrotominae). The larvae of aphidophagous Syrphidae also live on the surface of plants, searching for their prey and are often quite brightly coloured. The red coloration of some larval Chironomidae is due to haemoglobin in the haemolymph. Similarly the brownish colour of some Tabanidae is due to coloration of the haemolymph. Some Tipulidae have dense microtrichia on the cuticle which may give them a grey or golden (some Limoniinae) appearance.

In addition to hairs and bristles, which may be modified, the cuticle of Diptera larvae may have minute spicules, and scale-like, larger projections. These may be arranged in groups or patterns and thus be of use taxonomically. Tubercles or larger fleshy processes may also be present on the body segments, especially on the last segment where they may form a series around the spiracles: their particular arrangement can be of use in identification.

Some cuticular outgrowths may be used in locomotion. True jointed thoracic legs are never present in Diptera, but two types of false legs have evolved. *Prolegs* usually occur in pairs, ventrally, on the thoracic and anal segments, and sometimes on the abdominal segments (figs 201, 938). These prolegs bear one or more locomotory spinules at their apices (figs 152–156, 938, 945). *Creeping welts* are transverse swollen ridges usually found on the anterior ventral margins and sometimes the anterior dorsal margins of the first seven body segments. These locomotory welts usually have transverse rows of spinules, the microstructure and arrangement of which may have diagnostic importance (figs 529, 564). Larval creeping welts are commonest in Schizophora but also occur in some Nematocera, and Brachycera-Orthorrhapha. Some non-British species (e.g. Blephariceridae and some Psychodidae) have developed suction discs which anchor them in swiftly flowing water. Other backwardly directed bristles or spines or cuticular ridges may also assist in locomotion. Roberts (1971b) discusses locomotion by apodous cyclorrhaphan maggots.

Respiratory System

There are seven main types of respiratory system in the larvae of Diptera (fig. 1) and these may vary not only between taxa or habitat types occupied but also between instars of the same species. The systems described below refer to the final instar larvae. Detailed discussions of respiratory systems and their systematic importance are provided by Keilin (1944) and Whitten (1959).

The *holopneustic* type is the basic system in which 10 pairs of spiracles are present, located on the prothorax, metathorax and eight of the abdominal segments (not on segment 9 in British genera). This condition occurs only in Bibionidae (figs 1, 74) and the non-British Pachyneuridae and Cramptonomyidae. In larval descriptions the prothoracic spiracles are called the *anterior spiracles* and those on the anal segment are termed the *posterior spiracles*. Both pairs are larger than the other, abdominal, spiracles.

In the *peripneustic* system the metathoracic spiracles are absent and this is characteristic of Cecidomyiidae, Mycetophilidae (sub-family Ditomyiinae), Scatopsidae and the non-British Synneuridae and Pachyneuridae other than *Pachyneura*.

Posterior spiracles are lacking in the *hemipneustic* system which is represented by Sciaridae and most Mycetophilidae.

The *amphipneustic* system has only the anterior and posterior pairs of spiracles. It is the commonest system in Diptera and typical of Anisopodidae, Psychodidae, Thaumaleidae, Trichoceridae (and the non-British Axymiidae and Tanyderidae) in the Nematocera and most other Diptera.

In the *propneustic* condition only anterior spiracles are present. This respiratory system occurs only in some Mycetophilidae (*Diadocidia* species and some Sciophilinae).

The *metapneustic* system in which only the posterior spiracles remain is found in some larvae living in aquatic or semi-aquatic conditions in the families Culicidae, Dixidae, Ptychopteridae, and Tipulidae in the Nematocera, and the Tabanidae in the Brachycera. The Tabanidae do have anterior spiracles but they are extruded just before pupation and it is not known if they are functional.

When spiracles are completely absent (although tracheae are always well-developed) the condition is said to be *apneustic*. Such larvae are aquatic (except Keroplatinae, Mycetophilidae) and include the Ceratopogonidae, some Chaoboridae (*Chaoborus*), most Chironomidae, Simuliidae (and the non-British Blephariceridae, Deuterophlebiidae and Nymphomyiidae) in the Nematocera; Athericidae and Empididae in the Brachycera; and some representatives of other families.

The respiratory system may differ between instars, e.g. Mycetophilidae and Sciaridae are metapneustic in the first instar, propneustic in the second and third instars and hemipneustic in the fourth (final) instar. In Cyclorrhapha the first instar larvae are metapneustic and the second and third (final) instar are usually amphipneustic.

Spiracles vary in structure and Keilin (1944) recognised three types (in final stage larvae). In the first type the spiracular opening through which the trachea of the previous instar is withdrawn becomes the spiracular opening of the following instar (e.g. Culicidae, Tabanidae). In the second type the spiracular opening is closed and in the following instar forms a scar around which perforated oval or linear air intakes open (e.g. most Nematocera and Brachycera). In type three the spiracular opening of the second instar forms a scar near the inner margin of the spiracular plate and the number of air intakes opening around the scar is usually reduced (e.g. Cyclorrhapha).

A very useful 'spot character' of the larvae of most Cyclorrhapha is that in the three instars each posterior spiracle has one, two or three respiratory slits respectively (figs 786, 790). The *spiracular plate* upon which the posterior spiracles are situated has a margin or *peritreme*. The arrangement and shape of the spiracular slits and the state of the peritreme (complete or incomplete) provide valuable diagnostic characters in the Cyclorrhapha.

In the majority of the Nematocera the posterior spiracles are usually sessile but in the Brachycera and Cyclorrhapha they are raised above the body surface on short processes. Larvae living in liquid or semi-liquid media may have the spiracles each situated at the end of two short processes (Scatopsidae) or together at the end of a relatively short respiratory siphon (e.g. Psychodidae, Culicidae, Stratiomyidae, Tabanidae and Ephydridae) or at the end of a long and sometimes retractable siphon (e.g. Ptychopteridae; *Eristalis* and some other Syrphidae; Aulacigastridae).

Some Stratiomyidae exhibit another adaptation to an aquatic existence: they have the posterior spiracles enclosed in a small chamber (atrium), the opposing edges of which are fringed with hairs which enclose a bubble of air when the larva submerges (fig. 135). The same effect can be achieved by the anal lobes especially when they are fringed with hairs (e.g. Tipulidae (fig. 27) and Dolichopodidae (figs 208–209). The spiracular pit in *Sarcophaga* (fig. 781) may have a similar function.

The posterior spiracles of *Chrysogaster* (Syrphidae, fig. 258) and *Notiphila* (Ephydridae, figs 615–616) are modified into a respiratory spine used to pierce and draw air from tissues of aquatic plants. Structurally similar spines are found in some Tabanidae but are not situated at the point of air intake, and spiracular spines of unknown function are present in some Acalyptrates (e.g. Clusiidae, Lonchaeidae, Micropezidae and Psilidae).

In the Cyclorrhapha the anterior spiracles often have several openings, the number and arrangement of which may provide characters of taxonomic value.

In many aquatic or semi-aquatic larvae of Nematocera, *anal papillae* may be present, near or within the anus on the last abdominal segment. These appear to have mainly an osmoregulatory function (Wigglesworth, 1938; Brindle, 1952) but when well tracheated have been called *tracheal gills*, though the respiratory function is in doubt.

A list of the late Professor H. E. Hinton's important contributions to our understanding of respiratory systems in Diptera (and other insects) is included in the bibliography of his publications at the end of vol. 3 of his work on insect eggs (Hinton, 1981), and a few are cited at appropriate places in this *Handbook*.

Useful works on the identification of larvae are cited in the introduction and under each family below. A major work on the larvae of Cyclorrhapha has been published as this work goes to press (Ferrar, 1987).

Pupae

The pupae of Diptera are of two main types.

In *obtect* pupae (figs 1109–1148) the head appendages, wings and legs are visible and lie in sheaths attached to the surface of the body (e.g. Nematocera and Brachycera). Obtect pupae are mostly immobile although they can move by wriggling the abdomen. Pupae of this type may be enclosed in a silken cocoon covered with soil or other particles. Pupae of aquatic species may be able to swim actively (e.g. Culicidae, Chironomidae, Chaoboridae). The abdominal segments and head often have bristles or hairs which help the pupa move through or break out of the soil, wood or other medium in which it has developed. The adult emerges through a rectangular or T-shaped rupture (from which the name Orthorrhapha is derived: Gr. ortho—straight, raphe—suture).

The pupae of *Forcipomyia* and *Atrichopogon* retain the larval skin over the apical half of the body (fig. 1120). Only a few other Orthorrhapha do this, e.g. Stratiomyidae (entire cover), Scatopsidae (thorax free), *Dactylolabis* and *Cylindrotoma* (Tipulidae) (partially covered) and some Chironomidae that pupate inside a tube or case do not free themselves from a larval skin until they wriggle out to escape to the water surface.

The second type of pupa is found in Cyclorrhapha and is *exarate*, i.e. the appendages are free. However the pupa is rarely visible as pupation takes place inside the last larval skin or *puparium* (figs 792–793), 1149–1286) which is rounded, hardened and tanned. In some families the pupa or puparium may be concealed inside a cocoon made by the larva before pupariation (figs 1142, 1145, 1156, 1272). The adult emerges by inflating a large sac on its head, the *ptilinum*, which lifts a circular cap off the puparium (from which the name Cyclorrhapha is derived: Gr. cyclos—round; raphe—suture). The puparial cap splits in two, and one half contains the mouthparts of the final instar larva. The mouthparts, in conjunction with the posterior spiracles retained on the surface of the puparium, may render identification of puparia possible. This can be invaluable in certain types of investigation especially forensic and archaeological work (Smith, 1986b), when puparia are frequently the only material available for study.

Most pupae breathe entirely through the thoracic spiracles which are sometimes produced into pupal horns (figs 1110–1122, 1143–1145). In some aquatic species such pupal horns may be sharp and capable of piercing plant tissues in order to obtain oxygen.

The pupal stage is often neglected in descriptions of the immature stages unless it is the stage most frequently found (e.g. Asilidae, Sphaeroceridae) or of particular taxonomic or economic (especially medical) importance (e.g. Culicidae, Simuliidae, Chironomidae).

To facilitate approximate identification a range of pupae and puparia is illustrated (figs 1109–1286) for most families. Brauns (1954b) is useful for terrestrial species and other works dealing substantially with pupae are indicated under the appropriate families (see Ferrar, 1987 for Cyclorrhapha).

Classification, nomenclature and use of keys

As far possible the *sequence* of families, subfamilies, tribes and genera follows that of the Diptera *Check List* (Smith *et al.*, 1976) for the convenience of users of the *Handbook* series. Sometimes the only workable keys to larvae are based on a classification different from that now used for the adults (e.g. Syrphidae) and in such cases explanatory comments are given. Where recent taxonomic research on adults has led to changes in the nomenclature, status, or generic placing of well-known species (such as pests) adequate synonymy is cited under the appropriate family treatment. Colloquial names for pest species, plant crops and other familiar plants and animals are given in addition to their scientific names at the first (or most important) citation.

In using the keys it should constantly be borne in mind that many genera, species and even some families are unknown in the immature stages and therefore the full range of morphological variety is unknown. Particularly in the Acalyptratae couplets may lead to a choice of families and several families run through to more than one place in the keys. It is intended that identifications should be attempted by combining use of the keys with a consideration of habitat and pabulum (using the introductory sections in combination with the index) in conjunction with the figures. In this way it should be possible to identify many of the Diptera most commonly found as larvae or pupae, including all species of economic, agricultural, medical and veterinary importance. As far as possible I have aimed to include all those Diptera whose immature stages are regularly submitted to entomologists as 'economic enquiries'.

Notes on the illustrations

> 'As far as I am a judge, nothing would recommend entomology more than some neat plates that should well express the generic distinctions of insects according to Linnaeus; for I am well assured that many people would study insects, could they set out with a more adequate notion of those distinctions than can be conveyed at first by words alone.'
>
> Gilbert White, 1771

The illustrations are meant to supplement the text with the following aims:

(1) facilitating identification as far as family and tribe in conjunction with the keys;

(2) to show the range of form and to illustrate particular environmental adaptations;

(3) to facilitate the identification to genus and species of selected Diptera such as pest species, well known 'text-book' species and common readily encountered species of value for teaching or demonstration, or frequently found during faunistic surveys.

Attempts at identification by perusal of the whole insect figures alone should be practised with extreme caution making particular scrutiny of structural details and scanning *all* the figures. Convergence through adaptations to similar environmental requirements may result in remarkably similar superficial appearances between several taxonomically widely separated species, e.g. compare figs 1027 and 1059; figs 239 and 903; figs 201, 617 and 938 etc.

Allowance should be made for some variation in the structures illustrated, particularly in the pigmentation of the cephalopharyngeal skeleton. Apart from some expected variation within a species there is evidence of geographic variation. Published figures of the same species by different authors always show some slight differences. Skidmore (1985) frequently illustrates more than one example of mouthparts in species of Muscidae and the differences illustrate this point. Mandibular wear may occur in older larvae of a given instar (the sternal spatula of Cecidomyiidae may also become worn). The number of rays on an anterior spiracle may differ by one or two, even on each side of the same larva. The length of the caudal lobes may vary within a species in response to the amount of moisture in the habitat (see under Scatopsidae).

However, by careful use of keys, illustrations, text (introductory and under the family) and index the author believes it should be possible to identify nearly all Diptera larvae to family, most to genus and a large number to species, including all of the so-called 'pest' species.

To save space in the figure legends (and to avoid irksome abbreviations) the cephalopharyngeal skeleton is referred to as 'mouthparts' throughout and acknowledgements to published sources of many of the figures are given at the beginning of the book.

Key to suborders of British Diptera larvae

1 Mandibles usually moving against each other in a horizontal or oblique (Scatopsidae) plane and usually with two or more apical teeth (fig. 4). Head capsule usually complete and non-retractile (eucephalic) (fig. 2). Abdomen with at least 9 segments . . . . **NEMATOCERA** (p. 33)
Exceptions: in Forcipomyia *(Ceratopogonidae) the mandibles move vertically but the head capsule is complete and free; in Tipulidae the head capsule is partly or completely retractile and may be reduced but the mandibles move horizontally; in Cecidomyiidae the head capsule is often reduced but the mouthparts are indistinctly differentiated and the prothorax has a variously shaped ventral sternal spatula and the abdomen has at least nine segments.*

— Mandibles moving in a more or less vertical plane parallel to each other and usually hook or sickle-shaped, without secondary apical teeth and directed ventrally. Head capsule usually incomplete and retractile (hemicephalic). Abdomen with 8 segments 2
Exceptions: in Xylophagidae and Stratiomyidae the head capsule is strongly sclerotized and non-retractile but the mandibles move vertically; in Therevidae and Scenopinidae the head may be almost completely sclerotized and, due to secondary segmentation, the abdomen appears to consist of more than 8 segments.

2 Head capsule always with a distinct, even if incomplete, dorsal sclerotization; maxillae and maxillary palpi distinct and usually well developed (fig. 166); the sclerotized rods projecting posteriorly from the head into the body are not united; antennae well developed and situated on a sclerotized plate . . . . **BRACHYCERA** (p. 55)

— Head capsule not sclerotized dorsally; maxillary palpi usually absent or indistinct, maxillae fused with mandibles; the sclerotized rods projecting posteriorly from the head into the body are united in a cephalopharyngeal 'skeleton'; antennae reduced or absent and, if present, situated on a membranous area (figs 787–788) **CYCLORRHAPHA** (p. 71)
Exception: in Lonchopteridae the maxillary palpi are distinct but small.

Key to families for final stage larvae of British Nematocera

1 Head greatly reduced and lightly sclerotized; mouthparts indistinct but a variously shaped, prothoracic, 'sternal spatula' is usually present ventrally (figs 103–116). Larvae small, inactive; pink, red, orange, yellow or white in colour. Respiratory system peripneustic or apneustic. Frequently inhabiting plant galls but also under bark where larvae may occur in masses, also found in soil or humus (figs 101–122) . . . . . **Cecidomyiidae** (p. 52)

— Head usually distinct and forming a sclerotized capsule; without a sternal spatula; respiratory system variable 2

2 Head capsule complete or incomplete and reduced to a number of longitudinal sclerotized rods but always retractile, to some degree, into the thorax. Larvae usually medium to large in size, elongate; active (carnivorous species) or slow moving (herbivores); yellowish-whitish or dark brown to greyish in colour; respiratory system usually metapneustic, with one pair of spiracles on the last segment frequently surrounded by fleshy lobes (figs 10–29) or rarely apneustic (e.g. the aquatic *Antocha*); prolegs sometimes present (Pediciini) usually found in marshy soils but also in drier soils, in mosses, decayed or dead wood and sometimes aquatic (figs 9–29) . . . . **Tipulidae** (p. 35)

— Head capsule complete and non-retractile into the thorax; respiratory system usually otherwise 3

3 Abdomen long and slender with posterior margins of segments swollen and with a long retractile respiratory tube on the anal segment, terminating in small unbranched anal papillae; in saturated marshy soils and mud (fig. 41) . . . **Ptychopteridae** (p. 38)

— Abdomen not so long and slender; any respiratory tube much shorter, thicker, and non-retractile 4

4 Prolegs present on at least one body segment 5

— Prolegs absent 9

5 Paired prolegs on first two abdominal segments only; dorsum of abdomen may have rings (r) of setae on some segments; anal segment tapering posteriorly and with a dorsoventrally flattened leaf-like process (p) on each side. Very active larvae usually curved in a U-shape in life; on surface or slower moving water, on wet rocks or mosses (fig. 42) . . . . **Dixidae** (p. 39)

— Prolegs either on thoracic segments or on posterior abdominal segments 6

6 Head capsule with a pair of conspicuous, folding, dorsolateral mouth-brushes (labral fans) (fig. 69); abdomen conspicuously swollen distally; anal segment with circlet of minute hooked spines. Larvae sessile, usually anchored by the circlet of spines on the anal segment to pad of silk attached to stones, weed, etc. in flowing water (figs 68–69) . . . . **Simuliidae** (p. 45)

— Head capsule without such conspicuous mouth-brushes (Culicidae have hair tufts each side of the labrum); abdomen not conspicuously swollen distally; not sessile 7

7 Paired prolegs present on the first thoracic segment and on the last abdominal segment, with (figs 65–66) or without (fig. 67) (except some Orthocladiinae, see below) additional gills. Larvae active, aquatic or terrestrial; aquatic larvae frequently swim with a looping movement (figs 53–67) . . . . **Chironomidae** (p. 43)

— Prolegs on thoracic segments only, and not paired but fused and appearing bifurcated 8

8 Body smooth, almost parallel-sided; without prominent setae but with sclerotized darker dorsal areas; respiratory system amphipneustic with the anterior spiracles on a short stalk and the posterior spiracles opening into a transverse cleft between fingerlike processes on the 8th abdominal segment. On rocks, mosses, etc., washed by a film of water (hygropetricous); larval movement active and sinuous (fig. 47) . **Thaumaleidae** (p. 41)

— Body not smooth, less parallel-sided with conspicuous setae which may be long and filiform (figs 49) or spatulate (fig 48). Larvae slow; found in moist habitats, in soil, under bark, with water drops often adhering to the setae (figs 48–49) . . **Ceratopogonidae** (part) (p. 41)

9 Body slender (almost thread-like) with uniform bead-like segments and conspicuous setae present only on terminal abdominal segment. Movement active, sinuous; in wet mosses (e.g. *Sphagnum*), sand of river banks or sometimes freely aquatic (figs 50–52) . . . . **Ceratopogonidae** (part) (p. 41)

— Body not so slender or smooth 10

10 Thoracic segments fused and wider than the rest of the body 11

— Thoracic segments not fused nor distinctly wider than the rest of the body 12

11 Antennae (an) prehensile (adapted for holding or seizing), with long strong apical spines; without distinct mouth-brushes; thorax and 7th abdominal segment with paired pigmented air sacs (as). Larvae active, but hold a horizontal position in the water between movements; in still or slow moving water (figs 45–46) . . . . **Chaoboridae** (p. 39)

— Antennae not prehensile, without strong apical spines; with distinct mouth-brushes, one on each side of labrum (figs 43–44, br); no pigmented air sacs. Larva active but usually hold an oblique (fig. 44) (horizontal in *Anopheles* fig. 43) position at the surface of the water between movements; in still or slow moving water (figs 43–44) . . **Culicidae** (p. 39)

12 Body with short tubercles or spinous processes on all segments; anal segment with longer processes; respiratory system holopneustic with 10 pairs of spiracles. Larvae inactive, characteristically curved in life; usually communal in decaying organic matter, rich soil, plant roots, dung, etc. (figs 74–78) . . . . **Bibionidae** (p. 47)

— Body otherwise; less than 10 pairs of spiracles present 13

13 The two posterior spiracles each on the tip of a cylindrical process (except *Ectaetia* fig. 100). Larvae usually dark or at least brown or yellow and rather hairy; very inactive; in dung, soil or in drier habitats with decaying material, e.g. birds' nests, tree holes (figs 92–100) . . . . **Scatopsidae** (p. 50)

— The two posterior spiracles not on such processes 14

14 Last abdominal segment usually with a short non-retractile respiratory tube (figs 30, 32) or tergites of body with numerous distinct transverse sclerotized plates (figs 31–39) (except *Trichomyia*, fig 40); sometimes body with numerous processes. Larvae rather inactive, in decaying organic matter in aquatic or semi-aquatic situations (figs 30–40) . . . . **Psychodidae** (p. 37)

— Last abdominal segment without such a tube; abdomen without distinct transverse sclerotized plates 15

15 Abdominal segments subdivided superficially into 3 more or less equal parts (fig. 5); posterior spiracles surrounded by four fleshy lobes (figs 6–8). Larva whitish to brownish, slow moving; in drier dung, soil, or in moist habitats with decaying organic material (figs 2–8) . . . . **Trichoceridae** (p. 35)

— Abdominal segments not subdivided superficially into three more or less equal parts . 16

16 Abdominal segments 2–6 divided superficially into two unequal parts (figs 70–71); posterior spiracles surrounded by 5 reduced lobes (figs 72–73). Larvae slender, active; in moist habitats where decaying organic material occurs, in deliquescent fungi, or in drier habitats such as dung, soil, old plant stems, etc. (figs 70–73) . . . . . **Anisopodidae** (p. 46)

— Abdominal segments not so divided; sometimes superficially ringed but in this case the rings are narrow, darker and equal; anal segment without lobes. Larvae usually white with contrasting darker, often black head capsule 17

17 Head capsule ventrally with epicranial plates meeting only at one point (or not meeting, Diadocidiinae) so that the posterior tentorial bridge is absent (fig. 86); or if the bridge is partly formed the abdominal creeping welts have sclerotized spicules. Larvae usually white, sometimes dull yellow to bright green; usually in fungi, under bark, in silken webs in holes in old tree trunks, in soil, decaying plants, roots etc . . **Mycetophilidae** (p. 47)

— Head capsule ventrally meeting at two points, the posterior tentorial bridge (ptb) being complete (figs 87–88) or nearly complete; abdominal creeping welts without sclerotized spicules. Larvae white with black head capsule; in decaying plant material, animal excrement, rotten wood attacked by fungus, some in old nests of mammals and birds, sometimes mass movements in large columns . . . . **Sciaridae** (p. 50)

Notes on families of Nematocera

Trichoceridae

(Figs: larvae 2–8, egg 968, pupa 1109)

The family Trichoceridae (winter-gnats) contains about 112 species in 5 genera of which 9 species in 2 genera are known in the larval stages. In Britain 2 genera are represented: *Diazosoma hirtipenne* Siebke which is unknown in the larval stage and *Trichocera* with 9 species of which 6 are known in the immature stages.

Trichocerid larvae are cylindrical and a little depressed, yellowish white to reddish brown in colour and amphipneustic. The cuticle is covered with fine pubescence. The posterior spiracles are surrounded by four fleshy lobes. In *T. saltator* (Harris) the dorso-lateral lobes are pigmented right up to the spiracle (fig. 7), in *T. hiemalis* (De Geer) the pigmentation ends short of the spiracle (fig. 6) and in the remaining species the lobes are unpigmented (fig. 8).

The larvae are saprophagous and feed on decaying organic material. They have been found in potatoes, turnips and mangold-wurzels which have partly decayed when stored in pits during the winter. *T. saltator* and *T. regelationis* (L.) occur in dung; *T. annulata* (Meigen) and *T. saltator* have been recorded from human corpses and probably occur on other carrion during the winter; I have received *T. saltator* from a bottle of milk. Larvae also occur in fresh and decomposing fungi.

The morphology of the larva and pupa of *T. hiemalis* is described by Keilin & Tate (1940). Keys to species are provided by Brindle (1962f), C. Dahl (1973) and Smith (1986b).

Tipulidae

(Figs: larvae 9–29, eggs 969–973, pupae 1110–1111, emergence of adult 1327)

The Tipulidae (crane-flies) is the largest family of Diptera (see also Tachinidae) with about 13,500 described species of which 303 species, representing 41 genera, occur in the British Isles. Of the British fauna about 150 species, representing 39 genera, are known in the larval stage. Larvae of the subfamilies Tipulinae and Cylindrotominae are fairly well known but in the Limoniinae many species are unknown in the immature stages. Larvae of the three sub-families may be separated as follows (after Brindle, 1967).

1 Posterior spiracular disc with six lobes which are flattened or cylindrical, sometimes reduced in size and rarely entirely sclerotized (figs 10–14) . . . . **Tipulinae**

— Spiracular disc with five or fewer lobes 2

2 Body with prominent processes, at least half as long as the body width and arranged in longitudinal rows (figs 17–20) . . . . **Cylindrotominae**

— Body without prominent processes; at most with tubercles which are much shorter than half the body width (figs 21–29) . . . . **Limoniinae**

Tipulinae. The larvae of this subfamily include the familiar 'leather jackets' and are very similar in appearance: usually cylindrical, rarely depressed; with a tough unpigmented cuticle, usually clothed in short, usually dense, pubescence. The colour may vary with the type of soil in which the larvae are found. There are invariably 6 anal lobes around the posterior spiracles. These lobes vary in size and degree of sclerotization according to the habitat in which the larvae are found. Soil is the main larval habitat with divergence into decaying wood (*Ctenophora*) and mosses (*Dolichopeza*), while some are aquatic (*Prionocera, Tipula maxima* Poda). In pasture soil some species attack the roots of cereals, root crops, vegetables such as *Brassica*, and also damage many herbaceous garden plants. The main pest species is *Tipula paludosa* Meigen which occurs in all soil types (clay, marl, peat, sand). The worst attacks occur in the spring, especially on young plants of crops sown on freshly ploughed grassland when the leather jacket population may be as high as hundreds of thousands per acre. Usually leatherjackets feed on roots and underground stems just below the soil surface but on warm nights they will feed on the surface, cutting off the plants at soil level. Sometimes, especially after heavy rain, they will be forced up through cracks in concrete, between paving stones etc and become trapped on the surface in very large numbers on hard areas into which they cannot burrow, such as paths and concrete surrounds of houses, and thus be reported as a nuisance.

Brindle (1967) keys the genera and species of this subfamily. The common 'pest' species usually found in pasture soil or gardens may be identified as follows.

1 Dorsum of prothorax with two raised welts (fig. 16). (*N. appendiculata* (Pierre) (= *maculata* Meigen) is a common garden species) . . . . **Nephrotoma** spp.
— Dorsum of prothorax without raised welts (fig. 15) . . . . (**Tipula** sp.) 2
2 Dorsal pairs (dl) of anal lobes sclerotized to tip (fig. 13) . . . . . **T. vernalis** Meigen
— Dorsal lobes not sclerotized 3
3 Only the lateral pair (lp) of anal papillae elongated, the ventral (vp) being rounded (fig. 10) . . . . **T. paludosa** Meigen
— At least two pairs of elongated, tapering, anal papillae, lateral (lp) and ventral (vp) . 4
4 Pigmented marks between spiracles obvious (fig. 12), pigmented borders of anal lobes darker, disc whitish yellow, larva yellowish brown in colour, not translucent . . . . **T. czizeki** De Jong
— Pigmented marks between spiracles weak, often absent (fig. 11), pigmented borders of anal lobes lighter, disc whitish, larva greyish, rather translucent . . . . **T. oleracea** L.

Cylindrotominae. The four British species of this subfamily have very distinctive caterpillar-like larvae which feed openly on the leaves of marsh plants.

Diogma glabrata (Meigen) (fig. 17) is green in colour and occurs in terrestrial mosses, usually on stones in limestone woodlands; *Triogma trisulcata* (Schummel) is dark brown or brownish green and occurs in semi-aquatic mosses (e.g. *Hypnum cuspidatum*) on moors; *Phalacrocera replicata* (L.) (fig. 19) is dark brown, paler below and is found on aquatic mosses (e.g. *Hypnum fluitans* or *Sphagnum*) in acid pools on moors or in woodlands; *Cylindrotoma distinctissima* Meigen is light green, darker dorsally and feeds on the leaves of *Caltha, Viola, Stellaria, Anemone*, etc.

Brindle (1967) keys the British genera and species.

Limoniinae. The larvae of this subfamily can be approximately separated into four tribes as below.

Brindle (1967) keys the British genera and species so far described as larvae and Crisp & Lloyd (1954) give much useful biological information.

Limoniini — larvae without obvious anal lobes, frequently living in silken tubes, herbivorous. Larvae occur in wet earth, decaying vegetation immersed in water or mud, on partly submerged stones in shallow streams, on piles and bridge piers where they feed on algae. Larvae of *Limonia (Geranomyia) unicolor* Haliday feed on algae on marine structures washed by the tide. *L. nubeculosa* Meigen (fig. 29) is a very common species beneath leaves in woods. There are 58 British species in 7 genera in this tribe of which some 25 species of *Limonia s. l.* are unknown in the larval stage.

Pediciini — larvae with two anal lobes, free living and carnivorous. The larva of *Pedicia rivosa* L. (fig. 25) has four pairs of creeping welts or tubercles which lack ventral hook-like spines at the tip. It is fairly common is aquatic or semi-aquatic mosses or in decaying vegetation in boggy places near streams and springs, where it feeds mainly on Diptera larvae (e.g. Chironomidae, Ceratopogonidae). Another common species *Dicranota bimaculata* Schummel has 5 pairs of well developed ventral pseudopods, which have prominent curved rows of hook-like spines at the tip (Figs 22–23). It is found in aquatic mosses or in marshy soils, mud or gravel near streams and rivers, where it feeds mainly on small worms (Oligochaeta). *Ula* occurs in fungi. There are 19 British species in the 3 genera in this tribe of which some species of *Dicranota* are unknown in the larval stage.

Hexatomini — larvae with 4 anal lobes, free living and carnivorous. The larvae of *Hexatoma* (fig. 27) are greenish and occur in sand by the edges of rivers and streams and share with the subgenera *Phylidorea* and *Elaeophila* of *Limnophila* and some *Pilaria* species the characteristic swollen penultimate abdominal segment (though this may occur only in preserved larvae). There are 42 British species in 8 genera of which the larvae of 11 species (4 *Paradelphomyia*, 2 *Pilaria*, 5 *Limnophila s. l.*) are unknown.

Eriopterini — larvae with 5 anal lobes, free living, herbivorous. This, the largest tribe, is the least well known in the immature stages because of their smaller size and burrowing habits. However, they can occasionally occur in large numbers, e.g. *Rhypholophus haemorrhoidalis* Zetterstedt (almost black in colour) and *Erioptera lutea* Meigen. The larvae and pupae of *E. squalida* Loew have piercing spiracles with which they obtain oxygen from the roots of aquatic plants (*Glyceria maxima*) (Houlihan, 1969). Of the 96 British species in 14 genera only 18 species in 9 genera are known as larvae.

Psychodidae

(Figs: larvae 30–40, egg 974, pupa 1112)

The family Psychodidae (moth-flies) contains some 1200 world species of which 84 species representing some 16 genera occur in the British Isles. Larvae of the British species may be grouped into three sub-families and separated as follows.

1	Abdomen ending in a tubular siphon which bears the posterior spiracles at its apex and a pair of fan-like brushes (figs 30–37)	**Psychodinae**
—	Abdomen not ending in a tubular siphon; posterior spiracles on each side of 8th abdominal segment	2
2	Body without conspicuous setae (fig. 40)	**Trichomyiinae**
—	Body with conspicuous setae (fig. 39)	**Sycoracinae**

Psychodinae. The genus *Psychoda* contains 15 British species of which the larvae of 13 are described and keyed by Satchell (1947). *Psychoda alternata* Say, *Ps. albipennis* Zetterstedt) (= *severini* Tonnoir) and *Ps. cinerea* Banks are frequently found in sewage bacteria beds. *Ps. alternata* (figs. 30, 31) is known as the trickling filter fly (see also under Phoridae) and the larvae also occur in rotting seaweed and the sodden refuse of disused farm feeding troughs, washings from animal cages, kitchen sink U-traps, etc.; it appears to show a preference for foul and wet habitats but not cow dung. Several species of *Psychoda* regularly breed in cow dung and others occur in decaying vegetation. The common *Ps. albipennis* (figs 32–33) has been reared from horse and cow dung and rotting carrots; it has also been involved in cases of human urogenital myiasis (Zumpt, 1965). The larva of *Ps. brevicornis* Tonnoir (figs 35–36) is adapted to feeding on the surface of dung and differs from other dung-feeding species in having a lateral fringe of hairs to keep it afloat on the semi-liquid medium and only a short respiratory siphon. *Ps. surcoufi* Tonnoir is another cow dung species, but larvae occasionally occur in milk bottles (see also Phoridae and Drosophilidae for this habit). *Ps. lobata* Tonnoir occurs in fungi.

Satchell (1949) described 15 of the 24 British species of *Pericoma* then recognised but Vaillant (1971–1976) has since transferred several species to other genera. The larvae are heavily pigmented and occur amongst clumps of damp moss and algal mats bordering the margins of streams where several species may be found in numbers quite close together. *P. trivialis* Eaton (figs 37–38) is a common species, the larvae of which may be seen creeping about on the surface of mud, though the mud particles trapped in the dorsal setae may render them inconspicuous apart from the winding tracks left by their movements. The larvae of *P. trifasciata* (Meigen) and *P. calcilega* Feuerborn are normally thickly encrusted with lime.

The larva of *Philosepedon humeralis* (Meigen) (fig. 34), the only British representative of the genus, feeds in dead snails (Vaillant, 1961; Smith & Grensted, 1963).

Only three of the 17 British species of *Telmatoscopus* are known in the larval stage; they should be sought at the edges of ponds or lakes where the ground is moist and occasionally submerged, though Withers (1986) records *T. tristis* Meigen and *T. advenus* Eaton from tree rot-holes.

Jung (1956) keys and describes some *Panimerus, Threticus* and *Clytocerus* larvae. The immature stages of other British genera and species remain undescribed from native material but Vaillant (1971–1976) should be consulted for descriptions of some and notes on the likely habitats in which to search for others (but frequently under names differing from the British Check List).

Trichomyiinae. The larva of *Trichomyia urbica* Curtis, the only British species, is found in the rotting wood of fallen trees where it makes a gallery running in the direction of the grain (Keilin & Tate 1937). The body, unlike that of other Psychodidae, is devoid of long setae and the head is strongly chitinized (fig. 40).

Sycoracinae. The larvae of this subfamily are associated with fast streams and waterfalls where they live on rocks in the splash zone or near the surface. *Sycorax silacea* Curtis (fig. 39), the only British representative of the subfamily, resembles a small water louse (*Asellus*) and is found among mosses or rotting leaves in such situations.

An account of the British species of Psychodidae, by Mr P. Withers, is in press.

Ptychopteridae

(Figs: larva 41, pupa 1113)

The family Ptychopteridae contains more than 60 world species in three genera. In Britain the family is represented by only the genus *Ptychoptera* with 7 species of which 6 have been described in the larval stage.

The larva (fig. 41) is very distinctive, with a long, narrow cylindrical body terminating in a long retractile respiratory siphon. It is whitish-grey in colour, frequently with a pair of brownish eye-spots. The respiratory system is metapneustic. Small prolegs, each with a single hook-like spine (vh) are present on abdominal segments 1–3. The presence of lateral and median brushes on the labrum, and of setal brushes on the mandibles (md) and maxillae suggest a detritus feeding habit.

Ptychoptera larvae are semi-aquatic and inhabit saturated mud, or shallow muddy pools in marshes, *Sphagnum* pools, or the margins of streams. Larvae of *P. contaminata* (L.) prefer mud covered with water and having a high organic content; they are usually common around farmyard pools and similar situations. *P. albimana* (F.) is usually found in mud without a high organic content, e.g. open marshes, thin woodland; *P. lacustris* Meigen and *P. paludosa* Meigen (and *P. longicauda* Tonnoir *teste* R.I. Vane-Wright) occur most frequently in woodland streams, in medium or dense shade; *P. scutellaris* Meigen is restricted to acid pools with *Sphagnum*, often at high altitudes in upland marshes; *P. minuta* Tonnoir has been found in a drainage channel around peaty fields.

Brindle (1962d, 1966) and Hansen (1981) provide keys to the known British larvae with descriptions and ecological notes and Miall (1985) gives some interesting behavioural notes.

Dixidae

(Figs: larva 42, pupa 1114)

Most of the 200 known species of Dixidae are Holarctic. Three genera are recognised, two of which occur in Britain: *Dixa* with 6 species and *Dixella* with 8 species. The immature stages of all British species are known.

The larvae are aquatic and are found at the surface of the water which has earned them the common name of meniscus midges. The resting larva adopts a U-shaped position (fig. 42) and joins the drift when disturbed. They are usually in contact with a plant, leaf, stone or piece of wood, where they feed on microscopic organic particles and microorganisms swept in by the labral brushes. *Dixa* is usually found in running water (though always marginal) and *Dixella* in still water, while both genera occur in slow-moving water. *Dixa* larvae sometimes form a significant component of the invertebrate fauna occurring in the downstream drift in rivers and streams.

Disney (1975) keys the British species in the larval, pupal and adult stages. The two genera may be separated as follows.

1 Usually five (3–7) or six (2–7) of the abdominal segments each with a dorsal ring or 'crown' of hairs (fig. 42,r) (poorly developed along anterior and posterior sectors in *D. puberula* Loew) . . . . **Dixa**

— Abdominal segments without dorsal rings of setae . . . . **Dixella**

Chaoboridae

(Figs: larvae 45–46, eggs 975, pupa 1115)

Most of the 100 or so known species of Chaoboridae occur in the Neotropical region. The group was formerly regarded as a subfamily of the Culicidae but is now almost universally accepted as separate family. Three subfamilies are recognised, only one of which (Chaoborinae) occurs in Britain, where it is represented by two genera, *Chaoborus* with 4 species and *Mochlonyx* with 2 species.

Chaoborus larvae have long been known as 'phantom' larvae because of the remarkably transparent body. The larvae of *Mochlonyx* are less transparent than *Chaoborus*. Hydrostatic organs enable chaoborid larvae to float in a horizontal position in mid-water waiting for their prey (mosquito and mayfly larvae, *Daphnia*, *Cypris*, etc). The larvae of *Chaoborus* are found in a wide variety of lakes and ponds while *Mochlonyx* larvae prefer pools in woodland (*M. culiciformis* De Geer) or acid moorland (*M. fuliginosus* Felt). Larvae of the two genera may be separated by the following couplet.

1 Thorax not greatly swollen, and not much wider than abdomen; head longer and narrower, eyes smaller; anal segment without siphon; respiratory system apneustic (fig. 45) . . . . **Chaoborus** Lichtenstein

— Thorax greatly swollen and much wider than abdomen (fig. 46); head shorter and broader, eyes larger, anal segment with siphon; respiratory system metapneustic . . . . **Mochlonyx** Loew

Brindle (1962) keys the larvae of all the British species of the family and gives notes on their ecology, and Miall (1895) also gives an account of the immature stages.

Culicidae

(Figs: larvae 43, 44; eggs 976–978; pupa 1116; adult emergence 1329)

Over 3000 species of true mosquitoes have been described and three subfamilies of worldwide distribution are recognised. Two subfamilies occur in Britain: Anophelinae, represented by a single genus (*Anopheles*) with 5 species, and Culicinae, with 5 genera and 27 species. Larvae of the two subfamilies found in Britain may be distinguished as follows:

1 Eighth abdominal segment without an elongate dorsal siphon (fig. 43), larvae resting horizontal to the water surface . . . . **Anophelinae**
— Eighth abdominal segment with a dorsal siphon which is longer than broad (fig. 44), larvae resting obliquely to the surface . . . . **Culicinae**

The final stage (fourth instar) larvae of the British species are keyed by Snow (1984); Cranston *et al.* (1987) provide keys to fourth instar larvae, pupae and adults.

All mosquito larvae are aquatic but occur in a variety of habitats and ecologically may be referred to four groups.

1. Domestic species (adults overwinter indoors): *Anopheles atroparvus* van Thiel (brackish water), *A. messeae* Falleroni (permanent ponds, slow streams), *Culiseta (=Theobaldia) annulata* Schrank (foul or brackish water in stagnant ponds, tanks, waterbutts, etc.), *Culex pipiens* L. typical form (natural and artificial collections of fresh, foul or brackish water), *C. pipiens* form *molestus* Forskal (usually in water below ground level in semi darkness).
2. Salt-marsh species (on or near coasts): *Aedes caspius* Pallas (brackish water, also in sewage effluents), *A. detritus* (Haliday) (brackish or saline water), *A. dorsalis* (Meigen) (brackish water).
3. Arboreal species (tree-holes): *Anopheles plumbeus* Stephens, *Aedes geniculatus* (Olivier), *Orthopodomyia pulcripalpis* (Rondani).
4. Rural species (non-domestic, in ground waters usually away from coasts): all the remaining species.

Some species on the British List have only been recorded once or twice, but because of their medical importance are worthy of further attention. *Aedes aegypti* (L.) is the principal vector of urban yellow fever abroad and although temperature requirements preclude it from becoming established in Britain under natural conditions, there was a local outbreak of yellow fever in Swansea in 1865, almost certainly from a single generation introduced from a ship. The species is extensively cultured in laboratories and escapes may occur. Larvae of *Anopheles algeriensis* Theobald have been recorded only once from three localities in Norfolk where they occurred (and persisted for some years) in extensive shallow puddles among thick sedges on the marshes adjoining Hickling Broad. This species is doubtfully indigenous but investigations by a resident in the area would be worthwhile as it is one of the species capable of transmitting malaria and the disease used to occur in East Anglia. The species has recently been discovered in Anglesey (Morgan, 1987). Locally contracted cases of malaria can still occur in the U.K. in the vicinity of airports when mosquitoes are inadvertantly imported in aircraft. *Aedes leucomelas* Meigen has only been recorded once from Britain (Widmerpool, Notts, May 1919) and *Culex modestus* Ficalbi has only been recorded in 1944–1945 in the Portsmouth area.

Apart from these 'exotic' species there is still much to be learned about the larvae of most mosquitoes, especially on their precise feeding habits and distribution.

The larvae of *Anopheles* collect their food at the surface and of Culicines below the water surface. Two different methods of feeding are adopted: by nibbling algae, dead leaves, etc. (e.g. *Aedes*, except *A. cinereus* Meigen) or by movements of the mouth brushes (figs 43, 44, br) which create a whirlpool bringing floating organic particles into the mouth (remaining genera and species).

Mattingly (1969) has drawn attention to the interesting problem of mouthbrush polymorphism and particle size of food taken, which can apparently vary during a life-history and requires further investigation.

There is an active mosquito recording scheme (organiser Dr Keith Snow, Northeast London Polytechnic) which prospective researchers on the family are recommended to support.

The eggs of Anophelinae have floats and are laid singly (fig. 978). Eggs of Culicinae lack floats and may be laid singly on soil etc. in seasonally dry pools (*Aedes*, fig 977) or in batches or rafts on the surface of the water (*Culex*, fig 976). Christophers (1945) has written on the structure and function of *Culex* egg rafts.

The pupa (fig. 1116) is comma shaped and swims with violent lashing movements of the abdomen. It rests at the surface where it takes in air through respiratory trumpets which extend internally into the thoracic spiracles. In Anophelinae the trumpets are more or less conical; in Culicinae they are more or less cylindrical.

While this *Handbook* was in press an important work on the larval habitats of mosquitoes appeared (Laird, 1988).

Thaumaleidae

(Figs: larva 47, pupa 1117)

The 60 known species of Thaumaleidae are mostly Holarctic in distribution. Five genera are recognised of which only one, *Thaumalea*, is represented in Britain by 3 species.

The immature stages are aquatic. The larvae (fig. 47) resemble those of Chironomidae but have spiracles on the prothoracic and terminal abdominal segments and the thoracic prolegs are unpaired (see key). They are found where clean water flows in thin films over rocks so that their backs are exposed above the surface. They feed on vegetable debris and diatoms. Saunders (1923) describes the larva of *Th. testacea* Macquart but immature stages of the other two species are undescribed.

Ceratopogonidae

(Figs: larvae 48–52, egg 979, pupae 1118–1120)

About 4000 species of Ceratopogonidae (biting midges) have been described throughout the world, and 154 species in 17 genera (several divided into numerous subgenera) occur in Britain. Four subfamilies are recognised of which Leptoconopinae does not occur in Britain. The larvae lack functional spiracles and respiration is cuticular or via anal blood-gills.

The immature stages of most genera are aquatic and are found in streams, ponds, lakes, salt-marshes or water in tree holes. Some genera have terrestrial immature stages and others are semi-aquatic in wet soil, rotting wet wood or other decomposing vegetable matter. The adults of some genera are of medical and veterinary importance due to their habit of sucking vertebrate blood (e.g. *Culicoides* in Britain) and their potential role in disease transmission. Because of this, the larvae of the family, especially the blood-sucking genera, have attracted a certain amount of research but much remains to be done. The subfamilies occurring in Britain may be identified in the larval stages by the following key.

1 Thoracic prolegs present; body with conspicuous hairs often arising from raised tubercles (figs 48–49), often terrestrial . . . . **Forcipomyiinae**

— Thoracic prolegs absent; body without conspicuous body hairs or tubercles . . . 2

2 Posterior proleg present with spines and hooklets (fig. 50). Usually crawling **Dasyheleinae**

— Posterior proleg absent, but last segment with hairs; body very smooth, whitish or translucent (figs 51–52). Usually fast swimming with snake-like motion **Ceratopogoninae**

Forcipomyiinae. This subfamily contains only two British genera, i.e. *Forcipomyia* (fig. 48) and *Atrichopogon* (fig. 49), which are mostly terrestrial (abroad, the subgenus

Trichohelea of *Forcipomyia* is truly aquatic). The larvae of *Forcipomyia* have bulbous tips to some hairs (fig. 48, detail) within which a hygroscopic substance collects moisture from the atmosphere. The water flowing down the pedicel of the hair keeps the skin moist and facilitates cuticular respiration. These beads of moisture give the larva and pupa a striking appearance when first exposed. The larvae are gregarious (20–100 or more) in habit and pupate together (fig. 1120). They are found in dark cavities where the atmosphere approaches saturation and favours the development of moulds and other fungi on which the larvae feed. There are 4 instars before pupation. Habitats include under bark (*F. bipunctata* L., *F. picea* Winnertz, *F. nigra* Winnertz), in rotting tap-roots of *Angelica* etc. (*F. radicicola* Edwards), rotting fungi (*F. ciliata* Winnertz), drying horse and cow manure (*F. brevipennis* Macquart). *F. braueri* (Wasmann) and *F. myrmecophila* (Egger) occur in ants' nests. *F. pulchrithorax* Edwards lives in the granular, solidifying sap in open wounds on elm, chestnut and ash trees. Saunders (1924) gives detailed descriptions of the immature stages of several species.

Larvae of *Atrichopogon* (fig. 49) have the body segments flattened in cross section. They are found in moist soil at the water's edge and among accumulations of floating plants.

The pupae of *Forcipomyia* and *Atrichopogon* retain the larval skin over the apical half of the body (fig. 1120). Few Diptera do this (see introductory section on pupae).

Dasyheleinae. This subfamily has only one genus, *Dasyhelea* (fig. 50).

Keilin (1921) reviews the larval habitats, including those of the following British species: *D. bensoni* Edwards (? *diplosis* Keiffer, among filamentous algae in a brackish pool); *D. dufouri* (Laboulbène) (in thick sap in wounds on elm); *D. flavifrons* (Guérin-Méneville) (in sap of beech and horse-chestnut); *D. versicolor* (Winnertz) (in humus around roots of *Spiraea ulmaria* and *Angelica*, from scum on surface of aquarium and (as *obscura* Winnertz) from elm sap, hornbeam sap and a water filled hole in an oak tree). *D. bilineata* Goetghebuer has been reared from the axil-waters of teasels (*Dipsacus fullonum* L.) by Disney & Wirth (1982). I have also seen *Dasyhelea* larvae from water in an old frying-pan used as a bird bath. The identity of the species recorded from water-filled tree-holes by Kitching (1972) is uncertain.

Ceratopogoninae. This subfamily is divided into five tribes. The Culicoidini contains *Culicoides*, the only genus occurring in Britain with blood-sucking adult females (divided into six subgenera). The larvae (fig. 52) are long, smooth, dull whitish or translucent, progress with a snake-like lashing motion and are mostly aquatic.

Kettle & Lawson (1952) key the larvae and pupae of 28 of the British species of *Culicoides*, distinguish some other genera of the subfamily, and classify the larval habitats as follows (some genera from other tribes are also included):

1. Bogland with ground cover of the mosses *Sphagnum* and *Polytrichum* penetrated by *Juncus articulatus* (*s. l.*): *Culicoides impunctatus* Goetghebuer (dominant), *C. clintoni* Boorman (= *C. truncorum* Edwards, of Kettle & Lawson, 1952), *C. heliophilus* Edwards, *C. albicans* (Winnertz), *C. obsoletus* (Meigen) and *Ceratopogon* spp.
2. Freshwater marsh without *Sphagnum* and *Polytrichum*, but with meadow plants e.g. *Cardamine pratensis* L. and *Ranunculus* spp. and sometimes with abundant *Juncus* spp.: *Culicoides kibunensis* Tokunaga (= *cubitalis* Edwards) (dominant), *C. pallidicornis* Kieffer, *C. obsoletus*, *C. pulicaris* (L.), *C. delta* Edwards, *C. punctatus* (Meigen), *C. odibilis* Austen, *Stilobezzia* spp., *Ceratopogon* spp. and *Serromyia* spp.
3. Areas continually under water, e.g. swamp: *C. kibunensis* (dominant when *Carex riparia* cover present), *C. odibilis* (dominant when *Carex* cover absent), *C. pulicaris*, *C. punctatus*, *C. fascipennis* (Staeger) (dominant in two swamps on margins of lochs).
4. On areas of bare mud: *C. odibilis* (dominant), *C. kibunensis*, *C. pallidicornis*, *C. pulicaris*, *C. stigma* (Meigen) and if there is slight organic pollution C. *nebeculosus* (Meigen) is dominant.

5. Coastal salt marshes: *C. circumscriptus* Kieffer and *C. salinarius* Kieffer (dominant on muddy sites), *C. maritimus* Kieffer and *C. halophilus* Kieffer (on vegetated sites).
6. Dry cakes of cow dung: *C. chiopterus* (Meigen), *C. dewulfi* Goetghebuer (= *pseudochiopterus* Downes & Kettle).

Additional categories not included by Kettle & Lawson are as follows:

7. Tree-holes: *C. fagineus* Edwards, *C. truncorum* Edwards, *C. obsoletus* (damp debris).
8. Temporary pools in pasture: *C. vexans* (Staeger), ? *C. brunnicans* Edwards (? small streams).
9. Fungi (large Agaricaceae, Polyporaceae, Boletaceae): *C. scoticus* Downes & Kettle; *C. obsoletus*.
10. Sap in tree wounds: *C. chiopterus* (on elm) (see also 6 above).

The larvae of the remaining tribes should be sought as follows:

Ceratopogonini: *Ceratopogon* and *Isohelea* in swampy banks of lakes, rivers and streams and in *Sphagnum* bogs.
Stilobezziini: *Monohelea* in *Sphagnum* bogs and swampy parts of forest streams; *Serromyia* in margins of shallow waters and swamps;*Stilobezzia* in moist soil, often overgrown with moss along the margins of rivers and streams, silted up ditches, etc.
Heteromyiini: *Clinohelea* in heavily vegetated overgrown meadows; sedgy boggy parts of flowing water in river flood plains.
Sphaeromyiini: *Mallochohelea inermis* (Kieffer) and *M. munda* (Loew) in lakes and *M. setigera* (Loew) in rivers; *Probezzia* in rivers in sandy areas and among dense weeds; *Sphaeromias* in lakes (*S. fasciatus* Meigen in the depths).
Palpomyiini: *Palpomyia* in lakes and rivers; *Bezzia* mostly in lakes, some in swamps and forest pools.

There is plenty of scope for careful research on larval ecology and systematics in this important family. The biting adults of *Culicoides* can make life miserable for residents and visitors in northern temperature regions (e.g. *C. impunctatus* in the highlands of Scotland). A useful modern introductory chapter on the family is provided by Kettle (1984: 137–158) and Atchley *et al.* (1981) give a full bibliography of Ceratopogonidae.
Keys to genera are provided by Glukhova (1977, 1979).

Chironomidae

(Figs: larvae 53–67, eggs 980–982, pupa 1121)

Over 5000 species of Chironomidae (non-biting midges) have so far been described throughout the world. Seven subfamilies are recognised, six of which are represented in Britain by over 450 species in 120 genera.

Larval Chironomidae are the most abundant Diptera in aquatic ecosystems and often dominate the invertebrate fauna. Their occurrence in a wide range of ecological conditions has led to their use as indicator organisms in classifying lakes, river zonation, water quality, etc. This has led to an intense study of the immature stages of Chironomidae in recent years. Chironomid larvae are a major source of food for freshwater fish and may constitute as much as 80% of their total food requirements. The larvae of some species (e.g. *Metriocnemus hygropetricus* Kieffer) play an essential role, along with Psychodidae, as browsers in trickling filter sewage beds. Occasionally larvae may occur in the domestic fresh water supply and parthenogenetic *Paratanytarsus* (= *Stylotanytarsus*), including apparently paedogenetic pupal forms, can complete their life cycles entirely within the system. (See introductory sections on larvae, and agricultural and medical importance.)

Not all Chironomidae have aquatic life-histories and the larvae of terrestrial species are not so well known. There is much scope for research in the elucidation of life-histories providing that larvae are reared through to adults, males of which can now be reliably identified by the key in Pinder (1978). A typical pupa is illustrated (fig. 1121) and a key to pupal exuviae is provided by Langton (1984).

Eggs are laid in a protective gelatinous matrix and each subfamily appears to have a characteristic shape of egg and arrangement within the mass, e.g. linear type (Orthocladiinae, Diamesinae); compact type — spherical, tear or fig-shaped, or occasionally attached to a solid object by a gelatinous stalk (Tanypodinae, Chironominae) (figs 980–982).

The life-histories of Chironomidae are reviewed by Oliver (1971) and a bibliography of Chironomidae is provided by Fittkau *et al.* (1976). Keys to larvae and pupae are provided by various authors in Wiederholm (1983, 1986). These are cited below, under subfamilies. This comprehensive work will also eventually cover pupae and adults, and reliable keys beyond genus are cited.

The subfamilies may be distinguished in the larval stage as follows (after Cranston 1982).

1	Antenna retractile into head capsule (fig, 53, an); ligula strongly developed (fig. 53, lg)	**Tanypodinae**
—	Antenna not retractile; ligula not strongly developed	2
2	Premandibles absent; procerci 8–10 times as high as wide (fig. 59, pc) . .	**Podonominae**
—	Premandibles present (fig. 54, pm); procerci rarely more than 4 times as high as wide	3
3	Third antennal segment annulate (fig. 56)	**Diamesinae (Diamesini)**
—	Third antennal segment not annulate	4
4	Anterior part of labrum (fig. 54, la) with a transverse row of 'scales' (fig. 57)	**Diamesinae (Protanypini)**
—	Labrum without this row of 'scales'	5
5	Ventral part of the mentum (fig. 54, m) expanded laterally to form ventromental plates which are usually striated (fig. 55)	**Chironominae**
—	Ventromental plates not striated	6
6	Ventromental plates well developed, extending beyond mentum by at least half of the width of the flattened mentum	**Prodiamesinae**
—	Ventromental plates smaller, never extending beyond mentum by as much as half width of flattened mentum	7
7	Hypopharynx (fig. 54, h) with an apical group of elongate, serrate hairs (fig. 58)	**Telmatogetoninae**
—	Hypopharynx with a few shorter hairs	**Orthocladiinae**

Tanypodinae. Larvae of this subfamily are aquatic, may be red with haemoglobin, and do not construct tubes or cases. They prey on small Crustacea, oligochaete worms and often on the larvae of other Chironomidae. Adaptations to the predaceous habit include the retractile antennae and rather long stilt-like prolegs, the latter giving rise to a rapid jerky motion (fig. 65). The pupae resemble those of mosquitoes and are free-living active swimmers. Larvae of Tanypodinae are keyed (to genera) by Fittkau & Roback (in Wiederholm, 1983: 33–110).

Podonominae and Diamesinae. Larvae of these small subfamilies appear to be generally adapted for life in cold conditions and are found in mossy mountain springs and cold streams. *Lasiodiamesa sphagnicola* (Kieffer), however, favours warmer pools in *Sphagnum* bogs. Larvae of Podonominae feed on diatoms, are free-living and very strong swimmers (even as pupae). Larvae of Podonominae are keyed by Brundin (in Wiederholm, 1983: 25–31) and Diamesinae (to genera) by Oliver (in Wiederholm, 1983: 115–138).

Orthocladiinae. Some larvae of this subfamily are terrestrial, usually in moss covered soil. Larvae of *Bryophaenocladius* have been reported as attacking the roots of greenhouse plants, stored potatoes, mosses, liverworts and commercial lettuce crops and are able to 'skip' like a cheese-skipper (*Piophila*). I have seen larvae (probably *Smittia* sp.)

reported as attacking: young plants of barley in Aberdeenshire (M.W. Shaw, pers. comm.); central shoots of winter corn in Lincolnshire (G. Murdoch, pers. comm.); winter wheat in Newcastle upon Tyne (4% of seed failed to germinate following 2 year ley, J.P. Rogerson, pers. comm.); and associated with rose-roots in large numbers in Reading.

Many larvae of this subfamily have adapted to life in swift flowing rivers and streams (e.g. *Rheocricotopus, Eukiefferiella*). *Cardiocladius* larvae are free-living in waterfalls and swift currents where they pupate in strong cocoons spun on rocks, stones and water-plants. *Metriocnemus martinii* Thienemann larvae are found in water filled tree holes (especially beech); *M. ursinus* Holmgren occurs in moss. Larvae of *Clunio marinus* Haliday, *Halocladius* spp. and *Thalassosmittia thalassophila* (Goetghebuer) are marine. *Epoicocladius flavens* (Malloch) (= *ephemerae* Kieffer) larvae are found on mayfly nymphs which they do not harm; the fully grown larva spins a gelatinous cocoon on the thorax of the mayfly nymph in which it pupates. Keys to the known larvae of Orthocladiinae are provided by Cranston (1982) and Cranston, Oliver & Saether (in Wiederholm, 1983: 149–291).

Chironominae. Most larvae of this subfamily are red in colour, due to the presence of haemoglobin which assists survival in low oxygen concentrations. They live in tubes of mud or vegetable debris. In the tribe Chironomini the larvae are generally larger and include detritus feeders, filter feeders, symbionts, parasites and carnivores. The larvae of the common *Chironomus plumosus* L. and *C. dorsalis* Meigen live in mud in small stagnant pools. They construct fixed tubes of mud and vegetable debris respectively, but *C. plumosus* spins a sheet of salivary secretion across the tube and by undulations of the body draws phytoplankton and other particles into the net (fig. 61) (filter feeder). *C. dorsalis* (fig. 66) and other *Chironomus* species only take food from the end of their tubes (detritus feeders). The larva of *Glyptotendipes paripes* (Edwards) is found in the mollusc *Anodonta* (Beedham, 1966).

Larvae of the tribe Tanytarsini are smaller in size and are detritus or filter feeders. *Rheotanytarsus* species are filter feeders that construct tubes of fine silt particles attached to stones and plants. They spin nets across arms at the entrance of the tube and the natural water current brings food particles into the net, the water passing out through a hole at the end of the tube (figs 63–64).

Some larvae in the subfamily construct movable cases and adopt a mode of life similar to caddis larvae (e.g. *Zavrelia, Stempellina* and *Lauterborniella*). Larvae of Chironominae are keyed to genus by Pindar & Reiss (in Weiderholm, 1983: 293–435).

Telmatogetoninae. Larvae of the two British species (*Thalassomya frauenfeldii* Schiner, *Psamathiomya pectinata* Deby) of this subfamily are adapted to marine conditions and live on intertidal rocks where they feed on algae which they scrape from the rocks. Females of Telmatogetoninae are unique in the Chironomidae in laying eggs individually. Larvae of Telmatogetoninae are keyed to genus by Cranston (in Wiederholm, 1983: 17–22).

Marine habitats have also been invaded by larvae of Orthocladiinae (e.g. *Clunio*) and Chironominae (e.g. *Chironomus*).

Simuliidae

(Figs: larvae 68–69, egg 985, pupa 1122)

The family Simuliidae (black-flies) contains some 1450 species and has an almost cosmopolitan distribution. Two subfamilies are usually recognised, one of which (Simuliinae) is represented in Britain by 33 species contained in 3 genera (*Simulium, Prosimulium* and *Metacnephia*), but many sibling species, recognisable only on their chromosomes, are being found. The larvae are aquatic and usually found in running water including rapids and cascades. The three species of *Prosimulium* are found in hill streams. The commonest species of *Simulium* is *S. ornatum* Meigen, the larvae of which are found in all types of lowland water courses and are often abundant in small streams and flowing ditches. *Simulium vernum* Macquart and *S. cryophilum* Knoz are often abundant in many types of small streams. *S. equinum* (L.) is common, usually on rooted vegetation in large streams with a steady current and is frequently accompanied by *S. lineatum* (Meigen). *S. reptans* (L.) and *S. tuberosum* Lundström are common in larger stony rivers but the latter occurs usually above the limit of cultivation of the surrounding land and the former below, though there is an area of overlap. Other species are more specialised in their habitat and consequently less common, e.g. *S. costatum* Friederichs (spring-fed streams near source), *S. noelleri* Friederichs (lake or pond outlets).

The larvae are filter feeders on vegetable debris and diatoms which they strain from the water with their cephalic fans (figs 68–69). Occasionally they may ingest small larvae such as Chironomidae or even early instars of their own kind. There are six to eight larval instars in our species. There is a short pharate (see Introduction) stage (recognised by the much darker gill-spot) when the prepupa, still inside the last larval skin, spins its cocoon of silk, attached to a suitable substrate, inside which it pupates. The pupa has long filamentous gills (fig. 1122).

The eggs are eccentric ovoid in shape (fig. 985) and may be laid singly and loosely or in batches stuck to the substrate; they are white when laid but darker later. Many species pass the winter as eggs but some do so as slowly growing larvae.

Most adult female Simuliidae suck blood and their biting of man and animals causes irritation sometimes followed by toxic and allergic reactions. In tropical Africa and tropical America they transmit the disease onchocerciasis (river blindness). In Britain they are known to transmit the nematode *Onchocerca gutturosa* to cattle (without serious results) and certain Protozoa (e.g. *Leucocytozoon*) among birds. This medical and veterinary importance has led to a considerable amount of work on their immature stages for the purpose of survey and control work throughout the world. The *Simulium* fauna of an area is best established by searching for their larvae and pupae in freshwater systems from small trickles to large rivers. Thorough surveys such as that of Crosskey (1985) in the London area would be worthwhile projects and add much to our knowledge of the ecology and distribution of the family.

L. Davies (1968) keys the British species in the larval, pupal and adult stages, but the keys to early stages are difficult to use and are currently under revision by the Freshwater Biological Association. Ladle & Bass (1975) have described the larva of a new *Metacnephia*. The Diptera Check List in the *Handbook* series should be consulted for nomenclatorial changes.

Anisopodidae

(Figs: larvae 70–73, egg 986, pupa 1123)

The family Anisopodidae contains about 100 species in six genera of which 5 species in 2 genera occur in Britain. Two subfamilies are recognised, the larvae of which may be separated as follows.

1 Anal segment rather truncate posteriorly; posterior spiracular disc larger and with distinct lobes (fig. 72); lines drawn through the axes of the diagonal posterior spiracles would intersect on disc . . . . **Anisopodinae**
One genus, Sylvicola (= Anisopus)

— Anal segment elongated and more rounded posteriorly; posterior spiracular disc small, without distinct lobes; lines drawn through axes of posterior spiracles would not intersect on disc (fig. 73) . . . . **Mycetobiinae**
One genus and species, Mycetobia pallipes *Meigen*

Anisopodid larvae all have a perianal shield (of thickened hypodermal cells) on the ventral surface of the anal segment, which spreads laterally with a sinuate margin (fig. 71, S).

The larvae of *Sylvicola* species (fig. 70) are yellowish in colour but the underlying organs impart a reddish tinge with dark brownish thoracic markings. They are usually associated with decaying vegetable matter such as potatoes, beet, decaying roots of *Angelica* and burdock, mouldy decaying honeycombs, cardboard, fungi, decaying leaves in tree rot-holes, slime flux from tree wounds, but have also been found in cider and home-made wines, and liver that had been preserved in formalin for seven years (partly projecting and mouldy). *Sylvicola fenestralis* (Scopoli) has occurred in cases of urogenital myiasis (Smith & Taylor, 1966, Morris, R.F. 1986). *Sylvicola punctatus* (F.) frequently occurs in dung. The remaining two British species are unknown in the immature stages. The larvae of *Sylvicola* are often found in company with *Scatopse notata* (L.) (Scatopsidae), *Lonchaea chorea* (F.) (Lonchaeidae), Mycetophilidae and Sphaeroceridae.

Larvae of *Mycetobia pallipes* Meigen (fig. 71) occur in slime or exudations on the surface or under wet bark on decaying trees.

The eggs of *Sylvicola* (fig. 986) and *Mycetobia* are enclosed in a gelatinous mass. The pupae are free and found in the same media as the larvae.

Keilin & Tate (1940) give detailed descriptions of the immature stages of *Sylvicola fenestralis* and *Mycetobia pallipes*; Brindle (1962f) gives keys to species.

Bibionidae

(Figs: larvae 74–78, eggs 983–984, pupa 1124)

The family Bibionidae contains nearly 700 species in 8 genera throughout the world. Three subfamilies are recognized but only one of these (Bibioninae) is present in Britain, represented by the two genera *Bibio* and *Dilophus*. Larvae of *Bibio* have two openings to the posterior spiracles and larger body processes in transverse rows (figs 74, 78), while those of *Dilophus* have three spiracular openings (fig. 77) and shorter body processes except for one dorso-lateral series.

Both genera are herbivorous, often on plant roots, and live in soil, wood debris, dung, etc. The larvae are slow moving and gregarious, being usually found clustered together.

The eggs of Bibionidae (fig. 983) are laid in masses and appear rather opalescent. The newly hatched larva of *Bibio* (fig. 76) has conspicuous long hairs but that of *Dilophus* is short haired (fig. 75). There are four larval instars. Male pupae of *Dilophus* have 3 pointed processes on the head and female pupae have a single process, but this is better developed than the single process present in the pupae of both sexes of *Bibio* (fig. 1124).

Bibio larvae are usually found in woodland soil but *B. johannis* (L.) occurs in soil or dung in open country. Larvae of both genera are occasionally pests of cereal and root crops (see Economic section and Freeman & Lane (1985). Morris, H.M. (1922) suggested that such cases were due to larvae being carried in manure applied to the plants.

Morris, H.M. (1917, 1921–1922) gives detailed descriptions of the immature stages. Brindle (1962a) gives specific keys to the larvae so far known (2 of the 4 species of *Dilophus* and 8 of the 14 of *Bibio*).

Mycetophilidae

(Figs: larvae 79–86, 89–91; egg 988; pupa 1125)

The family Mycetophilidae (fungus gnats) contains about 3400 described species with an almost cosmopolitan distribution. In Britain about 450 species in 65 genera and all seven accepted subfamilies have been recorded.

Larvae of six of the seven subfamilies (Manotinae not yet described) may be separated as follows (after Madwar 1937).

1 Larva with one pair of thoracic and 8 pairs of abdominal spiracles (8th pair with horned prominences in *Ditomyia*) (figs 79–80) . . . . **Ditomyiinae**
— Larva with one pair of thoracic and at most 7 pairs of abdominal spiracles, or without spiracles (Keroplatinae) 2
2 Antennae well developed, composed of three segments (fig. 81) . . . . **Bolitophilinae**
— Antennae rudimentary, composed of one segment 3
3 Larva free; locomotory pads present (fig. 82) . . . . **Mycetophilinae**
— Larva enclosed in slimy tube, or in web; pads absent 4
4 Larva without spiracles, vermiform (worm-shaped) . . . . **Keroplatinae**
— Larva with spiracles, not vermiform 5
5 Larva peripneustic (fig. 1) . . . . most **Sciophilinae**
— Larva propneustic (fig. 1) 6
6 Epicranial plates meeting as usual on ventral surface (fig. 86) . . . . (Genus *Speolepta*) **Sciophilinae**
— Epicranial plates not meeting on ventral surface . . . . **Diadocidiinae**

The larvae of Mycetophilidae are mostly found in the larger fungi and it is probable that even when found elsewhere the majority are feeding on microfungi or fungal hyphae.

Chandler (in Stubbs & Chandler, 1978) lists fungus associations for 130 British species of Mycetophilidae and Hutson *et al.* (1980) give considerable information on life histories. Madwar (1937) and Laštovka (1971) describe some immature stages.

There are three recognisable stages in the development of a soft fungal fruiting body (sporophora): 1, fresh with no signs of decay; 2, decaying through age and damage (mostly by fungivores); 3, semi-liquid, advanced state of decay (some tougher fungi desiccate rather than rot and are unsuitable for fungus-gnats).

Most mycetophilids attack the first two stages but some species will continue to develop in the last stage of almost any rotting fungus (e.g. *Mycetophila fungorum* De Geer). Other habits and habitats are discussed below under subfamilies.

There is plenty of scope for research on the immature stages provided care is taken to identify the fungi and the adult flies correctly. Adults of all subfamilies except Mycetophilinae are keyed in Huston *et al.* (1980); other taxonomic literature is cited in that work.

Ditomyiinae. There are only two genera of this subfamily in Britain, each with a single species. The characteristic larvae of *Ditomyia fasciata* Meigen (fig. 80) have been reared from a variety of hard polyporaceous fungi including *Coriolus, Fomes, Daedalea, Polyporus, Bjerkandera, Trametes, Inonotus, Leptoporus. Symmerus annulatus* (Meigen) (fig. 79) is found in rotting logs.

Diadocidiinae. There is only one genus (*Diadocidia*) of this subfamily in Britain with three species, two of which are found in rotting wood and associated with the fungus *Peniophora*. The larva differs from that of other Mycetophilidae in having the epicranial plates separated ventrally.

Bolitophilinae. This subfamily has only one genus *Bolitophila* which is Holarctic in distribution. The known larvae are gregarious and have all been found in the soft fruiting bodies of fungi. *Bolitophila hybrida* (Meigen) is very common in *Paxillus involutus* (Batsch. ex Fr.) Fr. and *B. saundersi* Curtis (fig. 81) is usually found in *Hypholoma fasciculare* (Huds. ex Fr.) Quélet, but both species occur in other fungi.

Some species appear to be restricted to a few closely related fungi (i.e. are stenophagous), e.g. *Bolitophila cinerea* Meigen on *Hypholoma* and *Pholiota* spp.

Keroplatinae. There are seven British genera of Keroplatinae.

The larvae of this primitive and diverse subfamily spin webs, the strands of which are made sticky with drops of fluid containing oxalic acid.

Larvae of *Keroplatus* are flattened, somewhat luminous, and live under a large, flat, mucilaginous net on the underside of logs, usually with polyporaceous fungi. They feed partly on that fungus and partly on other invertebrates and pupate in a distinct dry cocoon.

Larvae of *Orfelia s.s.* species are found in turf, grass tussocks, under logs and boulders, in worm tunnels, among mosses and liverworts. Nothing is known of the biology of the other subgenera.

The larvae of *Macrocera* are poorly known, but have been found in turf, rotting wood and caves. They are predaceous but some are scavengers at first. The remaining genera should be sought under logs or rotting wood, though the immature stages of several are unknown.

Sciophilinae. This subfamily contains about one third of the British fauna, and is divided into five tribes of which four are represented in Britain. The immature stages are poorly known. The larvae are found on fungi or under bark, inhabit a small mucilaginous tube supported by threads and, in some species, covered by a dry irregular, sometimes communal, net.

Sciophila buxtoni Freeman occurs in tough lignicolous polypores, e.g. *Coriolus, Pseudotrametes* and *Daedaleopsis*. Extreme examples of polyphagous species are *Sciophila lutea* Macquart, *Rondaniella dimidiata* Meigen and *Docosia gilvipes* Haliday, larvae of the last species also being found in the nests of birds and mammals. *Mycomya* species have been bred from fungi associated with dead wood. Larvae of *Gnoriste* are found in mosses and some *Boletina* occur in mosses and liverworts as well as the more usual habitats such as rotting wood. *Speolepta leptogaster* feeds on algae and fungi in caves (see introductory section on caves).

Manotinae. The only British species of this subfamily is *Manota unifurcata* Lundström, which is rare and has been reared from a rotting beech with Myxomycetes (slime mould) but the larva is unknown (and therefore not included in the key).

Mycetophilinae. Larvae of this subfamily are mostly found in soft ground fungi but some, e.g. *Mycetophila ornata* Stephens, *Dynatosoma fuscicorne* (Meigen), prefer a wide range of lignicolous fungi. Other species are more specialised in the range of fungi in which they breed. *Mycetophila alea* (Laffoon), *Exechia nigroscutellata* Landrock and *Cordyla fasciata* Meigen are restricted to Russulaceae; *Mycetophila signatoides* Dziedzicki and *Exechia separata* Lundström are restricted to Boletaceae. A few species appear to be restricted to just one species of fungus (i.e. are monophagous) e.g. *Mycetophila cingulum* Meigen on *Polyporus squamosus* Fries; *Trichonta falcata* Lundström on *Stereum hirsutum* (Willd. ex Fries) and *T. apicalis* Strobl (=*vernalis* Landrock) on *Calocera cornea* (Batsch. ex. Fr.) Fries. *Mycetophila blanda* Winnertz is one of the few (see Ecology Section) Diptera that induce gall formation in fungi, in this case on *Lactarius deliciosus* L. ex Fries.

The slug-like larva (figs 83–84) of *Phronia flavicollis* Winnertz (=*strenua* Winnertz) lives on sodden, fallen and barkless branches, where it feeds on moulds. It bears a hard black conical case (figs 85, 89, 90) made from its own excrement. It leaves this case and spins a light silky cocoon prior to pupation. *Phronia braueri* Dziedzicki (?=*annulata* Winnertz) is found in similar situations but does not form a case. *Epicypta aterrima* (Zetterstedt), on rotten wood, forms a case similar to that of *P. flavicollis*. Some larvae (of this genus?) appear to live under a mucilaginous 'blob' (fig. 91) without forming a case. *Platurocypta* species and *Mycetophila vittipes* (Zetterstedt) feed on Myxomycetes (slime moulds).

Sciaridae

(Figs: larvae 87–88, egg 987, pupa 1126)

The family Sciaridae contains over 1000 species in over 50 genera and is represented in most regions of the world. In Britain about 100 species in 18 genera have so far been recorded but others are now being discovered following a recent *Handbook* to this long-neglected family (Freeman, 1983, 1987). For a long time sciarids were regarded as comprising a subfamily of the Mycetophilidae but they are now given family status.

The larvae are white with a sharply contrasting shiny black head and remarkably uniform general appearance (figs 87–88). The terminal abdominal segment is slightly lobate and is used as a leg in locomotion. There are four larval instars, the first metapneustic, the second and third propneustic and the fourth hemipneustic (see fig. 1). Diagnostic features are given in the key to families.

The larvae are usually associated with decaying vegetable matter, excrement, rotten wood and fungi.

Three species are recorded as pests of mushrooms: *Lycoriella solani* (Winnertz), *L. auripila* (Winnertz) and *Bradysia brunnipes* (Meigen). The larvae tunnel into the mushroom to feed, but more damage appears to be caused through the transmission of disease and mites associated with the bacterial breakdown of the fungi (Hussey, Read & Hesling, 1969). Larvae may still be recognizable after reconstitution in dehydrated mushroom soup!

Other species of economic importance through larvae damaging plants and seedlings in greenhouses include *Bradysia amoena* Winnertz, *B. brunnipes*, *B. paupera* Tuomikoski, *B. tritici* (Coquillett) (the mossfly of orchid growers), *Ctenosciara hyalipennis* (Meigen), *Lycoriella auripila* and *Pnyxia scabei* (Hopkins) (on cucumbers, Speyer, 1922).

Larvae of *Plastosciara* and *Xylosciara* are usually found under bark or in rotting wood, but *P. perniciosa* (Edwards) is a common greenhouse pest, destroying the roots and stems of cucumber seedlings. Adults of this species have also occurred in numbers indoors, possibly due to larvae feeding in decaying peat, used in the insulating lining of old fashioned steel safes. Adults indoors may also originate from larvae feeding in overdamp compost around potted plants.

The larvae of several species have been recorded from old nests of birds and mammals (Hicks, 1959–1971; Hackman, 1963) e.g. *Bradysia* spp., *Corynoptera* spp., *Lycoriella sagraria* (Felt), *L. lundstromi* (Frey), *Trichosia basdeni* Freeman, *T. coarctata* Winnertz. Most nests contain droppings and other decaying material which may attract them and of course some are lined with a mixture of mud and dung.

Occasionally mass movements of sciarid larvae have been reported in Europe, the larvae moving in columns 8–25 cm wide and 2–3 metres long. The species involved are *Sciara thomae* (L.) and *S. militaris* Nowicki. The former occurs fairly commonly in Britain, but the phenomenon has not yet been observed here and its cause or purpose is quite unknown.

There is plenty of scope for research on the immature stages of this family. Thomas (1930) describes the larva and pupa of *Bradysia aprica* (Winnertz) (as *Sciara nitidicollis*, see Freeman, 1983) from decaying celery roots. Madwar (1934) describes the larvae of *Pnyxia scabiei* and (1937) of *Lycoriella auripila*, *Heterosciara semialata* (Edwards), *Bradysia fenestralis* (Zetterstedt) and *Plastosciara perniciosa*. Very little has been done since.

Scatopsidae

(Figs: larvae 92–100, pupae, 1127–1128)

The Scatopsidae is a little known, little worked family. About 300 species have been described, contained in 18 genera. Four subfamilies are recognised but larvae of only two of these are known, so a key cannot be given and when more larvae are known even the family key may need emendation. All four subfamilies occur in Britain and such biological information as is available is given under these.

The immature stages of very few species are known. Of the 37 British species (in 15 genera) the larvae of only four have been adequately described.

Aspistinae. The immature stages are unknown. Adults of the only British species, *Aspistes berolinensis* Meigen, are rare and found in sandy places. In Britain the species has so far only been found in coastal sand dunes but continental records are from far inland. In Czechoslovakia adults have been reared from 'sifted litter' where it is thought there may be two generations a year.

Ectaetinae. Laurence (1953) describes the larva of *Ectaetia platyscelis* Loew (figs 96, 100) which he reared from a deposit of wet orange coloured detritus lying in a hole in a lime tree trunk. Adults of this and the other two British species of the genus (whose larvae remain unknown) have been reared from rotting trees.

Psectrosciarinae. The immature stages of Psectrosciarinae are unknown.

The subfamily is represented in Britain by three species of the genus *Anapausis*. *Anapausis soluta* (Loew) is common and widespread in the adult stage and is frequently found swarming in large number on fences and poles; it may also occur indoors where I have seen specimens that were found in cracks behind a kitchen sink. *A. talpae* Verrall was discovered swarming on a willow trunk.

Scatopsinae. The larva of *Scatopse notata* (L.) and *Coboldia fuscipes* (Meigen) have been found in a variety of decaying plant and animal materials, e.g. wasps' nests, bulbs and onions, green ginger damaged by water (Lyall, 1929), wastes from fruit and wine canneries, excrement and decomposing fungi. The larva of *S. notata* (figs 92, 97), described by Morris (1918), is somewhat flattened dorso-ventrally and dorsally has thick setae, arranged in a regular pattern, which are usually full of detritus when the larva is first found. It is peripneustic with one pair of prothoracic and eight pairs of abdominal spiracles. The larva of *Coboldia* is similar but the dorsal hairs are not arranged in a regular pattern (fig. 94). Bovien (1935) found that in *C. fuscipes* the length of the caudal spiracular processes varied with the degree of dampness of the breeding medium. In dry conditions they were short, but in wet conditions they were long and enabled the larvae to hang below the meniscus (like some other aquatic Nematocera).

The larva of *Rhexosa* has not yet been found in Britain but American species (fig. 93) have been found in the decaying bark of dead or dying deciduous trees. Lyall (1929) gives notes on *R. subnitens* (Verrall).

Apiloscatopse species have been reared from fungi: *A. flavicollis* (Meigen) from *Tricholoma pessundatum* Quélet and *A. scutellata* (Loew) from *Bjerkandera adusta*.

Parascatopse litorea (Edwards) (figs 95, 98) is a coastal species in Britain but the interesting larva has only recently been discovered and described from saltings in Poland (Szadziewski, 1979). The larvae were found in numbers (April-July) from salt soil covered with *Salicornia patula* Duval-Jouve and *Aster tripolium* L. Probably the larvae of both British species of the genus are to be sought in salt-marshes.

Adults of *Holoplagia transversalis* (Loew) have occasionally been found with ants (*Lasius fuliginosus* Latreille) and *H. richardsi* Edwards has been reared from rotting elm, but the immature stages are unknown.

Adults of *Reichertella geniculata* (Zetterstedt) have been found congregated on a poppy seed-head but the life-history is unknown. Wehrmeister (1924) figures the anal papillae (fig. 99) of *R. pulicaria* Loew but gives no habitat details.

Clearly, careful rearing from the habitats mentioned, especially rotting trees, should elucidate new life-histories in this neglected family.

Cecidomyiidae

(Figs: larvae 101–122, 125; eggs 989–990; pupae 123–124, 1129–1130; mines and galls 1289–1290, 1311–1315)

About 4500 species of Cecidomyiidae (gall midges) have so far been described throughout the world. Three subfamilies are recognised, all of which occur in Britain, and the larvae may be distinguished as follows.

1 Anus slit-like (fig. 102) and usually ventral (dorsal in some predaceous species, e.g. *Lestodiplosis*) 2
— Anus rounded, terminal (fig. 101) 3
2 Abdominal segment 8 with four dorsal papillae (fig. 103, dp), abdominal segments 1–7 with four posteroventral papillae (pv) (sometimes imperceptible); not gall-forming . . . . **Porricondylinae** (part)
— Abdominal segment 8 with two dorsal papillae; abdominal segments 1–7 with 2 posteroventral papillae; some are gall-forming . . . . **Cecidomyiinae**
3 Lateral papillae in groups of 2; anus usually protrusible; not gall-forming **Lestremiinae**
— Lateral papillae in groups of 3 (fig. 103, lp) anus non-protrusible; not gall-forming . . . . **Porricondylinae (Heteropezini)**

Cecidomyiid larvae are often brightly coloured red, orange, pink, yellow or sometimes white. The distinctive sternal spatula or 'breastbone' (figs 103–116) is present only in final (third) instar larvae and is absent in some species (e.g. *Contarinia geniculati* Reuter, a salmon pink larva in the florets of meadow foxtail and cocksfoot grasses) and in paedogenetic larvae (e.g. *Miastor, Mycophila*).

The spatula is best developed in soil-dwelling larvae where it is of use in tunnelling and excavating a pupal chamber. This can cause wear of the spatula and caution is then necessary in identification from this feature alone (Milne, 1961).

Eggs are usually small and ovoid and about 100 are produced by the adult females, except in paedogenetic forms, when they are few and large. Paedogenesis is more fully discussed in the introductory section on Immature Stages (p. 24).

There is still much to be done on the larvae of Cecidomyiidae, particularly on their description and detailed systematics. The series of books by H. F. Barnes (1946–1956) and Nijveldt (1969) is a mine of information and more specialised works are cited under each subfamily. Useful studies of gall midge communities, their life-histories and parasites are provided by Askew & Ruse (1974, on birch leaves), Hodges (1969, birch catkins), Milne (1960, clover), Otter (1938, knapweed), Parnell (1963, broom), and I. J. Wyatt (1964, mushrooms).

Lestremiinae. Larvae of this subfamily are poorly known but have been found in decaying wood and vegetation, plant wounds and fungi, including mushrooms.

Larvae of the mushroom infesting species are described and keyed by Wyatt (1964) (e.g. *Lestremia cinerea, Mycophila speyeri, M. barnesi*). *Mycophila* species are usually paedogenetic (i.e. with reproducing larvae, see Introduction and Porricondylinae below). The sternal spatulae (of the sexual cycle) of two of the mushroom pest species are illustrated (figs 113–114). *Monardia ulmaria* Edwards has been reared from rotten elm. The reddish larvae of *Campylomyza ormerodi* (Kieffer) (fig. 105) have been alleged to attack the tap root of red clover at ground level and the plant apex but this observation requires confirmation; *C. pumila* Winnertz has been reared from an Ascomycete from the United States. Adults of *Aprionus* species occur around old logs and stumps, especially beech. *Peromyia* species occur under bark and leaf litter and *P. fungicola* (Kieffer) (fig. 120) has been reared from a mould growing on the surface of a toadstool (*Lactarius*).

Porricondylinae. Larvae of this subfamily are mycetophagous in decaying vegetation and wood and may be secondary invaders in the living tissues of higher plants.

In his keys to mushroom infesting cecid larvae Wyatt (1964) includes *Heteropeza pygmaea* Winnertz and *Henria psalliotae* Wyatt, which are paedogenetic. He has also reviewed the phenomenon of paedogenesis in the family (Wyatt 1967) including the well known larvae of *Miastor* which are fairly easily found in numbers under the bark of rotting birch where they often form star-shaped clusters. The mother larvae increase in size merely by distention of the cuticle and the daughter larvae can be clearly seen inside (fig. 118). The striking larvae of *Parepidosis* (fig. 117) are found under bark and leaf litter.

Panelius (1965) covers the subfamily with notes on larvae and biology where known. Möhn (1955) gives detailed descriptions of larvae.

Cecidomyiinae. This subfamily contains the many gall-producing forms which earn the family its common name. Not all form galls however; some feed in the stems and flower heads of plants, others are mycetophagous and some are predators or parasitoids. Larvae of the tribe Oligotrophidi mostly live freely in flower heads or cause leaf rolls or swollen stems, but *Craneiobia corni* (Giraud) causes prominent galls on dogwood (fig. 1313).

The large genus *Dasineura* (136 British species) contains many species of economic importance (see table in Economic Section). The white larvae of *D. brassicae* (fig. 109) cause the 'bladder pod' condition which prevents normal seed development in cabbage, swede, turnip, rape and radish and has increased in importance with the increased growth of oil seed rape. *D. leguminicola* (fig. 110) attacks the inflorescences of red and white clover; the larvae are yellow at first, then become salmon pink. *D. trifolii* (fig. 111) forms galls on the leaves of clover plants which cause the leaflets to stick together; the larvae are white at first and later become orange. The red or orange larvae of *D. alopecuri* (fig. 112) feed and pupate in the florets of cocksfoot grass (*Dactylis glomerata* (L.)). The galls of *D. ulmaria* (Bremi) may be common on meadow sweet (*Spiraea*).

Mayetiola destructor (Say), the well known hessian fly (figs 116, 122, 1311), attacks the straw of wheat and causes widespread damage throughout the wheat growing areas of N. Africa, the U.S.A., New Zealand and part of Europe, but fortunately is less serious in Britain. The pupae (figs 123, 1130) are formed inside the last larval skin (which is more characteristic of Cyclorrhapha — see introductory section on pupae) and are sometimes called 'flax seeds' because of their superficial resemblance to such.

Rhabdophaga species (26 in Britain) (fig. 1315) are mostly associated with willows.

Rondaniola bursaria (Bremi) forms the galls frequently seen on ground ivy (*Glechoma hederacea* L.) (fig. 1314).

Sylvén (1975) deals with larval structures and habits of Oligotrophidi.

True galls, mostly on flowers and buds but also on leaves, are induced by larvae of the super-tribe Asphondyiidi.

The larvae of Lasiopterini and Oligotrophini mainly cause simple galls on twigs, petioles, midribs or leaves, a few occur in the seeds of Compositae and at least one species of Brachyneurini, *Brachyneurina peniophorae* Harris, forms galls in the fungus *Peniophora cinerea* (Fr.) Cook (Harris & Evans, 1979).

Members of the largest supertribe, the Cecidomyiidi, have a very wide range of habits, including free living, phytophagous and mycophagous forms, gall makers, predators and internal parasitoids. The large genus *Contarinia* (72 British species) contains most of the species of economic importance (see economic section and Harris, 1966), the larvae of which develop in malformed flowers of various Dicotyledons, especially Leguminosae (e.g. *C. pisi* on peas) (fig. 107); others develop in the spikelets of Gramineae (e.g. *C. tritici* on wheat (figs 108, 1312) (see also *Sitodiplosis* below), and *C. merceri* Barnes and *C. geniculati* (Reuter) on *Alopecurus*). Others are found in galls on trees or form galls in the leaves (e.g. *Putoniella pruni* Kaltenbach on plum) and inflorescences of Monocotyledons and Dicotyledons, and a few attack developing fruit (e.g. *Contarinia pyrivora* Riley on pear).

Cecidomyia species are associated with conifers. *C. pini* (fig. 121) larvae feed in resin masses on a number of species of Coniferae.

Myocecis ovalis Edwards induces a localized hyphal mat in the fungus *Hypoxylon rubiginosum* Pers ex Fr. (Evans, 1970). The bright red and orange larvae of *Mycodiplosis* species feed on rusts and mildews on a wide range of plants, including many agricultural crops. The commonest British species, *M. saundersi* Barnes, feeds on a rust on creeping thistle (*Cirsium arvense*).

Lestodiplosis (fig. 119) is another large genus (34 British species) found in a wide range of microhabitats. The extremely active larvae are predaceous on mites, certain beetle larvae and on other cecidomyiids. *Aphidoletes* and *Monobremia* larvae are specialized predators on aphids and *A. aphidimyza* (Rondani) (fig. 125) has been used as an effective biocontrol agent (Harris, 1982).

The larva of *Endopsylla agilis* de Meijere is an endoparasite of Psyllidae (Hom.) and that of *Endaphis perfidus* Kieffer is an endoparasite of aphids.

Sitodiplosis mosellana (Géhin) is another wheat blossom midge the larva of which can be distinguished by its colour (orange to red) from that of *Contarinia tritici* (yellow — see above) and the relative positions occupied in the wheat flower (fig. 1312).

Möhn (1955) gives detailed descriptions of larvae of Cecidomyiinae.

Key to families for final stage larvae of British Brachycera

1 Posterior spiracles close together and more or less concealed within a terminal fissure on the anal segment 2

— Posterior spiracles widely separated on the anal, penultimate or antepenultimate abdominal segment and not concealed (even if in a fissure) 4

2 Terminal fissure vertical; head capsule not strongly sclerotized, and retractile; body cylindrical with smooth cuticle; anterior seven segments all, or mostly, encircled by a row of projections which sometimes bear apical spicules and function as prolegs. Mainly in moist or wet soils, *Sphagnum*, etc.; inactive (figs 157–160) . . . . . . **Tabanidae** (p. 60)

— Terminal fissure transverse; head capsule strongly sclerotized, and non-retractile; body depressed with roughened cuticle 3

3 Anal slit on the central part of the anal segment bordered with teeth-like projections and a row of similar projections arranged transversely in front of the anal slit (fig. 141); thoracic tergites with a more or less well defined smooth area on the median part of each tergite; amphipneustic; under bark of decaying trees; inactive (figs 141–143) **Xylomyidae** (p. 58)

— Anal slit area without such teeth-like projections; thoracic tergites uniformly roughened (shagreened like shark-skin); holo- or peripneustic; inactive; terrestrial species broad and flattened (figs 126–130), in woodland debris, dung, compost heaps and other decaying vegetable material; aquatic species often having a tapering abdomen terminating in a respiratory siphon (figs 131–140) . . . . **Stratiomyidae** (p. 57)

4 Posterior spiracles on the last apparent body segment 5

— Posterior spiracles anterior to the last body segment 11

5 Head capsule very short and minute; body soft, broad, pear-shaped with enlarged abdomen; last abdominal segment without processes but with two distinct spiracles; anterior spiracle very small; inactive, endoparasites of spiders (the early stage larvae are free-living, active triungulins, elongated with long setae) (figs 177–182) . . . . **Acroceridae** (p. 64)

— Head capsule prominent; last abdominal segment usually with processes; free living . 6

6 Head and one or more thoracic tergites strongly sclerotized; posterior spiracles on a sclerotized plate with projecting processes; under bark of decayed trees, sometimes within old burrows; inactive (fig. 144) . . . . **Xylophagidae** (p. 58)

— Head not strongly sclerotized; posterior spiracles not on a sclerotized plate 7

7 Anal segment with two or four, usually pointed, fleshy lobes open at end in a concave cleft containing the posterior spiracles 8

— Anal segment otherwise 9

8 Lobes of anal segment subequal in size; soil dwelling (probably at least partially predaceous) (figs 145–151) . . . . **Rhagionidae** (p. 59)

— Lobes of anal segment with ventral pair longer and more strongly developed (fig. 206); mouthparts with metacephalic rods (upper rods) swollen or spatulate at tip (fig. 215); predaceous in damp soil, under bark, in decaying wood, some in wet sand on sea shore (figs 206–238) . . . . **Dolichopodidae** (p. 67)

9 Anal segment rounded at end with lateral furrows evident and sometimes a small median projection below the posterior spiracles (fig. 196); (or, *Ocydromia*, lacking lateral furrows and with a distinct lobe below spiracles in dung, fig. 193); terrestrial, predaceous (figs 189–205) . . . . **Empididae** (part) (p. 65)

— Anal segment usually with long float hairs, borne on obvious fleshy lobes; aquatic, predaceous 10

10 Larvae slightly flattened dorsoventrally; slender lateral and dorsolateral tubercles of progressively increasing size on abdominal segments 1–7; prolegs on all 8 abdominal segments; two large caudal tubercles fringed with hairs on terminal segment (figs 152–156) . . . . **Athericidae** (p. 59)

— Larvae not dorsoventrally flattened; no lateral or dorsolateral tubercles on segments 1–7; prolegs on 7 or 8 of the abdominal segments; tubercles on terminal segment smaller (figs 201–205) . . . . **Empididae** (part) (p. 65)

11 Posterior spiracles on the apparent penultimate segment; abdominal segments not sub-divided, the body consisting of 11 or 12 apparent segments, exclusive of the head . 12

— Posterior spiracles on the apparent antepenultimate segment; abdominal segments 1–6 sub-divided, the body thus apparently consisting of up to 20 segments, exclusive of the head 13

12 Thoracic segments each with two long setae, one on each side of ventrolateral margin; anal segment with six or more long setae; free living in soil or decayed wood; predaceous, ectoparasitic (figs 165–176) . . . . **Asilidae** (p. 61)

— Thoracic segments without, or with only weak setae; anal segment without setae; predators, parasites or inquilines in nests of bees and wasps or in egg cases of grasshoppers; resembling a bee or wasp grub; inactive (young larvae are slender, active, free-living triungulins with a long slender seta on each side of each thoracic segment and two very long setae on the anal segment, fig. 183) (figs 183–188) . . . . **Bombyliidae** (p. 64)

13 Dorsal extension of head capsule extending into the thorax from the head posteriorly, with a spatulate apex (fig. 162); head capsule with two ventral projections; in soil (often sandy); predaceous, active with snake-like movement or 'jumps' (figs 161–162) . . . . **Therevidae** (p. 63)

— Dorsal extension of head capsule extending into the thorax from the head posteriorly not spatulate at apex (fig. 163); head capsule without ventral projections; predaceous on insects in household stored foods, wood or fungi, active with movements as Therevidae (figs 163–164) . . . . **Scenopinidae** (p. 63)

Notes on families of Brachycera

Stratiomyidae

(Figs: larvae 126–140, eggs 991–992, emergence of adult 1330)

The family Stratiomyidae (soldier flies) contains some 2300 species of which 50 species in 12 genera occur in Britain. Six subfamilies are recognised, all of which are represented in Britain and distinguishable in the larval stage as follows (based on Rozkošný, 1982).

1 Last abdominal segment usually rectangular or elongated and tubelike, with a coronet of pinnate or plumose float-hairs at the apex. If the apical coronet is absent, then either the dorsal abdominal setae are in two transverse rows or the abdominal setae are flat with a frayed margin 2

— Last abdominal segment rounded posteriorly, without a coronet of float hairs at the apex. Dorsal and ventral abdominal setae arranged in one transverse row; never flat with frayed margin 3

2 Larvae with an apical coronet of setae (figs 132–133, 135, 139–140) . . **Stratiomyinae**

— Larvae without an apical coronet of setae (fig. 131); terrestrial, among semi-aquatic mosses on stones etc . . . . **Clitellariinae**

3 Body setae surrounded by bristle-like hairs which form more or less distinct tufts; anal segment fringed with fine setae (fig. 126). Terrestrial . . . . **Beridinae**

— Body setae not surrounded by bristle-like hairs; anal segment without marginal fringe 4

4 Large larvae (18–20 mm long) with a dense covering of adpressed yellow hairs; posterior spiracular opening almost apical (fig. 130) . . . . **Hermetiinae**

— Smaller larvae (at most 12 mm long), with surface-hairs sparse or absent; posterior spiracular opening dorsal 5

5 Medium sized larvae, with distinct ocular lobes (ol) (figs 128–129). Terrestrial . **Sarginae**

— Small larvae (4·5–7·5 mm long), without ocular lobes (fig. 127). Under bark . . . . **Pachygastrinae**

Keys to genera and species of larvae and puparia of European Stratiomyidae are provided by Rozkošný (1982, 1983), who also gives much biological information. Brindle (1959) provides a useful key to genera, including those now placed in other families. The pupae of Stratiomyidae are formed inside the last larval skin (see introductory section on pupae).

Beridinae. The larvae of *Beris* (fig. 126) live in compost, decaying vegetation, wet moss, etc. and *B. fuscipes* Meigen is the only British species unknown in this stage. The only other British genus is *Chorisops* with two species. The larvae of *C. tibialis* (Meigen) has been found among dead leaves and a puparium of *C. nagatomii* Rozkošný (1982, described since the Diptera Check List) was found in refuse washed up on a muddy stream bank (water meadows by River Test, P.J. Chandler).

Clitellariinae. Larvae of the reputedly British *Clitellaria ephippium* (F.) have been recorded on several occasions by continental authors in nests of the ant *Lasius fuliginosus* (Latreille) and also at the roots of a walnut tree and in forest soil. The larval stage appears to last 3 or 4 years.

Three of the four British species of *Nemotelus* (fig. 131) have been described in the larval stage by Brindle (1964b). The larvae occur in or on the mud of marshes and at least *N. uliginosus* (L.) and *N. notatus* Zetterstedt are found in estuarine marshes or inland in brine pits and similar habitats.

Oxycera larvae (fig. 132) occur in hygropetricous habitats, i.e. in mosses growing in water flowing down inclined rocks or in semi-aquatic mosses in marshes. All but two (*O. dives* Loew and *O. terminata* Meigen) are keyed in the larval stage by Brindle (1964b). (*O. nigripes* Verrall is synonymized with *O. pygmaea* (Fallén) by Rozkošný, 1983).

The larva of *Vanoyia tenuicornis* (Meigen) is unknown but should be sought along streams and marshes (including salt marshes) where the adults occur (often on the leaves of *Ligustrum*).

Pachygastrinae. Larvae of this subfamily (fig. 127) are found under the bark of decaying trees. Some species appear to be associated with particular species of trees and they would be a worthy subject for detailed investigation, e.g. *Neopachygaster meromelaena* (Dufour) (= *P. orbitalis* Wahlberg) (holly, willow); *Pachygaster atra* (Panzer) (elm); *Zabrachia* (= *Pachygaster*) *minutissima* Zetterstedt (pine); *Eupachygaster tarsalis* Zetterstedt (beech, poplar) and *Praomyia leachii* Curtis (oak). Brindle (1962b, 1966) keys all the British species.

Sarginae. The larva of the common *Chloromyia formosa* (Scopoli) is found in dung. *Microchrysa polita* (L.) (fig. 128) occurs in dung, grass-heaps, compost, garden refuse, under moss on old tree trunks, etc., and is the most commonly encountered larva of the family. *M. flavicornis* (Meigen) has been found in soil under moss on a tree trunk and may share the wide range of habitats favoured by *M. polita* but *M. flavicornis* is found in dung (pig, cow, horse).

Four of the six British species of *Sargus* are known in the larval stage from dung and decaying grass heaps. Roberts (1969) has studied the structure of the larval mouthparts of *Sargus* and concludes that it is a detritus feeder.

Brindle (1965e) keys the larvae of this subfamily.

Stratiomyinae. The larvae of this subfamily are all aquatic and live in shallow standing water and in ponds or marshes, where they feed on microscopic organisms.

Brindle (1964a) keys three of the British species of *Stratiomys* (figs 133–138) and Rozkošný (1982) includes all four.

A key to larvae of four of the six British species of *Odontomyia* (figs 139–140) is given by Brindle (1964a).

Hermetiinae. Although not included in the British Check List in the *Handbook* series, the larvae of *Hermetia illucens* (L.) (fig. 130) frequently come before entomologists who deal with economic enquiries involving food stuffs imported into Britain (see Medical and Veterinary Section and Smith & Chainey, 1989).

Xylomyidae

(Figs: larvae 141–143, pupa 1131)

Regarded until very recently as a subfamily of Stratiomyidae, this small but widely distributed family contains less than 100 species in 53 genera. Only one genus, *Xylomya* (= *Solva*) is represented in Britain, by 3 species.

The larvae (fig. 143) resemble Stratiomyidae with a shagreened cuticle but are distinguishable at once by the shiny smooth areas on the thorax and the toothed anus (figs 141–143). They are predaceous or saprophagous and live under the bark of trees (oak, poplar, elm, walnut) and in rotting logs.

Brindle (1961c) keys the British species.

Xylophagidae

(Figs: larva 144, pupa 1132)

This small family (until recently included in the Rhagionidae) consists of about 30 species in one genus (*Xylophagus*) and is restricted to the Holarctic region.

Three species of *Xylophagus* occur in Britain, two of which are known in the larval stages and keyed by Brindle (1961b, 1966); they occur in dead wood. *X. cinctus* De Geer (fig. 144) is restricted to pine trees but *X. ater* Meigen is found in deciduous trees including birch, oak, alder, beech and aspen. The larva of *X. junki* Szilády is unknown but may well be found in conifers since the only known British adult was found in Glenmore Forest, near Aviemore, Scotland.

There has been some controversy over the feeding habits of larval *Xylophagus* but they are certainly carnivorous, probably on beetle larvae. Downes (1953) records *X. ater* attacking a small staphylinid larva.

Rhagionidae

(Figs: larvae 145–151, egg 993, pupa 1133)

The Rhagionidae has a world-wide distribution with 500 species contained in some 20 genera. Four subfamilies are recognised of which two occur in Britain. No key to subfamilies is given since the larvae of some genera are unknown, but Brindle (1959) provides a partial key including those genera now removed to other families.

The larvae of *Rhagio* (fig. 145) and *Chrysopilus* (fig. 150) are carnivorous but are also said to feed on decaying vegetable material. However, from a study of the larval mouthparts, Roberts (1969) concludes that *Rhagio* is carnivorous, feeding on earthworms (Oligochaeta) and soft bodied insect larvae. Brindle (1962g) keys the larvae of four of the six British species of *Rhagio*. Hobby & Smith (1962a) describe the immature stages of *Chrysopilus cristatus* (F.), which differs from *Rhagio* (fig. 148) in the structure of the head capsule (figs 149–150). Larvae of both genera are found in leaf mould and moss and other woodland debris.

Ptiolina larvae feed on mosses on trees and stones. They are shining green in life and the anal segment has two fleshy lobes, one dorsal, one ventral (figs 147, 151).

The larva of *Spania* has not been described but is said to be small and to mine the leaves of liverworts (*Pellia*, etc.).

Symphoromyia larvae occur in damp soil. Some Alaskan species have been described by Sommerman (1962) and were found to feed on the larvae of other soil-dwelling Diptera.

Atherix and *Atrichops* of the Diptera Check List in the *Handbooks* series are treated here under Athericidae.

Athericidae

(Figs: larvae 152–156, eggs 994–995, pupa 1134)

Formerly included as a subfamily in the Rhagionidae this family contains some 80 world species in about 6 genera. Two genera occur in Britain, both aquatic in the immature stages.

The distinctive larvae of *Atherix* are found beneath and amongst stones on river beds. When fully grown they leave the water and burrow into light gravelly soil under moss on the river bank and pupate. The two British species are easily distinguished by the difference in the lengths of the lateral processes on the abdomen (figs 154–155). *Atherix ibis* (F.) is well known for the curious, and frequently described oviposition habits of the female. The flies gather in clusters on twigs and branches overhanging the water and remain there until they die in a mass of flies and eggs (fig. 994). The eggs (fig. 995) ultimately hatch and the young larvae fall into the water. Mackey & Brown (1980) describe the pupa and provide a key to pupae for the families of aquatic Brachycera. Brindle (1961d) keys the species of *Atherix*.

The larva of *Atrichops crassipes* (Meigen), the only other British representative of this family, remains undescribed, but its life history will probably prove similar to that of *Atherix*. Adults used to occur (1900–1904) on alders in a water-meadow near Ticehurst Road Station, Sussex, and near Milford-on-Sea, Hants, as well as a few localities in the New Forest (Hants). It has recently been rediscovered in some of the old localities, and Gibbs (1987) records it from the Kennet Valley in Berkshire.

Tabanidae

(Figs: larvae 157–160, eggs 996–997, pupa 1135)

The large family Tabanidae (horse-flies, clegs, deer flies) contains some 3500 species and is world-wide in distribution. Adult female Tabanidae suck blood and some are of veterinary and medical importance.

The larvae of Tabanidae are found in wet mud at the margins of ponds, lakes and streams, in sand on the sea shore or in tree-holes. The first two instars do not feed and moulting from first to second instar often takes place on the egg mass. The later instars are very active predators on worms, molluscs and larvae of other Diptera (including their own kind) but they do not feed on Crustacea or beetle larvae. The number of larval instars (fig. 157) ranges from 7 to 11 and varies, along with the time of larval development, even in the same species, according to a number of factors, e.g. food, temperature, humidity.

The larvae can survive for a long time without food (up to several months) and in unfavourable environmental conditions they can hibernate/aestivate several times, with additional larval instars.

Tabanid larvae can be roughly divided into three ecological groups:

1) Hydrophilous — developing only in water (e.g. *Chrysops*, some *Hybomitra*).
2) Semihydrophilous — with first and second instars on surface of water or moist soil and in third instar migrate into soil close to water (e.g. most European Tabanidae).
3) Edaphic — living in drier soil, usually far from water (e.g. some *Haematopota*).

Eggs (figs 996–997) are laid in masses which may consist of a single layer (some *Chrysops*), two or three layers (*Haematopota*) or three or four layers (other tabanids). The number of eggs laid ranges from 400 in small species to 1000 in the larger species.

There are 28 British species representing 5 genera. Two sub-families and three tribes occur in Britain, which may be distinguished in the mature larval stages as follows.

1 Four tubular pseudopods (ventro-lateral (vlp) and lateral pairs (lp)) on each abdominal segment except the last (fig. 159) . . . . **Chrysopsinae (Chrysopsini)**
— At least six tubular pseudopods (2 pairs ventro-lateral, plus a lateral pair) on all but the last abdominal segment (fig. 158) . . . . **Tabaninae** 2
2 Anal segment shorter than its own vertical height (fig. 157) . . . . . . **Haematopotini**
— Anal segment elongated, longer than its own vertical height (fig. 160) . . . **Tabanini**

The European Tabanidae have been monographed by Chvála *et al.* (1972) who include much biological information. Other important papers on larval Tabanidae are listed by Ježek (1977), who keys the last instar larvae and pupae of many species.

Chrysopsinae. Only one genus, *Chrysops*, occurs in Britain with four species. The larvae are usually found in mud or sand at the edges of streams and brooks and 3 of the 4 British species are described by Ježek (1970). The larva of *C. sepulcralis* (F.) is unknown but should be sought in swampy conditions, especially peat bogs, where the adults have a very local distribution.

Tabaninae

Haematopotini. Only one genus, *Haematopota*, with 4 species occurs in Britain.

The immature stages of the commonest species, *H. pluvialis* (L.) (the cleg or dun fly) have been studied in detail by Cameron (1934). The larvae of *H. crassicornis* Wahlberg also occur in marshy soil but the species is commoner than *H. pluvialis* in upland areas in the hilly districts of the north of England and Scotland. *H. grandis* Meigen and *H. bigoti* Gobert are salt marsh species in Britain but the larvae are undescribed.

Brindle (1961a) keys the larvae of three British species, including *H. italica* Meigen from salt marshes. *H. italica* however, included only as a dubious synonym of *H. grandis* in the British Check List, is regarded as a subspecies of *H. grandis* by Oldroyd in his key to adults in the *Handbook* series, and as a distinct species with larval habits resembling those of *H. pluvialis* by Chvála *et al.* (1972) (and the larva of *H. grandis* stated to be unknown). Clearly the genus *Haematopota* needs further attention by British Dipterists, accompanied by careful rearing from larvae but no genuine British adults of *H. italica* are known.

Tabanini. Only two of the 13 European (4 British) species of *Atylotus* are known in the larval stage. *A. fulvus* (Meigen) has been reared from the periphery of forest ponds in Czechoslovakia.

Ježek (1977) keys the last instar larvae and pupae of 8 of the 37 described European species of *Hybomitra*, including 4 of the 9 British species. *H. distinguenda* (Verrall) is a widespread and often numerous species whose larvae have been found in living or dead vegetation at the margins of marshes, forest ponds, marshy meadows, margins of drainage near cattle pens and in a moist rotten pine stump. *H. bimaculata* (Macquart), *H. ciureai* (Séguy) (accidentally indented as a synonym in the Check List) and *H. muehlfeldi* (Brauer) have all been found at the edges of ponds, usually submerged even during the winter months among frozen *Phragmites, Carex* and *Juncus.*

The immature stages of only 3 of the 8 British species of *Tabanus* have been adequately described. *T. autumnalis* L. has been found in a wide variety of substrates from totally organic soil in *Alnus* forest to the margins of forest ponds and drainage ditches. *T. bromius* L. occurs in the periphery of forest ponds and in molehills; *T. maculicornis* Zetterstedt has also been recorded from molehills, but usually in the margins of peat bogs and in forest meadows near lakes and streams; *T. miki* Brauer occurs in the mud of swamps and marshy meadows (with *Phragmites, Carex, Iris* and *Salix*).

Most of the ecological information given above comes from Czechoslovakian data included in the references cited in Ježek (1977). It is strange that the life-histories of this important family have been so neglected by British entomologists and clearly there is scope for a substantial research effort here.

Asilidae

(Figs: larvae 165–176, eggs 998–999, pupa 1136)

About 5000 species of Asilidae (robber flies) in over 400 genera and subgenera have been described throughout the world, of which 27 species in 15 genera occur in Britain.

The long white larvae prefer drier habitats, e.g. sandy soil, and are predaceous, although the Laphriinae, which occur in decayed wood, are considered to be saprophagous or herbivorous. A classic work on the immature stages is that of Melin (1923); Brindle (1962e) keys the known larvae of the British species. A useful world review of the known biology of Asilidae is provided by Knutson (1972). Many larvae are predaceous on beetle larvae but hardly any observations on larval food have been made for the genera occurring in Britain.

The higher classification of the adults of Asilidae based on adult structures appears to be very subjective, each specialist creating a different system, e.g. *Leptogaster* varies in status from tribe to separate family! For the purpose of this *Handbook* I follow Brindle (1962e) in recognising 4 subfamilies for the separation of the larval stages as follows.

1 Mandibles absent; maxillae (mx) widely separated distally being prevented from closer approximation by the strongly broadened basal part; outer margin of the maxillae with an incision in which lie the maxillary palps (mp) (figs 165–166) . . . . **Leptogastrinae**

— Mandibles (md) present; maxillae usually closely approximated along their length, basal part not broadened internally 2

2 Maxillae narrow, without a lateral incision (fig. 167); anal segment with a horizontal apical brown or white ridge (fig. 169, r) . . . . **Asilinae**

— Maxillae broad, with a lateral incision in which lie the maxillary palps (fig. 170); anal segment without an apical ridge 3

3 Abdominal segments 1–6 with an annular ring of 3 or 4 pairs of tubercles (fig. 171); anal segment with an apical sclerotised plate (figs 171–173) . . . . **Laphriinae**

— Abdominal segments 1–6 with only one pair of ventral tubercles; anal segment without an apical sclerotised plate (figs 174–176) . . . . **Dasypogoninae**

Leptogastrinae. There is only one British genus, *Leptogaster*, with two species, the larvae of which occur in sandy soil or meadows with dense ground vegetation (figs 165–166).

Dasypogoninae. The genera *Leptarthrus* (= *Isopogon*) and *Dasypogon* (= *Selidopogon*), each with one species, are unknown in the larval stages though *L. brevirostris* (Meigen) has been seen to oviposit on cocksfoot and the larvae should probably be sought in soil on chalk downland. Adults of *D. diadema* F. have not been found in Britain for well over a century but should the species still survive in Britain its larvae should be sought on the dunes of the Welsh coast.

Of the six British species of *Dioctria* only *D. rufipes* (De Geer) (figs 174–176) and *D. oelandica* (L.) are known in the larval stage and they occur in woodland soil (Brindle 1968, 1969a). The larva of *Lasiopogon cinctus* (F.) is not uncommon in sandy soils in pastures, woodlands and dunes, but also occurs in richer soils.

Laphriinae. The larvae (fig. 171) of this subfamily are found in the stumps of decayed trees. *Laphria flava* L. (figs 172–173) is found in decayed wood of pine, spruce or birch stumps in Scotland. *L. gilva* (L.) is found locally in southern England between the bark and wood of pine stumps. *L. marginata* (L.) is also restricted to southern England where it occurs in pine stumps or decayed deciduous wood.

Asilinae. All nine genera of the subfamily occurring in Britain are known in the larval stage, though not all are known from British species or material.

Larvae of *Asilus crabroniformis* (L.) are locally common in southern England in the sandy soils of pastures and heaths. One of the three species of *Epitriptus* (regarded as synonymous with *Machimus* by some workers), *E. cingulatus* (F.), is known in the larval stage and occurs in the sandy soils of meadows, grassy slopes, etc. *Eutolmus rufibarbis* (Meigen) is found in similar situations. The larvae of *Machimus atricapillus* (Fallén) and *Neoitamus cyanurus* (Loew) occur in sandy soils in open woodlands and the unknown larvae of the other rarer single species of each of these two genera will no doubt be found in similar situations. The larvae of *Pamponerus germanicus* (L.) (fig. 168) and *Philonicus albiceps* (Meigen) are found in sand dune soils and *Rhadiurgus variabilis* (Zetterstedt) occurs locally in sandy soils at the edges of pine woods in upland districts, chiefly in Scotland. The larva of *Dysmachus trigonus* (Meigen) is unknown but Melin (1923) found that of a Swedish species in sandy soils on the coast and inland heaths. In the British Museum (Nat. Hist.) collections there are two pupae of *D. trigonus* from St. Merryn, Cornwall, and Croyd, N. Devon, one labelled 'in sand' (coll. K. G. Blair ex coll L. Parmenter).

Therevidae

(Figs: larva 161–162, pupa 1140)

About 700 species of Therevidae (stiletto flies) have been described throughout the world, of which 13 species in 3 genera occur in Britain.

The life histories are very poorly known but the vermiform (worm- or snake-like) larvae (fig. 161), with abdominal segments 1–6 subdivided, occur in sandy to sandy-loam soils and are predators on a variety of arthropods and earthworms, with a preference (like Asilidae) for beetle larvae, especially of the families Elateridae, Scarabaeidae and Tenebrionidae. There are five larval stages in the life-histories so far studied.

Thereva is the genus most frequently encountered in the larval stage (figs 161–162). Fox Wilson (1924) conducted experiments on the feeding habits of *Thereva plebeia* (L.) and concluded that larvae fed on leaf-mould and humus in the soil and when this was scarce would attack living plants, e.g. cabbage and potato and other garden vegetables. However, it may well be that this only occurs in the absence of suitable invertebrate food, as the larvae are undoubtedly voracious predators and feed on various insect larvae including wireworms (Coleoptera, Elateridae) and their own kind. They are also capable of biting man, usually in sandy areas; Smith (1979a, 1986a) summarises these records and one more can be added from a dry rocky limestone area on Bunster Hill, Dovedale (K.N.A. Alexander, pers. comm.).

Collinge (1909) (overlooked by Fox Wilson) made observations on *Thereva nobilitata* F. from larvae sent in by gardeners and nurserymen from among the roots of various plants. He fed the larvae on Diptera larvae and small earthworms but noted that they preferred weevil larvae which were less active. The larvae of the remaining 8 species of *Thereva* are unknown but should be sought in sandy soil; *T. annulata* F. is common on coastal sand dunes.

Larvae of *Psilocephala melaleuca* (Loew) have been found in rotting stumps in the Windsor Forest–Ascot area of Berkshire, but have not been described.

The larva of *Dialineura anilis* (L.) is unknown, but should be sought on sandhills of the Welsh and Scottish coasts where adults are common.

Scenopinidae

(Figs: larva 163–164, egg 1000, pupa 1138)

Some 312 species of Scenopinidae (window flies, carpet flies) have been described throughout the world. The family is represented in Britain by 3 species in the single genus *Scenopinus*.

The slender snake-like larvae resemble those of Therevidae in having abdominal segments 1–6 subdivided (see key) and are predaceous on the larvae and pupae of clothes-moths, beetles and fleas. They are frequently found in carpets but since this can hardly be their 'natural' habitat it is assumed that the debris in birds' nests provided their original larval pabulum. They have been recorded most frequently from nests of house sparrows, swallows, pigeons, starlings and jackdaws (Hicks, 1959). Scenopinid larvae are notoriously resistant to desiccation and lack of oxygen. There is one record of involvement in human urogenital myiasis (Thompson, J.H. *et al.*, 1970).

Two of the three British species, *S. fenestralis* (L.) and *S. glabrifrons* Meigen, are world wide in distribution but only the larva of *S. fenestralis* (fig. 164) has been described in any detail (Séguy, 1921), while Zuranska (1979) has described the puparium.

Acroceridae

(Figs: larvae 177–182, eggs 1001, pupa 1139)

Some 475 species in 48 genera of Acroceridae have been described throughout the world. All are internal parasites of spiders (Araneae), particularly Lycosidae, but also of Theridiidae and Gnaphosidae. The black eggs (fig. 1001) may be laid in flight and scattered on the ground in large numbers or deposited in masses on grass stems, horsetails, twigs or tree trunks away from the intended hosts. The first instar larva (figs 179–181) is an active 'planidium' which seeks out and burrows into the host. These young larvae can jump for distances of 5 or 6 mm by bending and suddenly straightening the body, using caudal processes and a sucker attachment. They can also move along a spider's thread with a movement resembling that of a looper caterpillar. The larvae of some species are known to obtain their oxygen by applying their posterior spiracles to the spider's lung-books. There are three larval instars and the mature larva (fig. 177) usually emerges posteriorly from the spider's epigastric furrow area and pupates free of the host, often in a protective webbing spun by the host spider before its death.

Only three species (*Acrocera globulus* Panzer, *Ogcodes gibbosus* L. and *O. pallipes* Latreille) occur in Britain and these are very rarely seen even as adults. They occur in scattered localities from Herefordshire southwards and may be locally abundant.

Since spiders are so common it is strange that Acroceridae are so rarely encountered. Spiders are known to kill some of the larvae and the adult flies are frequently caught in their webs but in view of the large numbers of eggs laid (800–900 have been observed) the mortality seems high and a quantitative investigation would be worth while for anyone with access to a local colony.

Bombyliidae

(Figs: larvae 183–188, egg 1002, pupa 1137)

Nearly 4000 species of Bombyliidae (bee-flies) in some 194 genera have been described throughout the world. The family is best represented in arid and semi-arid regions. Few species are known in the immature stages but all are parasitic on the larvae or pupae (or both) of various species of Lepidoptera, Hymenoptera, Coleoptera, Diptera and Neuroptera, or predaceous on the egg pods of grasshoppers. There are 3 larval stages, the first being a planidium (fig. 183). As with Asilidae, the pupal stage (fig. 1137) is better described because so often only the pupal skin is recovered after a chance rearing. Hull (1973) provides generic keys to the pupal stage. Eggs (fig. 1002) are said to be produced in large numbers. Du Merle (1975) provides a host list for the immature stages.

Only 11 species in 5 genera occur in Britain. The higher classification of the Bombyliidae is rather unstable. Of the 12 or so subfamiles recognised 4 are represented in Britain but the larvae are too imperfectly known to construct a key.

Anthracinae. The only British member of this subfamily, the very rare (Leicestershire only) *Anthrax anthrax* (Schrank), has not been described in the larval stage, though the pupa is known. Abroad it has been reared from the nest of *Odynerus spinipes* (L.) (Hym., Vespidae); from both *Osmia nigriventris* (Zetterstedt) and its parasite *Stelis ornatula* Klug (both Hym., Apidae); and from nests of *Anthophora* and *Megachile* (both Hym., Apidae).

Bombyliinae. T. A. Chapman (1878) found pupae of *Bombylius major* L., the commonest British species, in the nest of the mining bee *Andrena labialis* Kirby. Other bees have been recorded as hosts on the continent, e.g. *A. humilis* Imhoff and *Colletes cunicularia* (L.). T. A. Chapman also observed females of a small brown species of *Bombylius* (probably *canescens* Mikan) laying its eggs in flight over a bank containing *Halictus* burrows. On the continent the immature stages of *B. minor* L. have been described from nests of *Colletes daviesana* Smith (Nielsen, J. C., 1903). The first stage larvae of *B. minor* feed on the pollen and honey store but in later instars attack the bee larvae.

Exoprosopinae. The larva (fig. 186) of *Thyridanthrax fenestratus* (Fallén) has been described by Séguy (1932). It has been recorded from the egg pods of grasshoppers in the Mediterranean area but Greathead (1963) has suggested that in at least some of these cases it may be parasitic on Diptera associated with the egg pods. The species has not been reared in Britain but adults occur locally on sandy commons in southern England. Grasshoppers and associated Diptera in such localities could well repay investigation.

Larvae of *Villa* species parasitize larvae of Lepidoptera (especially Noctuidae) and Coleoptera (Tenebrionidae). Of the three British species, only *V. circumdata* (Meigen) has been reared from a pyralid moth larva (in France).

Phthiriinae. *Phthiria pulicaria* Mikan is a sand-dune species and has been reared from *Scrobipalpula psilella* (Herrich-Schäffer) (Lep., Gelechiidae) on the continent.

Empididae

(Figs: larvae 189–205, eggs 1003–1004, pupae 1146–1148)

Over 3000 species of Empididae (dance flies) have been described throughout the world and many more await description. Over 350 species have so far been recorded in Britain. The family has usually been divided into 8 or 10 subfamilies of which 6 occur in Britain. Chvála (1983) has grouped these into distinct families: Microphoridae, Atelestidae (*Atelestus* is under Platypezidae in the *Check List*, larvae unknown), Hybotidae (including Ocydromiinae, Hybotinae and Tachydromiinae), and Empididae (including Oreogetoninae, Empidinae, Brachystomatinae (not British), Hemerodromiinae and Clinocerinae). The group is here treated as one family, since the immature stages are so poorly known and the available information is given under the six sub-family headings included in the *Check List* (Smith, 1976) in this *Handbook* series. The following key couplet will facilitate preliminary identification of larvae.

Keys to the few genera so far known in the larval stages are given by Smith (1969) and McAlpine *et al.* (1981).

1 Larvae terrestrial, with amphipneustic respiratory system (spiracles fairly conspicuous), without ventral abdominal pseudopods (figs 196–200) . . . . **Tachydromiinae, Hybotinae, Ocydromiinae, Empidinae**

— Larvae aquatic or semi-aquatic, with apneustic respiratory system (no spiracles) and with ventral abdominal pseudopods (figs 201–205) . . **Hemerodromiinae, Clinocerinae**

Tachydromiinae. There is no adequate description of a larva of this subfamily. I have seen *Crossopalpus curvipes* Meigen reared from a cocoon in a dead snail (*Cepaea nemoralis* L.) by R. A. Beaver and the mouth-parts and posterior spiracles, recovered from the cast skin, are illustrated (figs 190–192). Malloch (1917) figured the mouthparts of *Drapetis assimilis* Fallén (as *nigra* Meigen) which I have included for comparison (fig. 189). Malloch noted that the *Drapetis* larva occurs under bark or in decaying wood and makes a tough cocoon in which it pupates. Beling (1888) gives a brief description of the larva of *Platypalpus major* (Zetterstedt) found in soil under moss in a wood. The rarity or absence of males in some species of *Platypalpus* has led to the suggestion that they may be entirely parthenogenetic (*P. major* (Zetterstedt)) or at least so over part of their range (e.g. *P. candicans* (Fallén) in N. Europe, *P. cursitans* (F.) in central and southern Europe).

There are some records of reared adults which indicate where the larvae, which almost certainly are all predaceous, should be sought, e.g. *Crossopalpus*, dung, fungi (*C. nigritellus* Zetterstedt in young plasmodium of *Fuligo septica* Gmelin (Myxomycetes)); *Elaphropeza ephippiata* (Fallén), woodland soil (G. C. Varley); *Tachypeza nubila* (Meigen), under bark, in fungi (e.g. *Bjerkandera, Amanita, Paxillus, Hypholoma, Daldinia*).

The remaining genera should be sought where adults are known to occur, especially in soil and decaying wood, or soil under grass-tufts (*Stilpon*) sand on the sea shore, rivers or lakes (*Chersodromia*, some *Tachydromia*).

Hybotinae. The immature stages are unknown but the larvae of *Hybos* probably live in soil around woodland margins or scrubland. The larvae of *Syndyas* should be sought in cold *Sphagnum* bogs. *Syneches muscarius* (F.), the only British species of the genus, should be sought in wet meadows though only one locality is yet known in Britain (The Moors, Wool, Dorset).

Ocydromiinae. *Ocydromia glabricula* (Fallén) females are viviparous and scatter young larvae while in flight over dung, in which they develop (Hobby & Smith, 1962c). It is probable that the other British species of the genus, *O. melanopleura* Loew, is viviparous as Chvála (1983) has seen small dead larvae attached to the tip of the abdomen of dried female specimens.

Bicellaria, Trichina and *Trichinomyia* occur in moist shady places, in deciduous woodland and their larvae are probably in the soil. *Euthyneura, Oedalea* and *Leptopeza* have all been reared from rotten wood and probably *Oropezella* occurs there too, but the larvae of all remain undescribed.

Empidinae. The larvae of *Empis* (fig. 196) and *Rhamphomyia* (fig. 198) are predators, probably mostly on other Diptera larvae in woodland soil under leaf-litter (Hobby & Smith, 1961a, b, 1962b). Larvae of *Rh. sulcata* Meigen may occur in large numbers in freshly ploughed pasture soil (Smith, 1968). On the continent *Rh. dentipes* Zetterstedt has been reared from a beech stump and Dr B. R. Laurence has reared *Rh. crassirostris* (Fallén) from a pupa found under moss and liverworts on a tree stump.

The larvae of *Hilara* may be distinguished from *Empis* and *Rhamphomyia* by the larger posterior lobe (fig. 197) which is curved towards the tip; they are found in moist woodland soil under leaf litter, in mole casts and in decaying wood.

Hemerodromiinae. The larvae of this subfamily (except *Phyllodromia* (see below)) are aquatic and live in mosses in rivers and streams including hygropetricous habitats e.g. mosses growing in the water flowing down vertical rock faces or on the tufa (which they burrow into) deposited by lime-rich waters. The larvae have 7 pairs of retractable pseudopods on the abdominal segments but the arrangement and length of processes on the anal segment varies between genera and species (figs 202–205).

Hemerodromia unilineata (Zetterstedt) (fig. 202) larvae occur most commonly in mosses in deeper water where the current is slow. The larvae of *Chelifera trapezina* (Zetterstedt) are found in very fast flowing water, e.g. where the water runs down sloping artificial weirs. The striking pupae of these two genera have the spiracles of the prothorax and first seven abdominal segments modified into long slender gills (fig. 1146).

The larva of *Phyllodromia* is terrestrial and the anal segment has a large posterior lobe resembling *Hilara*. The immature stages of other British genera are unknown.

Brindle (1964c, 1969b) keys the immature stages (including Clinocerinae).

Clinocerinae. The larvae of this subfamily, like the Hemerodromiinae, are aquatic, but have 8 pairs (fig. 201) of abdominal pseudopods.

Vaillant (1967) has studied the ecological requirements of *Wiedemannia* in French rivers and streams and proposes seven ecological zones. He found that the immature stages of many species may be distributed along the same watercourse, depending upon the elevation, rate of flow, abundance of other aquatic fauna, and especially the maximal and minimal temperatures of the water throughout the year. Brindle (1969b) found larvae of *W. rhynchops* (Nowicki) in rivers and streams with a wide range of current speeds but they were fewer in numbers than Hemerodromiinae. *Wiedemannia* larvae have been found to feed on *Simulium* larvae (in Algeria).

The larva of *Clinocera stagnalis* (Haliday) has been found in a small shallow lake, also among filamentous algae on stones in a slow moving stream (in company with *Wiedemannia lota* Walker and probably feeding on chironomid larvae (Brindle 1973)).

Hinton (1950) showed that the pupa of *Clinocera* is adapted to survive both in and out of water, providing a certain level of relative humidity obtains. *C. bipunctata* (Haliday) pupates in mosses just above the water level and if the water level rises the pupa wriggles up through the mosses to a position just above the new level. Pupae of *W. rhynchops* have been found in similar situations and presumably react in a similar way. Brindle (1969b) suggests that the differences in pupation sites of Hemerodromiinae and Clinocerinae are correlated with the degree of development of the pupal spiracles (i.e. long gills in the former and of normal length in the latter).

Brindle (1964c, 1969b, 1973) provides keys to the then known genera and species of the subfamily. Vaillant (1952) has described the aquatic immature stages of *Dolichocephala ocellata* (Costa) (fig. 204) from France and provides a revised key to genera for the sub-family.

Dolichopodidae

(Figs: larvae 206–223, 226; eggs 1005–1006; cocoons 224, 228, 1142, 1145; pupae 225, 227, 1141–1145; stem mine 1291)

Some 4500 species of Dolichopodidae have been described throughout the world. The immature stages are not well known but the larvae appear to be predaceous and are found in damp soil, sand, rotting wood, under bark, in sap exudations on trees, and in cattle dung; some are stem-miners and some are aquatic, including the inter-tidal zone of the sea shore. Pupation usually takes place in a cocoon of sand, mud or a piece of wood (figs 224–228, 1142–1145). There are 267 British species in 38 genera. The family is divided into nine subfamilies in Britain but the immature stages are too poorly known to provide a key. Keys to genera for the larvae so far described are given in McAlpine *et al.* (1981). A useful 'spot' character for distinguishing most Dolichopodidae from other Brachycera larvae (especially Empididae with which they are often found), is the swollen posterior tip to each of the 'rods' of the mouthparts (fig. 215). Other larval and pupal differences are discussed by Dyte (1967).

Sciapodinae. Only the genus *Sciapus* occurs in Britain, represented by 8 species, one of which is known in the immature stages. Larvae of *Sciapus platypterus* (F.) were found in soil under leaves in a forest of beech trees in April by Beling who gave a brief description, later translated by Lundbeck (1912).

Dolichopodinae. Of the 53 species of *Dolichopus* occurring in Britain only 16 are known at all in the larval stages and these mostly from continental material. Few are adequately described. Early rearings by Beling, Brauer and others are summarised by Lundbeck (1912). *Dolichopus claviger* Stannius, *D. discifer* Stannius, *D. latelimbatus* Macquart, *D. lepidus* Staeger, *D. longicornis* Stannius, *D. popularis* Wiedemann and *D. ungulatus* (L.) have all been reared from soil in meadows or woods. In addition larvae and pupae of *D. popularis* have been found under moss on old 'stubs' of beeches and *D. ungulatus* has been found in hollow poplars. Vaillant (1950) described the egg (fig. 1006), larva and pupa of *D. griseipennis* Stannius reared from eggs laid in moist soil and the same species has been reared from wet grit (Dyte, 1959) and old cow dung (Laurence, 1953). Dyte (1959) has reared *D. nubilus* Meigen from intertidal mud in estuaries and from the muddy bank of a freshwater stream and he illustrates the pupa (fig. 1141). Dyte also records rearing *D. atratus* Meigen, *D. pennatus* Meigen, *D. signatus* Meigen and *D. trivialis* Haliday from freshwater mud or moist soil. Nielsen *et al.* (1954) found larvae of *D. plumipes* (Scopoli) (fig. 207) in numbers from a range of half-dry to wet soil in Iceland.

No larvae of the 22 British species of *Hercostomus* have been described but *H. cretifer* Walker has been reared from moss in a river bank by B. R. Laurence; *H. nigriplantis* Stannius has been reared from debris in the fork of a tree some 6 feet above the ground (Dyte, 1959) and the late Dr B. M. Hobby and myself have reared *H. cupreus* Fallén from woodland soil.

Of the 4 species of *Tachytrechus* occurring in Britain the immature stages of *Tachytrechus notatus* (Stannius) have been described by Vaillant (1949) from larvae found on wet rocks, in company with those of *Liancalus virens* (Scopoli) in Algeria. Lundbeck (1912) described the pupa of *T. insignis* (Stannius) which was found in a cocoon made of sand grains at the border of a lake in Denmark.

The immature stages of *Hypophyllus* and *Poecilobothrus* are unknown.

Hydrophorinae. The larvae and cocoons containing the pupae of *Hydrophorus oceanus* (Macquart) (figs 208–210, 223–225) occur in intertidal mud in estuaries or in sand on the sea shore (Tsacas, 1959; Dyte, 1959). However, since the adults of this species also occur inland the immature stages may be found on the stones of freshwater habitats. Probably larvae of the other 8 British species will be found to occupy similar habitats.

The immature stages of *Scellus notatus* (F.) are unknown but should probably be sought at the water's edge although the adults can be found in wet and dry places.

The immature stages of *Liancalus virens* are found in mosses on partly submerged wet rocks, and under waterfalls, etc., and are described by Vaillant (1948). The larva (fig. 213) is metapneustic and the pupa (fig. 1143) is hemipneustic. The prothoracic spiracles of the pupa are produced into two very long horns which project through a narrow opening at the anterior end of the cocoon (fig. 1142). Hinton (1950) found that the pupae, within their cocoons, can survive prolonged submergence if the water is well aerated and also prolonged periods of drying (2 days).

The immature stages of *Orthoceratium* and *Thinophilus* are unknown but should be sought on the seashore or salt-marshes.

Aphrosylinae. The one British genus, *Aphrosylus*, contains 4 species normally found on the sea shore. The larvae (fig. 214) have not been adequately described but have been reared from the littoral region, though some (e.g. *A. mitis* Verrall) may be estuarine. They are carnivores and sometimes *A. celtiber* Haliday lays eggs on limpets and in the shells of barnacles. Hinton (1967b) has studied the structure of the respiratory horns of the pupa of *Aphrosylus* (fig. 1144) in relation to those of other Dolichopodidae.

Medeterinae. The larvae of *Medetera* (fig. 216) are found under the bark of trees and logs, usually in the mines of Scolytidae and other beetles on whose larvae and pupae they feed. About 10 of the 27 British species have been reared from such situations but identifications of the older records are unreliable. R. A. Beaver (1966) has described the immature stages and life history of *M. nitida* (Macquart) and *M. impigra* Collin in association with the elm bark beetle *Scolytus scolytus* F. There is scope for much more research on other species of trees and their associated beetles and *Medetera*. Teskey (1976) provides a useful summary of recent work on this topic. Krivosheina (1974) describes and keys larvae of some Russian species including 5 that occur in Britain.

The larvae of *Thrypticus* are plant-miners in the stems (fig. 1291) of Monocotyledons associated with wet environments, e.g. *Eleocharis* and *Scirpus* (Cyperaceae), *Muhlenbergia* and *Phragmites* (Gramineae) and *Juncus* (Juncaceae). The female flies have a sharp sclerotised ovipositor for piercing the food plant and the larvae and pupae have secondary structural changes associated with the non-carnivorous life-style in this specialised habitat (e.g. peripneustic larvae with reduced mouthparts and without anal lobes; pointed abdominal structures on pupae; no cocoon formed). No larvae of the 7 British species have yet been described but Lübben (1908) has reared *T. smaragdinus* Gerstaecker and Dyte (1959) reviews work in America; another compact research project awaiting investigation.

The immature stages of *Cyrturella albosetosa* Strobl are unknown but its only known British locality is Chippenham Fen, Cambs.

Rhaphiinae. On the continent the larva of *Rhaphium crassipes* (Meigen) has been found in soil in a beech forest and *Rh. elegantulum* (Meigen) has been reared from a pupa found in sand at the edge of a pond (Lundbeck, 1912). None of the remaining 23 species of *Rhaphium* occurring in Britain are known in the immature stages but McAlpine *et al.* (1981) illustrate a Nearctic species (fig. 217).

Vaillant (1949) has described the larva of *Syntormon zelleri* Loew from wet rocks in company with *Liancalus* and *Tachytrechus* in France. The immature stages of the remaining 11 British *Syntormon* species are unknown.

Machaerium maritimae Haliday develops in the intertidal mud in estuaries (figs 226–228).

The larva of *Systenus* has a prominent pair of prolegs on the first abdominal segment (figs 219–220). Krivosheina (1973) describes and keys the larvae of *S. scholtzii* (Loew), *S. pallipes* Roser and *S. tener* Loew which are found in the accumulations of sap on tree trunks and in the humid rotten wood of tree holes. Lundbeck (1912) summarises the other early rearing records which include *S. scholtzii* from a beech fungus (by Verrall) and other British records.

Achalcus melanotrichus Mik has been reared from rotten debris in lime, elm or horse chestnut trees. *Bathycranium* and *Nematoproctus* are unknown in the immature stages.

Neurigoninae. The larva of *Neurigona* resembles *Thrypticus* in lacking anal lobes but unlike that genus is predaceous and has well developed mouthparts. Lundbeck (1912) gives a translation of Beling's brief description of the larva of *N. quadrifasciata* (F.) which was reared from soil under leaves in a forest of beech trees. The immature stages of the 3 other British species are unknown.

Diaphorinae. Dyte (1959) has reared *Argyra argentella* (Zetterstedt) and *A. confinis* (Zetterstedt) from mud, and the former from wet decaying sawdust near which dung had been dropped. Crisp & Lloyd (1954) reared *A. leucocephala* (Meigen) from mud but no larva has been adequately described. Dyte also notes that two American species of *Diaphorus* have been reared from human faeces but nothing of the life histories of the 4 British species of the genus or of the genera *Chrysotus* (19 spp.) or *Melanostolus* (1 sp.) is known.

Campsicneminae. *Campsicnemus curvipes* (Fallén) has been reared from mud (Crisp & Lloyd, 1954) and Nielsen *et al.* (1954) found larvae of what is probably *C. armatus* (Zetterstedt) (fig. 222) in the very wet soil of swamps and bogs near hot springs under mosses and grasses in Iceland. Nothing is known of the life-histories of the other 9 British members of the genus or any of the remaining 9 genera of the subfamily.

Key to families for final stage larvae of British Cyclorrhapha

1 Larva distinctly sclerotized, flattened dorsoventrally, with prominent segmentation and with obvious long processes 2
— Larva less distinctly sclerotized or flattened dorsoventrally, with or without processes 4
2 Tergal plates distinct (7 visible body segments), with thin striated lateral plates; first two segments and last segment with long filamentous processes; inactive, in moist decaying vegetable material, leaf-litter, etc. (figs 229–230) . . . . . **Lonchopteridae** (p. 76)
— Tergal plates distinct but without thin striated lateral margins and with lateral and dorsal processes not restricted to the first two and last segments 3
3 Posterior spiracles each on a short tuberculate dorsal process situated near the anterior margin of the last abdominal segment, this process terminating in three lobes each of which bears a spiracular opening; sometimes active; in decaying organic material often of animal origin (including carrion) and contaminated by urine or excrement (some Phoridae and Platypezidae may key out here but the lateral processes are usually unbranched and the posterior spiracles closer together) (figs 903–908) . . . . . **Fanniidae** (p. 133)
— Posterior spiracles each ending on a short slender spiculate tuberculate process arising caudally on the last abdominal segment; in the sap of tree wounds (fig. 593) . . . . **Periscelididae** (p. 104)
4 Posterior spiracles on a prominent large sclerotized plate; endoparasites of Hemiptera-Homoptera; inactive (some Tephritidae may key out here but are not parasites and have fan-like anterior spiracles) (figs 247–251) . . . . **Pipunculidae** (p. 79)
— Posterior spiracles otherwise 5
5 Anterior spiracles more dorsally situated on the prothoracic segment and therefore closer together; mandible with longitudinal axis at oblique or right angles to rest of cephalopharyngeal skeleton and usually with two or more pairs of equally sized teeth; mainly in leaf-mines (figs 650–668) . . . . **Agromyzidae** (p. 111)
— Anterior spiracles more lateral in position, or absent; mandibles normally in same plane as rest of cephalopharyngeal skeleton and if toothed the teeth are fewer and unequal in size 6
6 Posterior spiracles each with numerous pore-like openings; endoparasites in insects or mammals 7
— Posterior spiracle each with three slit-like openings (occasionally with up to six similar openings) 10
7 Posterior spiracles usually dome-shaped, either with circular wart-like protuberances each bearing several spiracular pores (some Tachinidae, e.g. *Pelatachina*, fig. 720, may key here, but are parasites of Lepidoptera), or with clusters of pores radiating from the ecdysal scar, or with a small stellar process near each spiracular plate, or with a pair of large laterally directed anal vesicles; endoparasites of bees and wasps; inactive (figs 282–292) . . . . **Conopidae** (p. 85)
— Posterior spiracles otherwise 8
8 Openings of posterior spiracle arranged in three radiating groups; endoparasites of Hemiptera-Heteroptera . . . . **Tachinidae** (part) (p. 118)
— Openings of posterior spiracle arranged circularly but not extending completely round the spiracular plate, the inner side of the plate more or less devoid of openings . . . 9
9 Posterior spiracles on dorsal surface of a transverse cleft of the terminal abdominal segment and are occluded within the cavity when opposing surfaces are brought together; endoparasites of sheep and deer (figs 683–692) . . . . **Oestridae** (p. 115)
— Posterior spiracles on evenly rounded terminal extremity of body where they are unprotected; endoparasites of cattle, horses and deer (figs 693–702) **Hypodermatidae** (p. 116)
10 Posterior spiracles close together on a fused process of varying length, from short to an elongate retractile tube (figs 252–281) . . . . **Syrphidae** (p. 80)
— Posterior spiracles not on a fused process and, if appearing fused, then lacking spicules, tubercles or dense pubescence 11
11 Neck region of larva with an incomplete U-shaped collar or ring (figs 395, 648, r) . . 12
— Neck region of larva without such a collar or ring 13
12 Larva more slender, anterior segments more obviously tapering towards head; numerous and obvious papillae laterally and ventrally on body; free living, feeding on aphids, coccids, etc., active (figs 385–395) . . . . **Chamaemyiidae** (p. 91)

— Larva short and broad, last segment broad and rounded, anterior segments not so tapering towards head; papillae smaller and confined to anterior segments; in wax cells of hive bees feeding on pollen paste, inactive (figs 647–649) . . . . **Braulidae** (p. 110)

13 Anterior spiracle simple, unbranched; larva oval in outline with branched lateral appendages or more or less parallel-sided, somewhat depressed, with or without short dorsal and lateral processes 14

— Anterior spiracle branched or absent 15

14 Posterior spiracles with four openings arranged radially around the ecdysal scar (fig. 241); in fungi; inactive (figs 241–246) . . . . **Platypezidae** (p. 78)

— Posterior spiracle with four openings arranged in two pairs, one behind the other (figs. 232); polyphagous saprophages; in fungi, dung, carrion, etc.; parasitic or predaceous on molluscs, spiders, millipedes, and other insects (figs 231–240) . . **Phoridae** (p. 76)

15 Margins of each posterior spiracular plate with a complete ring of branched setae; in decaying seaweed, etc. on beaches, active (figs 406–412) . . . . **Coelopidae** (p. 93)

— Margins of posterior spiracular plates without setae or setae present as isolated groups or tufts 16

16 Posterior spiracles on short processes ending in a sharp apex (Diastatidae may key here) 17

— Posterior spiracles otherwise 18

17 Anterior spiracles absent; aquatic, in plant stems, or as leaf-mines; or terrestrial and carnivorous; inactive or slightly active (figs 613–616) . . . . **Ephydridae** (part) (Notiphilinae) (p. 106)

— Anterior spiracles present; terrestrial, in leaf-mines; inactive (figs 633–634) . . . . **Drosophilidae** (part) (*Scaptomyza*) (p. 108)

18 Posterior spiracles on the inner side of a short process; other processes or tubercles may occur on the last segment; in decaying organic material of animal origin; active (figs 552–563) . . . . **Piophilidae** (part) (p. 101)

— Posterior spiracles not on inner side of a spiracular process 19

19 Posterior spiracles on elongated processes forming a pair of diverging branches from a cylindrical elongated base, or at least the branches are united at the base (in Canacidae, couplet 23, the spiracular branches are not forked or diverging but are on elongated processes); mouth-hooks with accessory sclerites (small sclerites below mouth-hooks) 20

— Posterior spiracles on the surface of the last segment of the abdomen, or on short processes which are not united at the base; mouth-hooks with or without accessory sclerites (*Limnophora*, Muscidae, fig. 949, has the posterior spiracles on diverging processes which *are* united basally, mouth-hooks with accessory sclerites, but occurs among moss in running water) 27

20 Mouth-hooks united by a sclerotized ventral arch (fig. 508, va); thoracic segments longer and narrower than the abdominal segments; dark coloured active larva with the body retractile, usually in ditches, ponds, etc., terrestrial, aquatic or semi-aquatic, feeding on snails and other molluscs (figs 475–518) . . . . **Sciomyzidae** (p. 96)

— Mouth-hooks not united by a sclerotized arch; thoracic segments not longer and narrower than the abdominal segments; not dark-coloured, active, retractile larva 21

21 Spines or setae present on at least the posterior body segments, apart from any on the segmental borders 22

— Cuticle smooth, without spines or setae on the surface of the body segments, although tubercles may be present 25

22 Posterior part of body obviously swollen, bulbous in shape; anterior spiracles with a more or less elongated cylindrical central axis from which arise lateral processes; in decaying organic material such as dung, carrion, etc.; active (figs. 447–474) . . **Sepsidae** (p. 95)

— Posterior part of body not obviously swollen; anterior spiracles usually more fan-shaped, sometimes elongated 23

23 Each posterior spiracle at the end of an elongated cylindrical process which projects from a tubular siphon derived from the last abdominal segment; ventral pseudopods often present; aquatic on plants, often anchored by the posterior pseudopods, or in semi-aquatic habitats which are contaminated with organic material 24

— Each posterior spiracle much shorter, without a basal tubular siphon derived from the last segment; in decaying organic material, such as fallen leaves (in which they may mine) or in birds' nests, occasionally phytophagous in roots and stems (figs 396–405) . . . . **Lauxaniidae** (p. 92)

24 Posterior spiracular process not forked, spiracles united (figs. 645–646) **Canacidae** (p. 110)
— Posterior spiracular process forked; spiracles not united (figs. 618–624) . . . . **Ephydridae** (part) (p. 106)
25 Anterior spiracles with a basal cylindrical part from the distal end of which arise several finer filaments, or anterior spiracles absent; saprophagous, in decaying fruit, or fruit-based food products, or other vegetable material, dung, fungi, etc.; active (figs 635–638) . . . . **Drosophilidae** (part) (p. 108)
— Anterior spiracles present but otherwise formed 26
26 Anterior spiracles with a very long slender central axis from which arise short lateral processes; posterior spiracles on an elongated siphon or process; body narrow, with ventral pseudopods; in sap from tree wounds, etc.; inactive (figs 590–591) . . . . **Aulacigastridae** (p. 104)
— Anterior spiracles with a long but broader central process, the distal end broadened and bearing the spiracular openings; no lateral processes; body broader, with ventral pseudopods; in larval tunnels of beetles (Scolytidae, etc.); inactive (figs 579–585) . . . . **Odiniidae** (p. 103)
27 Mouthparts usually with accessory sclerites (fig. 911, ob, ar) by mouth-hooks; posterior spiracular slits usually straight or sharply bent about midpoint (figs 925, 930) (sinuous in *Mesembrina*, figs 913–914); under bark, under moss, in soil, etc.; inactive . . . . **Muscidae** (part) (p. 134)
— Mouthparts without accessory sclerites by mouth-hooks (fig. 919); in doubtful cases then posterior spiracles with strongly sinuous slits (figs 956, 960) 28
28 Posterior spiracles with three strongly sinuous slits whose axes lie approximately parallel to the spiracular margins (figs 913, 916) . . . . . . **Muscidae** (Muscinae) (p. 134)
— Posterior spiracles with straight slits, or if openings are sinuous then their axes lie tangential to the outer spiracular margin 29
29 Each posterior spiracle with an obvious spine or lobe 30
— Each posterior spiracle without such a spine or lobe 32
30 Cephalopharyngeal skeleton vestigial, unpigmented, except the small mandibles; in decaying wood of fallen trees; inactive (fig. 578) . . . . **Clusiidae** (p. 103)
— Cephalopharyngeal skeleton normal and pigmented 31
31 Posterior spiracles with the slits short, oval in shape, and arranged almost at right angles to each other:
  (a) in plant roots and stems (figs 361–372) . . . . **Psilidae** (p. 90)
  (b) associated with trees . . . . **Lonchaeidae** (part) (p. 101)
  (c) in seaweed (figs 373–379) . . . . **Helcomyzidae** (part) (p. 91)
— Posterior spiracles with the openings radiating from the ecdysal scar at distinctly less than right angles, or irregularly or peripherally arranged:
  (a) in root-nodules of legumes or decaying organic material; inactive (figs 338–352) . . . . **Micropezidae** (p. 89)
  (b) in roots and bulbs (figs 336–337) . . . . **Otitidae** (part) (p. 88)
  (c) with bifid mouth-hooks in *Juncus, Carex*, etc.; or mining leaves of water lilies (figs 835–838; 849–851) . . . **Scathophagidae** (part) (*Cordilura, Hydromyza*) (p. 129)
  (d) in decaying wood (figs 607–609) . . . . **Diastatidae** (p. 108)
32 Anterior spiracle bicornuate (fig. 359), posterior spiracles each on a distinct process (fig. 356); ? saprophagous . . . . **Tanypezidae** (p. 90)
— Anterior spiracle otherwise, or if bicornuate (some Scathophagidae, fig. 840), then posterior spiracles not on raised processes 33
33 Posterior spiracles united, the three spiracular openings of each weakly or strongly bent; endoparasitic in horses; inactive (figs 703–711) . . . . . **Gasterophilidae** (p. 117)
— Posterior spiracles separate 34
34 Posterior spiracles in a distinct deep depression (fig. 781); in decaying organic matter of animal origin, carrion, etc.; active (figs 768, 785) . . . . **Sarcophagidae** (p. 125)
— Posterior spiracles not in a sunken depression 35
35 Apex of each posterior spiracular process separated into three, on each of which is an opening:
  (a) in excrement, carrion, or ants' nests (figs 639–644) . . . . . **Milichiidae** (p. 110)
  (b) in refuse in birds' nests (figs 586–589) . . . . **Carnidae** (p. 104)
  (c) plant feeders or predators of root aphids (figs 669–682) **Chloropidae** (part) (p. 113)
— Apex of each posterior spiracular process normal 36

36 Anterior spiracle with a more or less elongated central axis from which arise short or longer processes laterally; posterior spiracular openings short, elliptical; in carrion, dung, nests, etc., usually associated with decaying organic material (figs 519–530) . . . . **Sphaeroceridae** (p. 99)

— Not as above 37

37 Posterior spiracular openings rather sinuous, all openings more or less parallel to each other and to the outer margin of the spiracle; mouth-hooks strongly curved near base, rest of cephalopharyngeal skeleton united; under bark; inactive (figs 353–354) . . . . **Megamerinidae** (p. 90)

— Not as above 38

38 Posterior spiracles with three very short elliptical openings (some Anthomyiidae may key here, but are included in other half of couplet) 39

— Posterior spiracles with more elongated, slit-like openings 40

39 Anterior spiracles fan-like:
(a) phytophagous, esp. in Gramineae (figs 669–682) . . **Chloropidae** (part) (p. 113)
(b) predaceous on bark beetles or phytophagous in plants (figs 531–538) . . . . **Pallopteridae** (p. 100)
(c) in water-loving Gramineae (figs 594–606) . . . . **Anthomyzidae** (part) (p. 105)

— Anterior spiracles with central axis elongated:
(a) in Gramineae (figs 564–577) . . . . **Opomyzidae** (p. 102)
(b) in water-loving Gramineae (figs 594–606) . . . . **Anthomyzidae** (part) (p. 105)

40 Posterior spiracles on the surface of the last segment, not at all raised on short processes 41

— Posterior spiracles on the end of more or less obvious, though always short, processes 42

41 End of last abdominal segment with obvious tubercles arranged in a more or less circular sequence around the posterior surface; spiracular scar (button) usually in the rather narrow but strongly sclerotized spiracular border (peritreme); in decaying organic matter of animal origin, carrion, dung, wounds of animals, etc.; active maggots (figs 786–825) . . . . **Calliphoridae** (p. 127)

— End of last segment with less obvious tubercles; spiracular border without the spiracular scar which is always situated inside the border; in plant stems, roots, fruits, flower-heads, sometimes causing mines or galls (figs 293–314) . . . . **Tephritidae** (p. 86)

42 Endoparasitic in insects, woodlice (Isopoda), etc 43

— Free living larvae 44

43 Endoparasitic in insects (mainly) (figs 712–755) . . . . . . **Tachinidae** (part) (p. 118)

— Endoparasitic in woodlice (figs 756–767) . . . . **Rhinophoridae** (p. 124)

44 Body, including last abdominal segment, without obvious papillae or tubercles:
(a) in root nodules of legumes (*Rivellia*); in fungi, soil or dead wood (*Platystoma*) (figs 315–321) . . . . **Platystomatidae** (p. 88)
(b) in decaying vegetable matter or dung (figs 322–337) . . . **Otitidae** (part) (p. 88)
(c) under bark, in dung, plant roots and stems, conifer cones, fruits, etc. (figs 539–547) . . . . **Lonchaeidae** (part) (p. 101)
(d) in fungi, carrion, dung, decomposing matter (figs 413–446) . . . . **Heleomyzidae** (part) (p. 94)
(e) in decaying seaweed on beaches (figs 373–379) . . . **Helcomyzidae** (part) (p. 91)

— Body, including last segment, with a ring of papillae or tubercles around the spiracular field and with others on other segments; cuticle may have spines or hairs 45

45 Anterior spiracles (fig. 638) consisting of long filaments situated at the tip of an often long basal stem; in decaying or fermenting organic matter (figs 625–638) . . . . **Drosophilidae** (part) (p. 108)

— Anterior spiracles otherwise 46

46 Slits in posterior spiracles small, at right angles to each other and well separated basally; in fungi, dung, carrion, rotting wood and other decomposing material (figs 413–446) . . . . **Heleomyzidae** (part) (p. 94)

— Slits in posterior spiracles larger, usually at less than 90° to each other and more approximated basally 47

47 Cephalopharyngeal skeleton without a distinct sclerite (ventral arch) beneath the mouth-hooks (figs 548–551); sucking blood of nestling birds . . . . **Piophilidae** (part) (Neottiophilinae) (p. 101)

— Cephalopharyngeal skeleton with a distinct (often sub-triangular) ventral sclerite . 48

48 Anal fleshy lobes long, more equal in size, arranged with 8 evenly spaced around the discal plate, plus 2 more ventrally; in fungi, carrion (figs 380–384) . . **Dryomyzidae** (p. 91)

— Anal lobes otherwise 49

49 Anal lobes usually separate and simple; in dung, plant stems or leaf mines in docks, reeds, water-lilies, orchids, etc. (figs 829–854) . . . . **Scathophagidae** (part) (p. 129)

— Anal lobes sometimes joined basally or individual lobes bifurcate; in stems or roots of plants, leaf-mines, fungi or rotting wood (figs 855–878) . . . . **Anthomyiidae** (p. 130)

Families not included in the key

Hippoboscidae (p. 139) and **Nycteribiidae** (p. 140) larvae (prepupae) pupate soon after the female deposits them. Larvae have a large sclerotized spiracular plate and a distinct spiracular field and the spiracular openings are connected by branching tubular structures (fig. 967).

The immature stages of the following families are undescribed (see under each family for known habits):

Acartophthalmidae (? in fungi, dung, carrion) (see comment below)
Asteiidae (? in fungi, reeds, wood-detritus)
Camillidae (? in mammal nests, bird-guano)
Chyromyidae (? in bird and bat-guano)
Stenomicridae (? in water holding leaf-bases of Gramineae etc)
Tethinidae (saline habitats, shores, dunes etc)
Trixoscelidae (? bird-guano)

As this book goes to press a very important work on the immature stages of Cylorrhapha has appeared (Ferrar, 1987) and the immature stages of *Acartophthalmus bicolor* Oldenberg have been described from carrion (Ozerov, 1987).

Notes on families of Cyclorrhapha

Series **Aschiza**

Lonchopteridae

(Figs: 229–230, puparium 1149, pupa 1150)

This small family has only 37 described world species, all belonging to the single genus *Lonchoptera*. Seven species occur in Britain of which two are known in the immature stages. The larvae have been found under logs, among dead leaves and in decaying vegetable matter generally. They have also been found between the leaves of Brussels sprouts and on the moist surface of swede turnips, especially during wet weather. The transport of vegetables coupled with parthenogenetic reproduction in the adult may explain the cosmopolitan distribution of *L. furcata* (Fallén).

The larva (figs 229–230) is of a striking appearance, flattened ventrally with an arched back and long paired processes at each end. The larva of *L. lutea* Panzer has been described by Lubbock (1862) and de Meijere (1900) and that of *L. furcata* by Nielsen *et al.* (1954). No other species are known in the larval stage. Whitton (1956) describes the respiratory system, which is amphipneustic.

Phoridae

(Figs: larvae 231–240; egg 1007; puparia 1151,1152,1154; pupa 1153)

The Phoridae (scuttle-flies) is a large family with about 3,000 species so far described throughout the world. The life-histories are poorly known but the larvae show a very wide range of habits from polyphagous saprophages and fungus feeders to specialised predators, parasitoids and true parasites. Some 300 species in 22 genera occur in Britain. The subfamilies are ill-defined even in the adult stage and no larval key is offered but for convenience the immature stages are discussed under the 3 subfamilies recognised in the *Check List* (Smith, 1976). Disney (1979, 1983) reviews the biology of the British Phoridae and cites the original records for most of the comments below. Much careful work is needed in working out life-histories of this neglected but biologically important family now that good *Handbooks* to adults (Disney, 1983, 1989) are available.

Aenigmatiinae. The single British genus *Aenigmatias* is known to parasitize the pupae of ants, particularly wood ants (*Formica* spp.). The immature stages have not been adequately described and the identities of the three British species have been confused in recorded rearings.

Metopiniinae. This subfamily includes the large genus *Megaselia* (figs 231–233) with over 200 British species and a wide range of life-histories. *Megaselia rufipes* (Meigen) is the most frequently met of the polyphagous saprophage species with *M. giraudii* (Egger) a close second (records of both species as parasitoids are probably incorrect). The larvae of *M. halterata* (Wood) and *M. nigra* (Meigen) are known fungus feeders but other species occurring in fungus may be predators or parasites of other fungivorous Diptera. *M. aequalis* (Wood) and *M. ciliata* (Zetterstedt) feed on slug eggs; *M. melanocephala* (von Roser), *M. nasoni* (Malloch) and *M. pulicaria* (Fallén) feed on spider eggs; *M. fuscinervis* (Wood) attacks snails (*Vitraea*); *M. brevicostalis* (Wood) has been reared from deal snails (*Helix* and *Cepaea*). *M. flavicoxa* (Zetterstedt) and *M. obscuripennis* Wood parasitize larval Sciaridae (*Trichosia, Bradysia*); *M. paludosa* (Wood) parasitizes Tipulidae larvae. The larvae of some non-British species of *Megaselia* are parasitic on millipedes and predaceous on coccids.

The two British *Pseudacteon* species are parasitoids of adult worker ants; *P. brevicauda* Schmitz on *Myrmica ruginodis* Nylander and *M. scabrinodis* Nylander; *P. formicarum* on *Lasius flavus* (F.), *L. niger* (L.), *Formica sanguinea* Latreille and possibly other genera.

Phalacrotophora species parasitize the pupae of ladybird beetles (Coccinellidae).

The immature stages are undescribed for the genera *Beckerina, Gymnophora, Metopina, Plectanocnema* and *Woodiphora*. However, *Metopina* occurs in buried carrion (see Smith, 1986b) and *Woodiphora retroversa* (Wood) has been associated with a *Cossus* (Lepidoptera) excavation in a tree (Disney, 1983). The genus *Plastophora* of the Check List is now included in *Megaselia*.

Chonocephalus is a genus of about 40 species mainly found in the tropics and sub-tropics with 3 species in the Palaearctic Region. The larvae (fig. 234) of a few species have been reported in rotting fruits and rotting palm spadices and may thus come to the notice of economic entomologists. *C. heymonsi* Stobbe has occurred in a London hothouse.

Phorinae. The larvae (fig. 235) of *Anevrina* (4 British species) occur on vertebrate carrion and in the soil, particularly in mole nests.

Borophaga incrassata (Meigen) (figs 236–237) parasitizes the larvae of *Bibio marci* L. (Bibionidae) (Morris, 1922) but the immature stages of the other 5 British species are unknown though *B. irregularis* (Wood) has been reared from pupae under ash logs. *Chaetopleurophora* larvae have been found in dead snails.

Conicera tibialis Schmitz is the 'coffin fly' that breeds in coffined bodies and appears on the surface of the ground above the body after a year or more. This and other species have also been reared from other carrion. In addition *C. dauci* (Meigen) has been reared from fungi. Further information on the biology of *Conicera* in carrion, including human cadavers, is summarised by Smith (1986b).

Some species of *Diplonevra* breed in carrion; *D. funebris* (Meigen) has been reared from wasps' (*Vespula*) nests; *D. pilosella* Schmitz has been reared from a wounded earthworm; *D. nitidula* (Meigen) adults have been seen swarming over a dead earthworm, and have been reared from digested sewage sludge.

The tropical and sub-tropical genus *Dohrniphora* contains over 100 species. One species, *D. cornuta* (Bigot), has been spread by man and is now well established in Britain. The larvae (fig. 239) are found in sewage, compost, dead insects and snails, rotting ships' cargoes of rice, bran, cow peas, etc., vertebrate carrion, etc. and will attack the immature stages of other species that compete with it for food (e.g. *Psychoda alternata* in trickling filter sewage beds, Kloter *et al.*, 1977).

Gymnoptera longicostalis Schmitz breeds in bumble-bee nests (*Bombus*) and *G. vitripennis* (Meigen) in wasps' nests but both species have been reared from the same caterpiller of *Cossus cossus* (L.) (goat moth).

The larva of *Phora holosericea* Schmitz has been found preying upon root aphids some 20–40 cm below the soil surface (in Russia, Yarkulov, 1972). Apparently each larva consumes 80–85 aphids during its development. Nothing is known of the life-histories of the remaining 8 species of *Phora*. Early records of *P. aterrima* F. from carrion are misidentifications (of adults) of *Conicera*.

Larvae of *Spiniphora* live in dead snails but *S. bergenstammi* (Mik) (fig. 240) is frequently found by environmental health officers in milk bottles. The puparia (fig. 1154) are so firmly cemented to the inside of the bottle that they can survive the normal washing process. *S. bergenstammi* has also been reared from an old nest of a blackbird.

Several species of *Triphleba* breed in vertebrate carrion; *T. antricola* (Schmitz) also breeds in bat dung in caves; *T. lugubris* (Meigen) breeds in wasps' nests; *T. minuta* (F.) breeds in the fungus *Gymnopilus junonius* (Fries) (=*Pholiota spectabilis* Gillet); *T. gracilis* (Wiedemann) has been reared from puparia found under the bark of rotting larch and spruce logs.

The life-history of *Hypocera* is unknown. The genus *Citrago* is now included in *Triphleba*.

Platypezidae

(Figs: larvae 241–246, cocoon 1156, puparium 1157)

Some 200 species of Platypezidae (flat-footed flies) have been described throughout the world. In Britain there are 31 species (including *Atelestus*, see below) in 12 genera representing three subfamilies. All those Platypezidae known in the immature stages are fungus feeders. Kessel *et al.* (1973) survey what is known of the immature stages and key 10 genera.

Opetiinae. The immature stages and life-histories of this subfamily are unknown. *Opetia nigra* Miegen occurs in woodlands though the female is rarely seen. The genus probably belongs in the Empidoidea and discovery of the larva may resolve this problem (Disney, 1987). The three tiny species of *Microsania* are rarely seen except in the smoke of bonfires to which they are particularly attracted. The two species of *Atelestus* are usually beaten from the foliage of trees in the spring but this genus has recently been placed in a separate family, the Atelestidae (Chvála, 1983). Some rearing data are provided by Chandler (1973, and in Stubbs & Chandler, 1978) and Brindle (1961e) keys the few British species known in the larval stages.

Callomyiinae. The striking larvae of *Callomyia amoena* Meigen (fig. 245) feed on the surface of bark encrusting fungi (*Corticium* spp.) in damp situations. The host fungi of the other 3 species in the genus are not known. Members of the genus *Agathomyia* (fig. 246) appear to develop internally in the tougher Polyporaceae. *A. unicolor* Oldenberg and *A. falleni* (Zetterstedt) have both been reared from *Bjerkandera (Polyporus) adusta* Fries and *A. antennata* (Zetterstedt) probably develops in *Coriolus versicolor* Fries, which the adults frequent. The host fungi of the remaining 6 British species of *Agathomyia* are unknown.

Platypezinae. *Protoclythia* species attack soft fungi, chiefly the honey fungus *Armillaria mellea* Quélet from which both British species (*P. modesta* (Zetterstedt) and *P. rufa* (Meigen)) have been reared. Two of the four British species of *Platypeza* (figs 241–244) also breed in the honey fungus but in addition *P. fasciata* Meigen has been reared from a puff-ball (*Lycoperdon pyriforme* Schaeffer) and a *Boletus* sp. Dušek (1962) gives a good illustrated description of the larva and puparium of *P. fasciata*.

Plesioclythia dorsalis (Meigen) breeds in field mushrooms (*Agaricus* spp.) but on the continent it has also been reared from the giant puff-ball (*Langermannia gigantea* (Persoon) Rostkovius) and the cep (*Boletus edulis* Bulliard). I have also seen them in boxes of chocolates perhaps attracted by a fungal 'bloom' or more likely having wandered from nearby mushrooms in searching for a pupation site!

Paraplatypeza atra (Meigen) has been reared from *Pluteus cervinus* Quélet. *Orthovena furcata* (Fallén) breeds in *Polyporus squamosus* Fries, and adults have also been seen on or near other fungi (*Pleurotus sapidus* Sacc. and *Clitopilus prunulus* Quélet).

Polyporivora infumata (Haliday) and *P. picta* Meigen have been reared from *Coriolus versicolor*.

In spite of these rearings very few larval descriptions or studies of host fungus specificity have been published and there is scope for a research project here, perhaps coupled with other fungivorous Diptera, e.g. Mycetophilidae. Peter Chandler will be describing the immature stages of most of the above in his forthcoming volume in the *Fauna ent. Scand.* series.

Pipunculidae

(Figs: larvae 247–251, puparium 1155)

The family Pipunculidae contains about 600 species throughout the world. In Britain 74 species in 8 genera have so far been recorded but the family needs further careful study.

The larvae of pipunculids are endoparasites of Hemiptera-Homoptera, especially Cicadellidae (leaf-hoppers), Cercopidae (frog-hoppers) and Delphacidae. The biology of the family is poorly known and very few larval descriptions have been published, but classic work by Perkins (1905) in Hawaii has established their value in the biological control of the sugarcane leaf-hopper (*Perkinsiella saccharicida* Kirkaldy). Other economically important leaf-hoppers are attacked by Pipunculidae in other parts of the world. Except for *Eudorylas* each genus is confined to a single host-family and many species are host specific, though some may range over several genera. Clausen (1940), Coe (1966) and Askew (1971) review the biology of the family. Much careful rearing, coupled with a refined taxonomic study of the adults, is badly needed in this family which presents problems similar to those in the parasitic Hymenoptera.

Three subfamilies are represented in Britain.

Chalarinae. The genus *Chalarus* confines its attentions to Cicadellidae of the subfamily Typhlocybinae. Several of the 8 British species have been reared but early records are undoubtedly marred by misidentifications. Waloff (1975) records *C. spurius* Fallén from *Eupteryx notata* Curtis.

Verrallia species (fig. 247) confine their attentions to the family Cercopidae. Unlike other Pipunculidae this genus appears to attack adult Homoptera to the exclusion of the nymphal stages. *V. aucta* Fallén has been reared from the common British frog-hoppers *Philaenus spumarius* L. and *Neophilaenus lineatus* (L.). Whittaker (1969) and Waloff (1975) have studied the biology of *V. aucta* in these two frog-hopper species and what is probably *V. setosa* Verrall in *Neophilaenus campestris* (Fallén). *V. pilosa* Zetterstedt has been reared from a puparium found in a bird's nest, probably from a parasitized frog-hopper that had strayed or fallen in. No reliable rearing data are available for the remaining 3 British species.

Nephrocerinae. *Nephrocerus flavicornis* Zetterstedt is the largest British pipunculid which has led to some speculation on the identity of the homopteran host capable of sustaining its larva. Early in the century, when the only three British records of the species were from the New Forest it was thought that the rare and restricted New Forest cicada (*Cicadetta montana* (Scopoli)) was the probable host. Subsequent records of *N. flavicornis* suggest that our second largest homopteran, *Ledra aurita* (L.), may be the true host since it shares a predilection for oak woods and is fairly widely distributed from the New Forest to Suffolk.

Pipunculinae. *Tomosvaryella* (= *Alloneura*) has seven British species and Waloff (1975) has reared three of them from Cicadellidae: *T. sylvatica* (Meigen) from *Jassargus pseudocellaris* (Flor), *Errastunus ocellaris* (Fallén) and *Arthaldeus pascuellus* (Fallén); *T. palliditarsis* (Collin) from *Diplocolenus abdominalis* (F.); and *T. kuthyi* (Aczel) from *Psammotettix confinis* (Dahlbom). On the continent Coe (1966) records *T. sylvatica* from *Arthaldeus pascuellus* and an unidentified *Tomosvaryella* sp. from *Opsius* sp. (both hosts are Cicadellidae).

The only rearing records of *Dorylomorpha* (11 British species) are *D. rufipes* Meigen from *Cicadula quadrinotata* (F.) and *D. xanthopus* (Thomson) from an adult *Psammotettix confinis* (Waloff, 1975).

The genus *Pipunculus* contains seven species including two of the commonest British members of the family, *P. campestris* Latreille and *P. thomsoni* Becker. Nevertheless breeding records are few. In Germany *P. campestris* has been reared from the Cicadellidae *Macrosteles laevis* Ribaut, *Arthaldeus pascuellus* and *Cicadula quadrinotata* (Coe, 1966). Waloff (1975) adds *Euscelis plebejus* (Fallén), *Psammotettix confinis* and *Elymana sulphurella* (Zetterstedt) as hosts of *P. campestris* and also records *P. thomsoni* from *Elymana sulphurella*.

Cephalops species (13 British) select Delphacidae as hosts and rearing records are comparatively numerous. Coe (1966) records *C. semifumosus* (Kowarz) from *Ditropis pteridis* Boheman and *Conomelus anceps* Germar; *C. oberon* Coe from *D. pteridis*; *C. subultimus* Collin from *D. pteridis*; and (from Germany) *C. ultimus* (Becker) from *Eurysa lineata* Perris. Waloff (1975) records *C. curtifrons* Coe from *Stenocranus minutus* (F.) and *C. semifumosus* from the two hosts recorded by Coe (1966) and in addition *Javesella pellucida* (F.), *Megamelodes venosus* (Germar), *Laodelphax elegantulus* (Boheman), *Dicranotropis hamata* (Boheman), *Javesella* sp., and *Delphacodes fairmarei* (Perris). Rothschild (1964) describes the immature stages of *Cephalops semifumosus* Kowarz (fig. 248) and May (1979) those of *C. curtifrons* Coe. The latter appears to be specific to *Stenocranus minutus* in which 35% parasitism may occur.

Eudorylas species (21 British) (fig. 249) parasitize Cicadellidae. Waloff (1975) discusses the biology and lists hosts (mostly *Psammotettix confinis, Errastunus ocellaris* and *Arthaldeus pascuellus*) for *E. fascipes* (Zetterstedt), *E. jenkinsoni* Coe (= *E. obliquus* Coe), *E. obscurus* Coe, *E. subfascipes* Collin and *E. subterminalis* Collin. Coe (1966) lists some rearing records of *Eudorylas* from named cicadellid hosts in Germany.

Syrphidae

(Figs: larvae 252–281, eggs 1008–1012, puparia 1158–1164, pupa 1162, leaf mines 1292)

About 5,000 species of Syrphidae (hover-flies) have been described throughout the world. Of these some 242 species in 68 genera occur in Britain.

The larvae of some Syrphidae, especially aphidophagous species of the subfamily Syrphinae and the so called rat-tailed maggots (Eristalini), are quite well known but elsewhere knowledge is very irregular.

The following key to subfamilies, and tribes of Milesiinae, is based on Hartley (1961) with indications where the extra tribes recognised in the *Check List* (Smith, 1976) are there included. Notes on genera and species follow the tribal arrangement in the *Check List*. Keys to some genera and species for larvae with descriptions are provided by Dixon (1960) and Hartley (1961). For substantial, well illustrated, work on aphidophagous species see also Bhatia (1939) and Scott (1939). The continental works of Dušek & Laska (1967) and Goeldlin de Tiefenau (1974) are also very useful. Wood inhabiting species are keyed (in Russian) by Krivosheina & Mamaev (1967). Other work is cited below. Stubbs & Falk (1983) provide a useful summary of habitats of the early stages and key the adults.

Partial key to subfamilies and tribes of larval Syrphidae

(Modified from Hartley, 1961)

1 With piercing mouthparts. Posterior spiracles sessile, slits more or less radial and usually straight on slight ridges (except *Xanthogramma* where slits are convoluted but still distinctly radial); prothoracic spiracles very small. Prolegs vestigial or absent, without crochets; body often flattened and usually pointed anteriorly; usually with colour pattern which is lost on death. Predaceous, mainly on aphids (includes Syrphini, Chrysotoxini, Bacchini, Melanostomatini and Paragini. Pipizini also key out here) . . **Syrphinae**

— Without piercing mouthparts. Posterior spiracles on a telescopic breathing tube; or if sessile with the slits basically more or less circumferential, usually convoluted and sometimes subdivided or as numerous small apertures, not on raised ridges; prothoracic spiracles present or absent. Prolegs with crochets present or absent. Shape varied; never with colour pattern but sometimes with brownish cuticle . . . . **Milesiinae** 2

2 Anterior end pointed. Posterior spiracles with slits subdivided and radial. Prolegs well developed with few stout crochets. In nests of bees and wasps (figs 271–276) **Volucellini**

— Anterior end truncate or rounded. Posterior spiracles with slits undivided or if divided then the prolegs are absent 3

3 Body more or less hemispherical and flattened ventrally; pro- and mesothorax very reduced and only visible ventrally. Prolegs absent; pubescence usually as a lateral fringe; dorsal surface reticulated; metapneustic. In ants' nests (figs 269–270) . . . **Microdontini**

— Body more or less cylindrical, pro- and mesothorax well developed and similar in size to other segments 4

4 Abdomen abruptly tapering to a long telescopic breathing tube; anterior spiracles elongate and retractile. In stagnant foul water, liquid manure, rock pools, etc. (fig. 281) **Eristalini**

— Abdomen gradually tapering or truncate; if forming a distinct tail then the anterior spiracles are squat and not retractile 5

5 Metapneustic. Small white larvae (less than 10 mm) with long pubescence posteriorly; posterior spiracles convex or stylet-like on telescopic breathing tube. Larvae aquatic, piercing plant roots to obtain oxygen (figs 258–259) (*Chrysogaster*) . . . . **Chrysogasterini** (part)

— Amphipneustic (but anterior spiracle often very difficult to see). Larva otherwise . . 6

6 Body short (less than 8 mm) and flattened with abdomen gradually tapering posteriorly but not forming a distinct tail; prolegs and crochets present. Under wet decaying bark (*Sphegina*). In wet decaying manure etc (*Neoascia*) . . . . **Chrysogasterini** (part)

— Body longer (more than 10 mm) and more or less cylindrical or if short and flattened then truncate posteriorly and without prolegs 7

7 Abdominal prolegs large and partially fused in segmental pairs, with crochets of each pair confluent . . . . **Callicerini**

— Prolegs separate or absent, crochets never confluent (includes Cheilosiini, Eumerini, Merodontini, Sericomyiini, Xylotini, *Myolepta, Hammerschmidtia, Cheilosia*) . . . . **Milesiini** (s.lat.)

Syrphinae

Syrphini. The majority of genera and species in this tribe feed on aphids. The common *Syrphus ribesii* (L.) (fig. 253), *S. vitripennis* Meigen and *S. torvus* Osten Sacken are widely polyphagous, eating a great variety of aphids and occur on many trees, shrubs and herbs. Other genera with similarly polyphagous species include *Epistrophe* (fig. 254) (see Rotheray, 1986b) *Dasysyrphus* (fig. 255), *Episyrphus, Leucozona, Metasyrphus* (s.s.), *Scaeva* and *Sphaerophoria*. *Episyrphus balteatus* (De Geer) is found abundantly on cabbages and would be a good species for use in demonstration and teaching. Some are more specialist feeders, e.g. *Metasyrphus* s.g. *Lapposyrphus* on conifer aphids (*Adelges*); *Melangyna cincta* Fallén on *Phyllaphis fagi* on *Fagus silvatica*. The rare *Eriozona syrphoides* (Fallén) has been found to feed on the aphid *Cinaria pineae* (Panzer) in established (40 years old) spruce monocultures in Czechoslovakia (Kula, 1983). It would be a useful study to rear Syrphini and identify their aphid prey to establish the degree of specificity in habitat and in feeding, as Dušek & Laska (1966) have done in Czechoslovakia. The eggs, host range and oviposition behaviour have been studied by A. E. F. Chandler (1968). Some, e.g. *Sphaerophoria*, feed on other small Homoptera as well as Aphididae. *Parasyrphus nigritarsis* (Zetterstedt) attacks the eggs and larvae of certain chrysomelid beetles (Schneider, 1953); other members of the genus are unknown as larvae and would well repay investigation. Papers by Rotheray (1986– still appearing) should be studied.

The larval habits of some genera are unknown, but are probably aphidophagous, e.g. *Xanthogramma* has been found under turf and stones and in ants' nests (*Lasius* spp.).

Chrysotoxini. *Chrysotoxum* larvae appear to be of the aphidophagous type but the feeding habits are unknown. They have been found under compost heaps, stones, etc.

and Dixon (1960) reared *C. verralli* Collin from a larva found in an ants' nest (*Lasius niger* (L.)).

Bacchini. Larvae of *Baccha* have been found feeding among colonies of aphids: *Uromelan jaceae* (L.) on *Centaurea scabiosa* L. and *Brachycaudina napelli* (Schrank) on *Aconitum*.

Melanostomatini. Lucchese (1942) describes the larva of *Xanthandrus comtus* (Harris) which attacks caterpillars of *Acroclita naevana* Huebner and larvae of other small 'quasi-gregarious' tortricid moths.

Melanostoma species normally feed on aphids but *M. mellinum* (L.) has also been recorded attacking torpid adults of the flies *Musca domestica* L. and *Paregle cinerella* (Fallén) on umbels of *Daucus carota* L. When deprived the same species has been reported to take 'tortrix' larvae as prey. In the U.S.A. a non-British species has been reared on both aphids and decomposing chickweed, the latter being the more successful!

Platycheirus species are aphid feeders. Dixon (1960) describes the larvae of several species, but gives no information on plant hosts or aphid food. *P. scutatus* (Meigen) is common on potatoes, cabbages, etc. and *P. peltatus* (Meigen) shows a strong preference for brassicas. *P. (Pachysphyria) ambiguus* Fallén appears to specialize on aphids which curl up the leaves of *Prunus* (Dušek & Laska, 1966).

Lundbeck (1916) described the larva and puparium of *Pyrophaena granditarsa* Forster and the puparium of *P. rosarum* (F.), both of which he found in flood refuse in fens (in Denmark). The feeding habits remain unknown but they are thought to be aphidophagous.

Paragini. The larvae of *Paragus* species (fig. 256) are aphidophagous.

Milesiinae

Pipizini. The larvae of *Pipiza* species (fig. 257) seem to prefer aphids which secrete a waxy flocculence, e.g. woolly aphid (*Eriosoma*). *Pipizella* larvae confine their attention to subterranean aphids feeding on the roots of plants.

Heringia heringi (Zetterstedt) attacks the blister gall-forming aphid *Schizoneura lanuginosa* Hartig on elm (especially *Ulmus procera* Salisbury) and has been reared from an aphid gall on *Salix*, but the immature stages have not been adequately described.

The larvae of *Neocnemodon* usually feed on aphids of the family Pemphigidae (e.g. *Eriosoma*) on deciduous trees, but *N. latitarsis* (Egger) and *N. vitripennis* (Meigen) have been found attacking the woolly aphid *Dreyfusia piceae* (Ratzeburg) (Adelgidae) on silver fir (*Abies alba* Miller).

Triglyphus primus Loew larvae have been found feeding on aphids (*Cryptosiphum artemisiae* Buckton, =*gallarum* Kaltenbach) on *Artemisia vulgaris* L.

Cheilosiini. *Cheilosia* larvae are phytophagous. Smith (1979b) summarises the plant associations which are with the stem bases and roots of higher plants (especially Compositae) or leaf mines in Crassulaceae and some fungi. Some additional information is provided by Stubbs (1983) and Rotheray (1988a,b and in prep.) but host-plant information is still lacking for 20 of the 32 species occurring in Britain. The leaf-mining species is *C. semifasciata* Becker (fig. 1292) which attacks *Umbilicus rupestris* (Salisbury) Dandy (wall pennywort) and *Sedum telephium* L. (orpine). The species in fungi are closely related, e.g. *C. scutellata* (Fallén) and *C. soror* Zetterstedt (from truffles); *C. scutellata* and *C. longula* (Zetterstedt) in *Boletus* and allies (*Leccinum, Suillus* and *Gyroporus*).

The larvae of *Portevinia maculata* (Fallén) live in the underground portion of the leaf bases of *Allium ursinum* L. (ramsons or wild garlic) (Dr M. C. D. Speight, pers. comm.).

The common *Rhingia campestris* Meigen breeds in cow dung but nothing is known of the immature stages of the rare *Rh. rostrata* (L.).

The larvae of *Ferdinandea cuprea* (Scopoli) have been found in the sap of wounds on tree trunks especially trees infested with the goat moth (*Cossus cossus* L.) around the roots of which puparia have been found. It seems likely that the much rarer *F. ruficornis* (F.) breeds in similar situations.

The early stages of *Chamaesyrphus* are unknown but should be sought in the Caledonian pine woods where the adults occur among *Calluna*.

Chrysogasterinae. The larvae of *Myolepta* resemble the 'rat-tailed' maggots of the Eristalini but with a shorter anal siphon or 'tail'. They occur in wet tree rot-holes of beech and poplar.

The larvae of *Chrysogaster* are aquatic or semi-aquatic. Some species, e.g. *C. hirtella* Loew (figs 258–259), have the posterior spiracles adapted as a stylet for piercing aquatic plants in order to obtain oxygen but other species do not, e.g. *C. solstitialis* (Fallén) (fig. 260).

Orthonevra larvae (fig. 261) are found in mud containing decaying wood and other vegetation at the edge of ponds and streams in wooded areas. *Lejogaster* larvae have been found in the decaying vegetation of a floating mat of *Typha* and other plants in a pond. The posterior spiracles of these two genera are not modified into piercing stylets.

Larvae of *Brachyopa* live in sap runs or under dead bark, those of *Sphegina* in decaying wood and those of the rare *Hammerschmidtia* probably in dead wood of birch and aspen around which the adults have been found.

Lundbeck (1916) found larvae and pupae of *Neoascia geniculata* (Meigen) in flood refuse and it is assumed that they probably occur in marshy soils.

Callicerini. Coe (1938, 1939) found larvae of *Callicera* (figs 265–268) in a wet decaying cavity in the fork of a pine, some of which took five years to pupate. The posterior spiracles have straight slits and the anal papillae are very long. It is assumed that the other two members of the genus have similar life-histories; all are rare.

Pelecocerini. The immature stages of our only species, *Pelecocera tricincta* Meigen, are unknown.

Eumerini. The larvae of *Eumerus tuberculatus* Rondani and *E. strigatus* (Fallén) are well known pests of *Narcissus* bulbs and are known as small narcissus flies or lesser bulb flies (the large bulb-fly being *Merodon*). *E. strigatus* larvae (figs 262–264) also attack *Iris*, parsnip roots, onions and on the continent have attacked potatoes. The two species are not easily distinguished in the larval stages (Hodson, 1932a). The immature stages of the remaining two British species are unknown but presumably have similar habits and could well repay investigation. Larvae of other families (e.g. Scathophagidae) also occur in *Narcissus* bulbs (see index).

Microdontini. The remarkable larvae of *Microdon* (figs 269–270) live in ants' nests where they feed on the minute pellets of food discarded by the ants. The biology of *M. mutabilis* (L.) is described by Donisthorpe (1927) and that of *M. eggeri* Mik by Syms (1935).

Volucellini. *Volucella* larvae (figs 271–276) are scavengers in the nests of bumble bees (*Bombus*), social wasps (*Vespula*) and the hornet (*Vespa*). When wasps nest in roof spaces it is not uncommon for *Volucella* larvae (usually *V. inanis* L., which lacks the long anal papillae of other species, fig. 271) to leave the nests and appear (via light fittings) in the upstairs rooms of houses whence they may be sent in to entomologists for identification by environmental health officers. I have seen larvae of *V. pellucens*, which had obviously dropped from such a situation, served in a restaurant meal!

The classic and beautiful work on *Volucella* is by Künckel d'Herculais (1875–1881) but an illustrated key to species is provided by Hartley (1961).

Sericomyiini. *Sericomyia* species have larvae of the 'rat-tailed maggot' type similar to those of Eristalini. *S. lappona* (L.) has been found in disturbed peat lying in water at the end of a derelict cutting (Hartley, 1961).

The immature stages of *Arctophila fulva* (Harris) are unknown, but a female has been seen ovipositing in deep, water-filled horse hoofprints along a shaded muddy path near a stream (Stubbs & Falk, 1983).

Xylotini. *Xylota* larvae resemble those of *Syritta* (see below) and have been found in very wet decomposing silage, wet sawdust of an old saw pit, exudate and rot-holes of yew (*Taxus baccata* L.), and wet decaying beech stumps (*Fagus sylvatica* L.).

Larvae of *Xylotomima nemorum* (F.) have been found overwintering under bark of recently felled logs and branches lying in wet situations.

The short-tailed larvae of a non-British species of *Brachypalpus* has been found in the decaying wood of willow trees (on the continent).

The very rare *Caliprobola speciosa* (Rossi) has been reared from a rotten beech stump.

Syritta pipiens (L.) (figs 277–278) breeds in various kinds of decaying organic matter such as manure heaps and the edge of silage clamps where they may occur in very large numbers. They may also be found as saprophages in rotting bulbs (they do not attack healthy bulbs) where they could be confused with *Eumerus* larvae (see above).

The puparium of *Tropidia scita* (Harris) was found among flood refuse by Lundbeck (1916) and an American species has been reared from human excrement near the mouth of a sewer and also in masses of rotting potatoes.

Pocota has a short-tailed larva which has been found in rot-holes high above the ground in various trees (Aubertin, 1928). *Criorhina berberina* (F.) has been reared from the slimy decay at the base of a fallen birch (*Betula*) trunk. The larva appears to be of the short-tailed type, whereas the larvae of some North American species are rat-tailed.

The early stages of *Blera fallax* (L.) are unknown but females have been seen laying eggs in sap exuding from beech and oak trees.

Merodontini. *Merodon equestris* (F.) is the large bulb fly (or Narcissus fly), the larvae (figs 279–280) of which attack narcissi and various other bulbs and can be a major pest to growers (see also *Eumerus*, the lesser bulb flies, above). Larvae have also been found in bulbs of the blue-bell (*Endymion nonscriptus* (L.)). Hodson (1932b) gives an account of the biology. Eggs (fig. 1012) are laid on the neck of the bulb or on its dying leaves.

Eristalini. The genera of this tribe have larvae of the rat-tailed maggot type (fig. 281), which may be separated by the following simplified key (Hartley, 1961 and Dolezil, 1972 provide keys to some species):

1 Pubescence absent on dorsum of last six abdominal segments. Anterior spiracles especially long and pointed. Exclusively in tree rot-holes high above the ground and rarely seen until trees are felled . . . . *Mallota*

— Pubescence usually present on dorsum of abdominal segments. Anterior spiracles shorter. Larvae usually found in aquatic or semi-aquatic situations with high organic content occasionally in more accessible tree rot-holes 2

2 Abdominal prolegs with stout well sclerotized crochets in two distinct semicircular rows; anterior spiracle pale brownish . . . . *Myathropa*

— Abdominal prolegs with crochets in more than two distinct rows which are not semicircular on first three abdominal segments; if crochets tend to be in two rows then the anterior spiracles are dark brown 3
3 Tracheal trunks undulating (as seen through cuticle) . . . . *Helophilus*
— Tracheal trunks straight . . . *Parhelophilus, Anasimyia, Lejops, Eristalis, Eristalinus*

Mallota cimciciformis (Fallén) is another tree hole breeder, usually in elm or horse-chestnut, usually at a considerable height from the ground, and therefore rarely encountered until trees are felled.

Larvae of *Myathropa florea* (L.) are found in rot holes and leaf-filled water pockets in trees, especially beech, and also in wooden water butts with an accumulation of decaying leaves at the bottom.

Helophilus pendulus (L.) usually breeds in farmyard drains, very wet manure, decomposing silage etc. (sometimes in company with *Eristalis*). *H. hybridus* Loew and species of *Parhelophilus* and *Anasimyia* occur in ponds with a dense stand of *Typha* (reed mace). The larva of the rare *Lejops vittata* (Meigen) is unknown but should be sought in coastal marshes with growth of *Scirpus maritimus* among which adults have been found.

Eristalis tenax (L.) breeds in places with a high animal sewage content such as farmyard drains. It also breeds in the liquid putrefaction from carcases and (because of the bee-like adult) is the so called oxen-born bee of the ancients, which is shown coming from a lion carcase on the tin of a well known brand of golden syrup, accompanied by the quotation (from Samson) 'Out of the strong came forth sweetness' (see also Medical & Veterinary section). *E. pertinax* (Scopoli), *E. nemorum* (L.), *E. arbustorum* (L.) and *E. intricarius* (L.) breed in organically polluted (cattle droppings, etc.) drains and pools. Larvae of *E. abusivus* Collin have been found in mud at the edge of a moorland pond. The immature stages of other species require investigation.

Eristalinus sepulchralis (L.) occurs in ponds with a large amount of decayed vegetation, but usually with little sewage contamination. *E. aeneus* (Scopoli) occurs in seashore pools containing rotting seaweed.

Series **Schizophora**

Acalyptratae

Conopidae

(Figs: larvae 282–292, eggs 1013–1016, pupa 1165)

About 800 species of Conopidae in 47 genera have been described throughout the world and 25 species representing 7 genera in 2 sub-families occur in Britain. The British representatives of the family are internal parasites of adult bees and wasps. The immature stages are poorly known and only 4 British species in 4 genera have been described in the larval stage. The biology and known host records for world species are reviewed by Smith (1966) and other papers are cited below. Smith & Peterson (1987) provide keys to genera for the eggs and larvae so far described.

Conopinae. Larval mouthparts and posterior spiracles of *Conops vesicularis* L., recovered from the puparium, are described by Dušek (1964) (fig. 285). This species parasitises *Bombus muscorum* (L.). Host records for other British *Conops* species are *C. flavipes* L. on *Bombus lapidarius* (L.) and *Osmia*, and *C. quadrifasciatus* De Geer also on *Bombus lapidarius*. The hosts of *C. strigata* Wiedemann and *C. ceriaeformis* Meigen are unknown.

The hosts of the two British species of *Leopoldius* are unknown but the adults often occur on ivy blossom among wasps (*Vespula*) and on the continent *L. coronatus* Rondani has been seen ovipositing on and has been reared from *Vespula germanica* (F.).

Physocephala rufipes (F.) is parasitic on *Bombus* species. De Meijere (1912b) reared this species from *Bombus pascuorum* (Scopoli) (=*agrorum* (F.)) and *B. lapidarius* and described the immature stages. Cumber (1949) reared it from six species of *Bombus* in the London area and found that up to 13% of individuals of some species were parasitized. *P. nigra* (De Geer) is parasitic on *Bombus muscorum*.

Myopinae. De Meijere (1912b) described the immature stages of *Zodion cinereum* (F.) (figs 286–287) which he reared from *Hylaeus quadricinctus* (F.), *Halictus rubicundus* Christ and *Lasioglossum nigripes* Lepeletier (=*H. nylanderi* Pérez). In Russia the species has been recorded from the honey-bee, *Apis mellifera* L. (Zimina, 1968).

The larva of *Myopa* is unknown and the hosts of the 10 British species are unrecorded. However, in the British Museum (Natural History) collection there is a specimen of *M. fasciata* Miegen labelled 'Host: *Andrena cetii* Schrank=*marginata* Fab.' 'England: Devon, Bovey Tracey, ix.19?, R. C. L. Perkins (BM 1942–95)'. On the continent unidentified or non-British members of the genus have been reared or associated with species of *Eucera, Bombus, Andrena, Colletes* and *Vespula*.

The larva of *Thecophora* (figs 289–292) has been described only for a Nearctic species (Smith, 1966) associated with various *Halictus* and *Lasioglossum* species. In Britain *T. atra* (F.) and *T. fulvipes* Robineau-Desvoidy, and on the continent *T. pusilla* (Meigen), have all been found among *Halictus* colonies. In Russia two (non-British) species are recorded from the honey-bee, *Apis mellifera* (Zimina, 1968).

De Meijere (1912b) described the larva of *Sicus ferrugineus* (L.) (fig. 288) which has been recorded from seven species of *Bombus* on the continent.

Tephritidae

(Figs: larvae 293–314, eggs 1017–1020, puparia 1166–1168, mines 1293–1295, galls 1316–1317)

The Tephritidae (=Trypetidae) (fruit flies) contains some 4,500 species and of all the families of Diptera is said to cause the most economic damage to plants.

The larval habits of Tephritidae fall into four major groups as follows:

1. Developing in flower heads (mostly Compositae—thistles, sow-thistles, hawkweeds, etc.), e.g. *Urophora, Myopites, Xyphosia, Trupanea, Ensina, Noeeta, Tephritis*, etc.
2. Leaf-miners, e.g. *Euleia, Trypeta, Vidalia, Myoleja.*
3. Developing in stems or roots, e.g. *Oxyna, Campiglossa, Cerajocera, Dithryca, Platyparea, Platyparella.*
4. Developing in fruits, e.g. *Rhagoletis, Anomoia, Ceratitis*, etc.

Some of the non-British pest species are included below as they are frequently found in imported fruit and sent to entomologists for identification. There are 76 native British species representing 33 genera and 3 subfamilies.

A useful summary of the biology of fruit flies is provided by Christenson & Foote (1960). Phillips (1946), Varley (1937), Persson (1963), Dirlbeck & Dirlbeck (1962), Kandybina (1977) and G. H. Berg (1979) are useful for the identification of some Tephritid larvae that occur in Britain and further information, full host plant lists and some keys (to puparia) are provided in the British *Handbook* to the family (White, 1988). Although the host plants of most British species are known the immature stages of many are still inadequately described or unknown. Since White (1988) gives such a detailed treatment of the family my comments on host-plants and biology are restricted to the more frequently encountered genera and species, including those of economic importance.

Trypetinae

Ceratitini. *Ceratitis capitata* (Wiedemann), the well-known Mediterranean fruit fly, is not a native British species but its larvae (figs 293–296) occur in cherries, plums, peaches, apricots, pears, oranges and tomatoes imported into this country. Other non-British Tephritidae, e.g. *Dacus, Anestrepha*, occurring in imported fruits may be identified with the work of Berg (1979) and British records are discussed by White (1988) (see also *Rhagoletis cerasi* (L.) below).

Trypetini. *Anomoia* (= *Phagocarpus*) *purmunda* (Harris) larvae are found in the fruits ('haws') of hawthorn but also occur in the berries of *Berberis, Pyracantha* and *Cotoneaster. Platyparella discoidea* (F.) is said to occur in the stems of *Campanula latifolia* L. *Platyparea poeciloptera* (Schrank) is the horticulturalist's asparagus fly, the larvae (figs 297–299) of which damage the stems of asparagus (Lesne, 1913) (fig. 1293) though no attacks have been reported in Britain since the 1930s. *Euleia heracleii* (L.) is the celery fly, of economic importance to horticulturalists, the larvae of which, in addition to celery (*Apium graveolens* L.) also mine the leaves of parsnip (*Peucedanum sativum* Bentham & Hooker), *Heracleum sphondylium* L., *Sium latifolium* L., *Angelica sylvestris* L. and other Umbelliferae. *Acidia cognata* (Wiedemann) larvae mine the leaves of *Tussilago farfara* L. and *Petasites ovatus* Hill.

Trypeta and *Vidalia* species mine leaves of *Artemisia, Eupatorium, Senecio*, etc. *Rhagoletis alternata* (F.) larvae occur in the fruits ('hips') of wild and cultivated roses. *R. cerasi* (L.) is the European cherry fly and its larvae (figs 304–306) are frequently found in imported cherries. Larvae of *Gonioglossum wiedemanni* (Meigen) are found in the berries of *Bryonia dioica.*

Euphrantini. The larva of *Euphranta toxoneura* (Loew) is one of the very few tephritids that departs from the phytophagous habit and lives as a predator/brood parasite in sawfly galls of the genus *Pontania* (Kopelke, 1984, 1985).

Terelliini. Larvae of *Chaetostomella cylindrica* (Robineau-Desvoidy) occur in the flower-heads of *Centaurea. Chaetorellia* and *Cerajocera* larvae (figs 311–312) are found in the flower-heads of *Centaurea* and the latter also in *Arctium.* The larva of *Cerajocera ceratocera* Hendel has a very characteristic anal plate (fig. 312).

Larvae of *Orellia falcata* (Scopoli) are found in the root-stock of *Tragopogon pratense* L.

Terellia species occur in flower-heads as follows: *T. colon* (Meigen) in *Centaurea scabiosa* L.; *T. ruficauda* (F.) in *Cirsium; T. vectensis* Collin on *Serratula tinctoria* L.; *T. winthemi* (Meigen) on *Carduus acanthoides* L.

Xyphosia miliaria (Schrank) occurs in flower-heads of *Cirsium.*

Myopitinae

The larvae of *Urophora jaceana* (Hering), the knapweed gall fly (figs 307–310), form galls (fig. 1317) in the flower-heads of *Centaurea nigra* L. and this was the subject of a classical ecological study by Varley (1947). For many years *U. jaceana* was erroneously recorded as *U. solstitialis* (L.) which inhabits galls on *Carduus nutans* L. *U. cuspidata* (Meigen) and *U. quadrifasciata* (Meigen) also occur in the flower-heads of *Centaurea. U. spoliata* (Haliday) lives in the flower-heads of *Serratula tinctoria, U. stylata* (F.) in galls in flower-heads of *Cirsium vulgare* (Savé) Ten. and *U. cardui* (L.) forms galls on the stems of *Cirsium.*

Our two *Myopites* species form hard galls in the flower-heads of *Pulicaria dysenterica* L. and *Inula crithmoides* L. *Ensina sonchi* (L.) occurs in the flower-heads of a range of plants including *Hypochaeris, Sonchus, Picris, Leontodon, Tragopogon, Aster*, etc.

Tephritinae

Dithrycini. The larva of *Dythryca guttularis* (Meigen) forms a gall at the stem base of *Achillea millefolium* L. *Noeeta pupillata* (Fallén) is found in the swollen flower-heads of *Hieracium* spp.

Tephritini. *Icterica westermanni* (Meigen) occurs in the flower-heads of *Senecio* spp. The food-plant of *Acinia corniculata* (Zetterstedt) is probably *Centaurea nigra* (on the continent it has been reared from the related *C. jacea*).

Oxyna flavipennis (Loew) larvae live in fleshy galls on the roots of *Achillea millefolium* L. and those of *O. nebulosa* (Wiedemann) in galls on the rootstock of *Chrysanthemum leucanthemum* L. *O. parietina* (L.) larvae live in galls on the stems of *Artemisia* spp.

Campiglossa grandinata (Rondani) lives in a gall on the stems of *Solidago virgaurea* L. and *C. argyrocephala* (Loew) forms a rosette gall in the flowerhead of *Achillea ptarmica*.

Sphenella marginata (Fallén) is found in the swollen flower-heads of *Senecio* species.

Paroxyna are mostly found in flower-heads: *P. absinthii* (F.) on *Artemisia; P. loewiana* Hendel on *Solidago virgaurea* (L.); *P. plantaginis* (Haliday) on *Aster tripolium* L.; *P. producta* (Loew) on *Sonchus, Hypochoeris, Crepis, Taraxacum, Leontodon*, etc.

Larvae of *Tephritis* species occur in flower-heads of Compositae.

Trupanea amoena (Frauenfeld) occurs in flower-heads of *Lactuca, Picris* and *Sonchus. T. stellata* (Fuessly) is found in flower-heads of *Anthemis, Artemisia, Aster, Centaurea, Crepis, Hieracium, Matricaria* and *Senecio.*

Acanthiophilus helianthi (Rossi) occurs in flower-heads of *Centaurea.*

Platystomatidae

(Figs: larvae 315–321)

This is one of the largest families of Acalyptratae with over 1,000 species of which about 60 occur in the Palaearctic region but only 2 species representing 2 genera occur in the U.K., neither of which is known in the immature stages.

Platystoma seminationis (L.) has been reared from a fungus (*Tricholomopsis rutilans* Quélet). The larva of the European *P. lugubre* (Robineau-Desvoidy) was briefly described by Perris (1856) who found it on soil beneath a piece of dead wood (figs 315–316). Hennig (1945) described larval details from a puparium of *P. euphorbiinum* Enderlein from the Canary Isles (figs 317–319).

Larvae of *Rivellia* species (figs 320–321) have been found feeding on the root nodules of various leguminous plants in Zaire (Seeger & Maldague, 1960) and other countries, but the life-history of the only British species, *R. syngenesiae* (F.), is unknown.

Otitidae

(Figs: larvae 322–337, eggs 1021–1022, puparia 1169)

Over 500 species of Otitidae have been described throughout the world. The little that is known of their biology is summarised by Allen & Foote (1967). The immature stages have been found in decaying or damaged vegetable substances and in animal faeces. Twenty-one species in 11 genera representing two subfamilies occur in Britain.

Ulidiinae. The larvae of *Physiphora demandata* (F.) (figs 322–324) have been found in corn silage, clover fodder, rotting narcissus bulbs and dung (Allen, E. J. & Foote, 1967). The immature stages of *Ulidia erythrophthalma* Meigen and our two *Homalocephala* species are undescribed but puparia of *H. albitarsis* Zetterstedt have been found under the bark of dead and dying coniferous trees in Sweden.

Otitinae. The larva of *Myennis octopunctata* (Coquebert) (figs 325–328) was described by Vos de Wilde (1935) from larvae found under the bark of dead trees.

Seioptera vibrans (L.) has been reared from manure, decaying fruit, vegetables, narcissus bulbs, onions and dung. The larvae (figs 329–331) have been described by Lobanov (1958) and Allen & Foote (1967). The immature stages of *Herina* (7 British species) are unknown.

The larva of *Ceroxys urticae* (L.) (figs 332–335) has been found in manure and decaying vegetation and is described by Lobanov (1964).

Melieria species are unknown in the immature stages, as is the larva of *Tetanops myopinus* Fallén. The adult of *T. myopinus* is rarely seen in this country but occurs in coastal areas and has been seen resting on marram grass (Smith, 1955b). In North America *T. myopaeformis* (Röder) (figs 336–337) is an important pest of sugarbeet (Gojmerac, 1956) and *T. luridipennis* Loew has been reared from decaying narcissus bulbs. Lobanov (1972) has described the larva of *T. sintenisi* Becker.

The immature stages of *Otites guttata* (Meigen) and *Dorycera graminum* (F.) are undescribed but the latter is said to oviposit on the 'ovaries' of *Tamus* (Séguy, 1934).

Micropezidae

(Figs: larvae 338–352, puparia 1170–1171)

The Micropezidae contains some 450 species of which 9 species representing 3 genera in 3 subfamilies occur in Britain. The larvae are saprophagous in decaying vegetation and some are phytophagous on the root nodules of leguminous and other plants.

Micropezinae. The larva of *Micropeza corrigiolata* (L.) (figs 338–342) has been described by Müller (1957). They bore into the root nodules of leguminous crops, e.g. field pea (*Pisum arvense* L.), red clover (*Trifolium pratense* L.) and alfalfa (*Medicago sativa* L.). The immature stages of *M. lateralis* Meigen are unknown.

Taeniapterinae. The immature stages of the only British species, *Rainieria calceata* (Fallén), are unknown but larval details from a puparium of the Nearctic *R. antennaepes* (Say) found in the crotch of a large American elm have been described (Steyskal, 1964) and are illustrated here (figs 343–345).

Calobatinae. The larvae of *Calobata cibaria* (L.) (figs 346–347) and *C. petronella* (L.) (fig. 351) have been described by Brindle (1965a) from specimens found in a well decayed grass heap. Lobanov (1960) has also described the larva of *C. petronella* from 'refuses and strongly mineralized aggregations of swine manure' from which the third instar migrates into drier adjacent soil areas with decreased organic content for the pupose of hibernation. An interesting feature of the third stage larva of the Nearctic species *C. vittata* (Walker) is the presence of 4 slits in the posterior spiracle (fig. 352). The immature stages of the remaining 4 British species of the genus are unknown.

Megamerinidae

(Figs: larvae 353–354, puparium 1172)

Only 13 species of this family are known, 11 in the Oriental region and 2 Palaearctic species of which *Megamerina dolium* (F.) occurs in Britain.

The larvae live under the bark of dead and dying broad-leaved trees together with the larvae of other xylophilous Diptera and are apparently predaceous or necrophagous. Hennig (1943b) has described the larva of *M. dolium* (figs 353–354).

Tanypezidae

(Figs: larvae 355–360)

Twenty species of Tanypezidae have been described (mostly Neotropical) of which the only Palaearctic species, *Tanypeza longimana* Fallén, occurs in Britain. The larval stages (figs 355–360) have been reared in the laboratory on watermelon rind and pulp from eggs laid by a gravid female from a densely shaded colony of yellow skunk cabbage (*Lysichitum americanum* Hulton & St. John, Araceae) in the U.S.A. (Foote, 1970). None of the larvae formed puparia so it is not certain if they are naturally saprophagous. The species is rare in Britain and has been found among streamside vegetation.

Psilidae

(Figs: larvae 361–372, egg 1023, puparium 1173)

There are about 170 species of Psilidae worldwide of which 55 are Palaearctic and 26 of these species, representing 3 genera, occur in Britain. The larvae are phytophagous, usually boring in the roots of plants, and some are pests. Some species develop under the bark of trees.

De Meijere (1947) described a larva found in the base of a stem of *Juncus* as *Loxocera albiseta* (Schrank) (figs 361–363) but Brindle (1965d) suggests that this description could in fact refer to another *Loxocera* species, possibly *L. ichneumonea* (L.) (= *aristata* (Panzer)). It would be a useful exercise to rear any psilid larvae found in *Juncus* to settle this point, and perhaps elucidate the life-history of other species of the genus which remain unknown.

Psila rosae (F.) is the carrot fly (Ashby & Wright, 1946) which is a well-known pest in most fields, allotments and gardens where the larvae (figs 364–367) mine into the tap roots of carrots and render them unsaleable. Parsnips, turnips and the crowns and basal stems of celery are also attacked as well as wild Umbelliferae (e.g. *Anthriscus, Heracleum*). In carrots *P. rosae* larvae are yellow but from other plants they are white. Hardman *et al.* (1985) provide a bibliography of *P. rosae*. *Psila nigricornis* Meigen is the chrysanthemum stool miner which can be a serious horticultural pest. Under glass *P. nigricornis* and *P. rosae* may attack lettuce following chrysanthemums and celery respectively. *P. nigricornis* may also attack outdoor crops of lettuce (Margaret E. John *pers. comm.*). Osborne (1961) differentiates the larvae and puparia of the two species and notes that *P. bicolor* Meigen and *P. limbatella* (Zetterstedt) have also been found to attack chrysanthemums but unfortunately no larval descriptions of any of these other species of *Psila* occurring in Britain are available. See also *Napomyza* (Agromyzidae).

The larvae of *Chyliza vittata* Meigen (figs 368–372) occur in the stems of orchids (Vos de Wilde, 1935). Other species of *Chyliza* have been reared from orchids but the larvae are undescribed, e.g. *C. extenuatum* (Rossi) from bulbs of broomrape (*Orobanche*); *C. scutellata* F. from stems of the bird's-nest orchid (*Neottia nidus-avis* (L.)) and apparently the larva also causes woody galls on the stems of *Spiraea*. Several species of *Chyliza* have been reared from tree bark, sap or resin in North America and Winter

(1988) describes the larva of *C. fuscipennis* (Robineau-Desvoidy) from resinous wounds on conifers in Britain.

Helcomyzidae

(Figs: larvae 373–379, egg 1024, puparia 1174)

This is a very small family of 12 species found in the Holarctic region and sub-Antarctica (Falkland Is., Tierra del Fuego, S. Chile and Argentina). The larvae develop in rotting seaweeds on the sea shore. Two species representing 2 genera occur in Britain.

The larvae of *Helcomyza ustulata* Curtis (figs 373–375) live in small fairly dry seaweed (wrack) beds lying on the sand in the high tide position (Egglishaw, 1960b). Earlier descriptions of the supposed larva of this species were erroneous (see Egglishaw, 1960b; Smith, 1981).

The immature stages of *Heterocheila buccata* (Fallén) (figs 376–379) are described by Backlund (1945a) and Egglishaw (1960a). The latter gives a full account of the biology and ecology of the species. Larvae of *H. buccata* are found only among the deep stipes of the wrack string (*Laminaria*) which are often partly buried in damp sand. Apparently they do not occur among *Fucus* or the larger wrack beds.

Dryomyzidae

(Figs: larvae 380–384, eggs 1025–1027, puparium 1175)

This little-known family is confined to the Holarctic region and only 15 species have been described of which two, representing one genus, occur in Britain. The immature stages are associated with putrefying matter including excrement, carrion and rotting fungi, usually in woodland. An exception to this is the remarkable North American species *Oedoparena glauca* (Coquillett), the larva of which is a predator of intertidal barnacles (Burger *et al.*, 1980).

The larva of *Dryomyza analis* Fallén (figs 380–384) is described by Smith (1981) from a dead pheasant and the species has also been reared from dead shrews (Disney, 1973) and a dead fox (Smith, 1975). J. K. Barnes (1984) also describes the immature stages and biology in the U.S.A. where it has been successfully reared in the laboratory on hamburger, dead annelids, molluscs, insects, vertebrates and rotting fungi. However larvae failed to reach maturity when fed on rotting grass, decayed pumpkin flesh, decaying lettuce or cow manure. The egg (figs 1025–1026) bears dorsolateral flanges and is particularly well adapted to survive on the type of substrate chosen for oviposition.

D. flaveola (F.) has been reared from human and cow dung but only the egg (fig. 1027) has been described (Hinton, 1960, 1981). It has long anterior horns as do some Drosophilidae.

Chamaemyiidae

(Figs: larvae 385–395, eggs 1029–1030, puparia 1176–1179)

The Chamaemyiidae (silver flies) contain about 183 species with a cosmopolitan distribution. The larvae are important predators of aphids and Coccoidea (Homoptera) including many of the pest species. Twenty-five species representing 4 genera in 2 subfamilies occur in Britain.

Chamaemyiinae. Larvae of *Chamaemyia* feed on coccids living on grasses (Gramineae = Poaceae). In Russia, Tanasijtshuk (1970) has reared *C. geniculata* (Zetterstedt) (fig. 385) from a puparium found in the ovisac of a scale insect on cereal grass roots, and *C. juncorum* (Fallén) (fig. 386) from larvae feeding on scale insects

(*Balanococcus* sp.) on *Festuca ovina* L. (and possibly a *Metadenopus* sp. on *F. ovina* subsp. *sulcata*). Collin (1966) found *C. polystigma* (Meigen) to be predaceous upon *Pseudococcus phalaridis* Green. The immature stages of the remaining British species of the genus are unknown but those of *C. flavipalpis* Haliday should be sought on sandy coasts where the adults occur.

Acrometopia wahlbergi (Zetterstedt) is unknown in the immature stages but is probably predaceous on coccids or aphids on grasses among which the adults are usually found.

The larvae of *Parochthiphila coronata* (Loew) (figs 387–389) were found feeding on the scale insect *Pseudococcus aberrans* Goux in the leaf sheath of couch grass by Tanasijtshuk (1963) in Russia. The same author suggests that other members of the genus should be sought among scale insects in cereal leaf-sheaths and describes a new Russian species from such a situation in reeds.

Leucopinae. Tanasijtshuk (1959), from a study of *Leucopis* species in the Crimea, divides the genus into three biological groups:

1. The eggs are deposited in the colonies of different species of aphids living openly. The larvae crawl on twigs and leaves of the plant and feed on aphids. They pupate either on the plant or in the soil and hibernate as puparia. The number of generations per year is never less than two. *L. melanopus* Tanasijtshuk (fig. 391) belongs to this group.
2. The eggs are deposited inside aphid galls. Both the feeding of larvae on aphids, and pupation, take place inside the galls. The number of generations per year and hibernation habits unknown. *L. palumbi* Rondani (not British) belongs to this group.
3. The eggs are deposited in the ovisacs of coccids. The larvae develop and pupate in the ovisacs. There are two generations per year but hibernation habits are unknown. So far only the subgenus *Leucopomyia* is placed in this group.

A review of the British species including their known biology and habits is given by Smith (1963).

All the British species of *Leucopis* (*s.s.*) (fig. 390) have been reared as follows: *Leucopis albipuncta* Zetterstedt from a bright yellow larva found feeding on aphids on a poppy (specimen in BM(NH)); *L. atritarsis* Tanasijtshuk among aphids on nettles; *L. griseola* (Fallén) (fig. 392) from larvae feeding on the aphid *Eriosoma ulmi* (L.) on elm; *L. melanopus* Tanasijtshuk (fig. 391) feeding on *Dactynotus* sp. on *Lactuca viminae*, on *Brachycaudus cardui* (L.) on *Carduus*, *Aphis laburni* Kaltenbach on *Genista hispanica* L., *Myzus persicae* Sulz on henbane and on aphids from sage (all in the Crimea); *L. morgei* Smith from larvae feeding on the aphid *Myzus ornatus* Laing on *Cydonia speciosa* Sweet; *L. puncticornis* Meigen feeding on *Brachycaudus cardui* on *Cirsium vulgare*, *Microlophium evansii* (Theobald) and *Aphis urticata* Gmelin on *Urtica dioica* L.

Leucopis (Neoleucopis) obscura Haliday feeds on *Pineus (Adelges) pini* (Gmelin in Linnaeus) on Scots pine and the other two British members of this subgenus appear to do the same.

Leucopis (*Leucopomyia*) *silesiaca* Eggers has been reared from among *Eriococcus* sp. on grass and from a hibernating egg mass of *Eriopeltis festucae* (Fonscolombe). Tanasijtshuk (1965) describes the larva (figs 393–395).

Leucopis (*Lipoleucopis*) *praecox* de Meijere feeds on *Pineus pini* on pine trees.

Lauxaniidae

(Figs: larvae 396–405, egg 1028, puparium 1180)

About 1500 species of Lauxaniidae (= Sapromyzidae) have ben described throughout the world. Miller (1977) estimates that of these about 5% have been reared but the immature stages of only about 10 species have been described. The larval stages appear to be mostly saprophagous being found in fallen leaves, straw, rotting wood and birds' nests but a few are phytophagous in root collars, stems, leaves of clover, the ovaries of *Viola* and the leaf-like phylloclades of *Opuntia* cacti. No species appears to have any economic importance which probably explains the neglect of so large a family. I have seen probable lauxaniid larvae from rotting tissue at the base of winter barley stems and from the petiole of oil-seed rape but these appeared to be saprophagous (J. A. Whiteway, pers. comm.). In Britain 46 species occur representing 11 genera. The immature stages and biology are reviewed by Miller & Foote (1975, 1976), and Miller (1977).

The immature stages of *Trigonometopus frontalis* (Meigen) are unknown but may be associated with reeds (*Phragmites*) among which the adults occur.

Minettia inusta (Meigen) has been reared from the nest of a mole; *M. lupulina* (F.) from mines in leaf litter (*Acer, Prunus, Alnus*) and *M. plumicornis* (Fallén) from rotting leaves. The remaining seven British species have not been reared and only *Minettia lupulina* (Holarctic) has been described in the immature stages (Miller & Foote, 1976) and is illustrated here (figs 401–402).

Sapromyza apicalis (Robineau-Desvoidy) has been reared from garden earth; *S. basalis* Zetterstedt from deciduous leaf litter; *S. obsoleta* Fallén from rotting vegetable matter and *S. sordida* Haliday from wrens' nests. Larval habitats of the remaining six British species are unrecorded and none of the larvae have been described. Some larval details of the European *S. quadripunctata* (L.) are very poorly illustrated by Perris (1852) who found the larva in rotting straw.

Peplomyza litura (Meigen) has been reared from a larva mining the withered leaf of crab apple and the larval mouthparts are here illustrated from a puparium among A. H. Hamm's material in the Hope Entomological Collections at Oxford (fig. 400).

Aulogastromyia anisodactyla (Loew) and the rare *Cnemacantha muscaria* (Fallén) are unknown in the immature stages.

Six of the 10 British *Lyciella* species have been reared as follows: *L. affinis* (Zetterstedt) from a rotting birch stump; *L. decempunctata* (Fallén) from thrush and blackbird nests and thistle (*Carlina*) heads; *L. decipiens* (Loew) from rotting leaves; *L. pallidiventris* (Fallén) under rotten bark, garden earth and flood refuse; *L. rorida* (Fallén) from rotting leaves, under bark of decayed tree trunk, earth, moss on rocks; *L. subfasciata* (Zetterstedt) from rotting tree leaves. *L. rorida* (figs 396–399) is the only British species for which the immature stages have been described (Hennig, 1952).

Tricholauxania praeusta (Fallén) has been reared from rotting tree leaves and (?) cow dung.

Larvae of *Calliopum aeneum* (Fallén) have been found in *Viola* ovaries; leaves, stems, bases and root-collars of clover (*Trifolium*); rotting tree leaves and crab apple leaf litter. *C. simillimum* (Collin) has been reared from a robin's nest. Nothing is known of the two remaining British *Calliopum* species and none has been described in the immature stages.

Lauxania cylindricornis (F.) has been reared from witches' broom on black spruce (*Picea mariana* (Miller)) in Canada and Teskey (1976) gives a brief unillustrated description of the larva.

Of the 5 British species of *Homoneura* only *H. notata* (Fallén) has been reared from larvae found in rotting tree leaves. Several Nearctic species have been reared from similar sources (*Acer, Prunus, Alnus*, etc.) and the larva of *H. americana* (Wiedemann) (Nearctic) is illustrated here (figs 403–404).

Coelopidae

(Figs: larvae 406–412, puparium 1181)

The small family Coelopidae (seaweed flies) contains 20 species in about 10 genera and is represented in all regions except the Oriental. The larvae develop in decaying seaweeds on seashores. Although adults may sometimes occur inland in large swarms, attracted to particular chemicals (e.g. trichlorethylene), it is doubtful if they ever breed away from their special seashore niche (Oldroyd, 1954). Only 3 species in 2 genera occur in Britain.

The immature stages of *Malacomyia sciomyzina* (Haliday) are unknown but this species undoubtedly breeds in rotting seaweed where the adults occur sparingly in mostly southern coastal localities.

Egglishaw (1960a) and Burnet (1961) have studied the biology of the two British species *Coelopa frigida* (F.) (figs 406–409) and *C. pilipes* Haliday (figs 410–412). Larvae of both species occur in wrack banks rather than the wrack string, though rarely together and then only a few of *C. pilipes* will be present. *C. frigida* larvae, however, are never found among a large number of *C. pilipes*.

In spite of several detailed studies on wrack fauna (e.g. Backlund, 1945b, Egglishaw, 1960–1961) the establishment of the precise ecological requirements of each species of the several families involved (Coelopidae, Helcomyzidae, Sepsidae (*Orygma*)) still needs refinement and the subject is an excellent one for the purposes of research, teaching and demonstration.

Work on *Coelopa* genetics, started at Newcastle in the late 1950s by Dr Ursula Philip, was continued by Dr Barrie Burnet who is now at Sheffield. Genetic and other studies are also in progress at Nottingham and yielding information on the biology of the immature stages of Ceolopidae (e.g. Butlin & Day, 1984).

Heleomyzidae

(Figs: larvae 413–446, puparia 1182–1183)

This is a cosmopolitan family of over 500 species in some 65 genera of which 56 species in 16 genera occur in Britain. The classification and nomenclature of the family has been considerably revised since the British Check List appeared. Gorodkov (in Soós & Papp, 1984) should now be consulted. Following Gorodkov the genera are grouped here under 3 subfamilies but since so few immature stages are known his tribal classification is omitted.

The fungus hosts of the family are fully listed by Chandler (in Stubbs & Chandler, 1978). Hackman (1963, 1967) records adult Heleomyzidae found in the burrows and nests of small mammals and Hicks (1959–1971) lists those found in birds' nests. An interesting review of the larval habits of Nearctic Heleomyzidae is given by Garnett & Foote (1967). A key to some species (in Russian) is provided by Lobanov (1970c).

Heleomyzinae. The larvae of this subfamily are presumably saprophagous and have been recorded from carrion, faeces, mammals' burrows and birds' nests; they also occur in caves.

Heleomyza serrata (L.) (figs 413–418) has been reared from the fungus *Fistulina* but is usually found in other media, e.g. birds' nests, caves and soil.

Neoleria ruficauda (Zetterstedt) visits fungi and carrion and *N. inscripta* (Meigen) (figs 419–423) although an uncommon fly was reared in numbers from a dead fox (Smith, 1975).

Scoliocentra villosa (Meigen) (figs 424–428) has been reared from dead hens at the entrance to a fox-hole (Skidmore, 1967) and Séguy (1934) records the fly from bat roosts and rabbit holes. The adult has been found in every month of the year, frequently in caves, which has earned it the common name of cave-fly.

Oecothea fenestralis (Fallén) (figs 429–434) is another carrion feeding species found in mammal burrows and caves.

Suillinae. Larvae of this subfamily mostly develop in fungi but on the Continent *Suillia lurida* Meigen is a pest of onion and garlic and is figured here (figs 435–436) as it may be imported. *S. humilis* (Meigen), *S. pallida* (Fallén) and *S. ustulata* (Meigen) have been reared from truffles (*Tuber*). *S. bicolor* (Zetterstedt), *S. fuscicornis* (Zetterstedt) and *S. variegata* (Loew) are polyphagous on many agarics, boleti, etc. Other species appear to be more restricted in the range of their fungus hosts but some have been reared from other pabula, e.g. *S. ustulata* from dead elder stem and *S. variegata* from roots of *Aster*.

Heteromyzinae. *Heteromyza oculata* Fallén has been reared from an unidentified lignicolous fungus.

Tephrochlamys flavipes (Zetterstedt) is recorded from several agarics, soft polypores, *Tuber* and bird and mammal nests; *T. tarsalis* (Zetterstedt) (figs 437–441) from several agarics and birds' nests; *T. rufiventris* (Meigen) (figs 442–446), one of the commonest species of the family, from *Hypoxylon fragiforme* and a wide range of decaying animal or vegetable matter.

Trixoscelidae

This small family was formerly included in the Heleomyzidae and is still regarded as such by some workers. It contains some 70 species mostly found in the Holarctic and Afrotropical regions. Nothing is known of the immature stages but *Trixoscelis canescens* (Loew) was reared from a blackbird's nest by the late E. B. Basden and Dr A. G. Irwin has reared a species from soil derived from feral pigeon guano. Two of the four British species (*T. obscurella* (Fallén) and *T. marginella* (Fallén)) appear to have a coastal distribution (see p. 9).

Chyromyidae

Another small family (about 40 species) which is represented in most regions and in Britain by 6 species in 3 genera. The immature stages are undescribed but the larvae are said to develop in guano near the nests or roosting places of birds, in mammal burrows and under the bark of trees. Dr A. G. Irwin has reared a *Chyromya* from damp droppings of Daubenton's bat.

Ardö (1957) regards *Chyromya minima* (Becker) as restricted to sand-dunes and Séguy (1934) regards *C. flava* (L.), *C. oppidana* (Scopoli) and *Gymnochyromyia inermis* Collin as cave-dwellers (troglobionts) and birds' nests dwellers (nidicoles). Hicks (1959) records *C. flava* and *G. inermis* from birds' nests ('owl'; and wren, hedge-sparrow, blackbird, greenfinch, etc., respectively). Adults of *Aphaniosoma socium* Collin and *A. propinquans* Collin are recorded from sea-shore flowers (*Convolvulus* and *Matricaria*).

Sepsidae

(Figs: larvae 447–474, eggs 1031–1033, puparia 1184–1185)

This family contains some 240 species in 21 genera and is well represented in all the zoogeographical regions. Their wide distribution is undoubtedly due to their close association with animal faeces in which they mostly breed. Twenty-seven species in 6 genera are known from the British Isles.

The larvae of several species have been described by Hennig (1949), Schumann (1962), Brindle (1965b), Mangan (1977) and Ozerov (1986). Pont's (1979) *Handbook* to adults includes a substantial section on the life histories and immature stages.

Orygma luctuosum Meigen (figs 447–450) breeds on the sea-shore in the smaller drier beds of decomposing wrack and was until recently included in the Coelopidae.

Saltella sphondylii (Schrank) (figs 451–453) breeds in cow dung.

Little is known of the biology and immature stages of the 11 British species of *Themira*, but probably most develop in mud alongside ponds and streams, especially if this is enriched with dung or sewage effluent. *T. putris* (L.) (figs 454–456) and *T. nigricornis* (Meigen) have been recorded from human excrement and the former breeds in the sludge and seepage from sewage works and can produce vast numbers of adults which may become a nuisance by invading nearby houses. Larvae of *T. annulipes* Meigen occur in soil especially if enriched by cattle droppings, sewage overflows, etc. *T. minor* Haliday occurs in cow dung and trampled dung and soil from cattle feeding pens. *T. leachi* (Meigen) probably breeds in cow dung upon which the females may frequently be seen and it has been reared from manured soil, human excrement and grass cuttings. *T. nigricornis* has also been reared from garden soil and dung (human and chicken) and *T. putris* has been reared from birds' nests. Adults of *T. biloba* Anderson, recently added to the British List (Pont, 1986) were swept off guano on a coot's nest. *T. lucida* Staegar and *T. superba* Haliday seem also to be associated with waterfowl droppings though the immature stages are unknown. Abroad several species have been reared from the dung of cows, pigs, humans and small mammals.

The rare *Meroplius minutus* Wiedemann (=*stercorarius* Robineau-Desvoidy) (figs 457–460) has been reared from human faeces, cow, pig and (accumulations of) rabbit dung.

Nemopoda nitidula (Fallén) (figs 461–465) has been reared from human excrement, dead snails, carrion and (mainly rotting) fungi.

All *Sepsis* species (figs 466–474) breed in mammal dung, preferably cow dung, but also including horse dung (*S. fulgens* Meigen, *S. violacea* Meigen), chicken dung (*S. violacea, S. fulgens*), pig dung (*S. fulgens, S. punctum* (F.), *S. violacea*), human faeces (*S. punctum*), sewage and pig swill (*S. fulgens*), sheep dung (*S. cynipsea* (L.), in upland areas), small mammal droppings (*S. punctum, S. neocynipsea* Melander & Spuler, the latter also allegedly in small mammal carrion).

The eggs of Sepsidae (figs 1031–1033) have long respiratory horns (*Orygma* has 2) often much longer than the egg itself. All are plastron bearing (except *Saltella*) and are adapted for atmospheric respiration and for extracting dissolved oxygen from ambient water when the egg is submerged (Hinton, 1960, 1961, 1981).

Sciomyzidae

(Figs: larvae 475–518, eggs 1034–1036, puparia 1186–1189, cover)

Over 470 species of Sciomyzidae (snail killing flies) have been described throughout the world. C. O. Berg & Knutson (1978) provide a useful summary of the state of knowledge of the biology and systematics of the family which has increased rapidly over the past 30 years.

The discovery that their larvae feed on living aquatic and terrestrial molluscs gave them a medical and veterinary significance in the possible control of schistosomiasis (in Africa, South America and the Far East) and other snail-borne diseases. The natural food of over 200 species is now known and the immature stages of many species have been described in detail.

The larval morphology reflects their mode of life. Free-living larvae have wart-like tubercles on the body and elongate lobes on the anal segments. Aquatic forms have conspicuous branched float hairs on the posterior spiracular plate. Larvae living as parasitoids have a mostly transparent integument without conspicuous tubercles but with a transverse patch of spinules on each segment of the body.

Sixty-five species in 23 genera representing 3 subfamilies occur in Britain. Rozkošný (1967) provides keys to larvae and puparia of some genera and species.

Salticellinae. *Salticella fasciata* (Meigen) (figs 475–479) was the first species of the family to be associated with molluscs when Perris (1850) reared adults from puparia found in the shells of *Theba pisana* (Müller). Knutson, Stephenson & Berg (1970) described the immature stages and recorded them from several species of snails found on dunes or in dry habitats (e.g. *Theba pisana, Helicella candicans* (Pfieffer), *H. virgata* (de Costa) and *H. hortensis* (Müller), all Helicellidae) on which they may feed as solitary, internal parasitoids or they may be saprophagous on dead tissue.

Phaeomyiinae. Nothing is published on the biology or immature stages of the two British species of *Pelidnoptera*, but Dr Peter Baily has recently reared a species from millipedes in Portugal.

Sciomyzinae

Sciomyzini. *Colobaea bifasciella* (Fallén) has a highly specialized parasitoid larva which feeds as a solitary individual and each larva consumes only one snail. One or two eggs are laid across the sutures of the shell of exposed *Lymnaea palustris* Müller or *L. trunculata* Müller. The larva enters the shell and feeds on the mucus, extra pallial fluid, or the less vital tissues. Later the vital tissues are consumed, the snail dies and the larva consumes the decaying tissues; then, after about 25 days, it pupates within the shell. The adult emerges some two or three weeks later. Although more than one egg may be laid only one larva feeds and it is thought that it kills any other larvae as they enter the shell.

C. punctata (Lundbeck) has been recorded from *Planorbis albus* Müller, *Lymnaea peregra* (Müller) and young *P. corneus* (L.). *C. pectoralis* (Zetterstedt) and *C. distincta* (Meigen) (fig. 480) have been reared from *Anisus vortex* (L.) and *A. spirorbis* (L.) respectively.

Of the 16 species of *Pherbellia* occurring in Britain the life histories and immature stages of 9 species have been described (Bratt *et al.* 1969). Eggs are laid in mosses, etc. and the larvae seek out and may eat up to 4 snails during their development.

Most of the common species of *Pherbellia* feed on hygrophilous and exposed aquatic snails, whereas the uncommon species eat terrestrial snails.

Some snails eaten in natural conditions are indicated as follows:- Terrestrial species: *Pherbellia dubia* (Fallén) (figs 482–483) (*Cochlicopa, Discus, Hygromia, Oxychilus, Retinella*); *P. knutsoni* Verbeke (*Cochlicella, Helicella*); *P. scutellaris* (von Roser) (*Clausilia*). Aquatic and hygrophilous species: *Pherbellia dorsata* (Zetterstedt) (*Planorbis*); *P. schoenherri* (Fallén) (fig. 481) (*Succinea*); *P. scutellaris* and *P. ventralis* (Fallén) (figs 484–485) (*Lymnaea*). Full lists including snails eaten or rejected in laboratory conditions are given by Bratt *et al.* (1969) and O. Beaver (1972) gives further information on some British species.

The larvae of *Pteromicra* species are polyphagous predators of small aquatic and hygrophilous, non-operculate snails and may kill and consume up to 3 snails during their development. The common *P. angustipennis* (Staeger) (figs 486–489) feeds on *Planorbis contortus* (L.), young *P. planorbis* (L.), *P. vortex* (L.), *Hygromia hispida* (L.), *Succinea* sp., *Segmentina nitida* (Müller), and *Lymnaea truncatula* (Müller). *Pteromicra glabricula* (Fallén) feeds on *Planorbis vortex, P. contortus*, young individuals of *Physa fontinalis* (L.), *Planorbis planorbis, Lymnaea palustris, L. peregra* (Müller), *L. truncatula*, and the terrestrial snails *Discus rotundatus* (Müller) and *Succinea* sp. *Pteromicra leucopeza* (Meigen) larvae have been found in *Planorbis contortus*, and *Pteromicra pectorosa* (Hendel) feeds on *Segmentina nitida* and *Planorbis vortex*. The immature stages of *Pteromicra* are fully described by Rozkošný & Knutson (1970).

All known larvae of *Sciomyza* feed on terrestrial snails of the family Succineidae and the immature stages are described by Foote (1959). The two British species are known to attack living snails of the genus *Oxyloma* (in Alaska). *Sciomyza simplex* Fallén (figs 490–492) is probably a predator (several attacking more than one snail) rather than parasitoid (one snail per larva) but the feeding status of *S. dryomyzina* Zetterstedt is not yet clear.

The larva of *Tetanura pallidiventris* Fallén (figs 493–494) feeds on terrestrial snails of the genera *Cochlicopa, Discus* and *Retinella* and may have some use as a biological control agent as one of the host snails, *Cochlicopa lubrica* (Müller), is an intermediate host of the sheep lancet fluke, *Dicrocoelium dendriticum* (Rudolphi) (Trematoda). Knutson (1970a) describes the immature stages and biology. Eggs are laid directly onto the retracted soft parts of the host snail. The puparia vary in shape according to whether they were formed inside or outside of the host's shell; and those formed inside vary further with the shape of the host shell. A puparium formed in the elongate shell of *Cochlicopa lubrica* is illustrated (fig. 1188).

Tetanocerini. Larvae of *Antichaeta* feed exclusively on the eggs of snails and appear to be the only insects to do so (though the phorids *Megaselia aequalis* and *M. ciliata* feed on slug eggs and that large and enterprising genus may well possess an as yet undetected snail egg predator). The eggs (fig. 1036) are enclosed in a gelatinous substance and are deposited on egg capsules or egg masses of the snails. *A. analis* (Meigen) larvae feed on the eggs of *Lymnaea truncatula* (and in the laboratory on *L. stagnalis* (L.) and *Succinea* sp.) and *A. brevipennis* (Zetterstedt) (figs 495–498) feeds on egg masses of *Succinea* sp. (and in the laboratory in egg capsules of *Lymnaea truncatula*). Knutson (1966) describes the immature stages and detailed biology of the genus.

Coremacera tristis (Harris) (=*marginata* F.) (figs 499–503) has been reared on a number of terrestrial snails in the laboratory (Knutson, 1973).

Dictya umbrarum (L.) was reared by Lundbeck (1923) from floating puparia and is presumed to attack aquatic snails as do the larvae of some Nearctic species described by Valley & Berg (1977).

Larvae of the genus *Elgiva* (figs 504–506) attack aquatic pulmonate snails of the families Lymnaeidae, Physidae and Planorbidae. The larvae are air-breathers and float just beneath the surface film of quiet waters and they forage in and on *Lemna* mats. They quickly kill snails and commence feeding and when replete move on to other snails; each larva may kill 12–23 snails during its development. The puparia (fig. 1187, cover) are well adapted for flotation and have the posterior spiracles uplifted. Knutson & Berg (1964) describe the immature stages and biology of the genus.

The larvae of *Hydromya dorsalis* (F.) (figs 507–509) are found in shallow, flowing water where they kill and feed upon aquatic pulmonate snails, especially *Lymnaea* spp. (Knutson & Berg, 1963).

Knutsonia species (except *K. lineata*) are also predators of aquatic pulmonate snails and a larva may consume as many as 40 snails during the 21–77 days of its development. The larvae of both British species, *K. albiseta* (Scopoli) and *K. lineata* (Fallén) (figs 510–511) are described by Knutson & Berg (1967) but they were unable to rear *K. lineata* on gastropod molluscs and it has since been established (Foote & Knutson, 1970) that this species is exceptional in feeding only on bivalve clams (*Pisidium*), a habit also shared by the genus *Renocera* (see below). During the 37–53 days of larval life *K. lineata* killed and ate 21–31 individual clams (1·5–4·0 mm in greatest diameter).

The larvae of *Limnia, Pherbina* and *Psacadina* are predaceous on hygrophilous and exposed aquatic snails at the shoreline or on the water surface. Knutson, Rozkošný & Berg (1975) describe the immature stages of *Pherbina* and *Psacadina*. *Pherbina coryleti* (Scopoli), one of the commonest European sciomyzids, is illustrated here (figs 512–514).

The larva of *Renocera striata* (Meigen) is an aquatic predator of sphaeriid clams. The other two British species may also be presumed to be so as Foote (1976) has shown that the habit is shared by American species. *Renocera* and *Knutsonia lineata* (discussed above) are the only insects known to kill and feed on bivalve molluscs. The only other insect found associated with clams is the larva of the chironomid *Glyptotendipes paripes* (Edwards) found between the shell and mantle of *Anodonta cygnea* L. (Beedham, 1966).

Sepedon larvae are predators of aquatic snails and the two British species are included in Neff & Berg (1966).

British representatives of the genus *Tetanocera* include one slug-killing species, *T. elata* (F.) (fig. 515), and two North American species also share this habit (Knutson, Stephenson & Berg, 1965; Rozkošný, 1965; Stephenson & Knutson, 1966). Other members of the genus range over the usually snail-killing habits of the family as follows: *T. ferruginea* Fallén (figs 516–518), *T. hyalipennis* von Roser, *T. robusta* Loew (aquatic snails); *T. arrogans* (Meigen), *T. silvatica* Meigen, *T. unicolor* Loew (hygrophilous and exposed aquatic snails); *T. phyllophora* Melander (terrestrial snails). The biology of *T. punctifrons* Rondani requires description and further elucidation (O. Beaver, 1972).

The biology and immature stages of *Trypetoptera punctulata* (Scopoli) remain unknown.

Nothing is known of the immature stages of the two British species of *Dichetophora* or of *Ectinocera borealis* (Zetterstedt).

The immature stages of *Euthycera fumigata* (Scopoli) are unknown but the larva may attack slugs as the European species *E. chaerophyli* (F.) appears to do (Knutson, 1970b) (see also under *Tetanocera* above).

Much is known of the biology and life-histories of this fascinating family but much detail still needs to be added, particularly on which species of snail are selected as food in the field rather than in the laboratory.

Techniques for laboratory rearing are described by Willomitzer (1970) and Willomitzer & Rozkošný (1977). The distribution of the family in Britain is given by Stephenson & Knutson (1970).

Sphaeroceridae

(Figs: larvae 519–530, eggs 1037–1042, puparia 1190–1193)

About 1000 species of Sphaeroceridae have been described from all regions of the world. Many anthropophilic species have a wide distribution having been introduced by man into continents in which they are not endemic. Their propensity for breeding in dung no doubt enabled the flies to follow caravan routes overland and shipping routes in the holds of cargo ships carrying cattle and other domestic animals. The larvae are generally saprophagous and in addition to dung will develop in mud, forest litter, fungi, decaying vegetable refuse, seaweed, in caves, in the runs of mammals, in the nests of birds, mammals and insects, and in carrion.

Some 114 species in 33 genera and 3 subfamilies occur in Britain. The immature stages are not well known and there are more descriptions of the distinctive puparia (figs 1190–1193), (Goddard, 1938; Okely, 1974) than any other stage. Puparia are frequently found during archaeological excavations (see section on fossils). Some larvae have been described by Schumann (1962), and Pitkin (1987) reviews and reproduces illustrations of most of the described immature stages of the family in his *Handbook* to the British species. Carrion and dung frequenting species of possible forensic significance are discussed by Smith (1986b). An American species has been involved in a case of human intestinal myiasis (Micks & McKibben, 1956).

The following comments are confined to actual field rearing records since the adults are frequently found on media in which they do not necessarily breed. Pitkin (1987) should be consulted for a review of adult habits. In the laboratory boiled grass-cuttings have proved a successful medium on which to rear larvae when their natural pabulum is unknown.

Sphaerocerinae. *Sphaerocera curvipes* Latreille (fig. 519) is a common species that has been reared from cow dung and human excrement. *Ischiolepta pusilla* (Fallén) has been reared from human excrement and dead snails. *Lotobia pallidiventris* (Meigen) has been reared from cow-dung.

Copromyzinae. *Lotophila* (= *Copromyza*) *atra* (Meigen) (figs 520–522) has been reared from cow-dung. *Crumomyia nitida* has been reared from horse-dung and fungi; *C. pedestris* (Meigen) has been reared from dead snails. *Copromyza similis* (Collin) has been reared from cow-dung, *C. equina* Fallén from horse and cow-dung and *C. stercoraria* (Meigen) from human excrement.

Limosininae. The following species breed in cow dung: *Coproica acutangula* (Zetterstedt) (figs 523–524), *C. lugubris* (Haliday), *C. vagans* (Haliday), *Elachisoma aterrima* (Haliday), *Halidayina spinipennis* (Haliday), *Chaetopodella scutellaris* (Haliday) (figs 525–526), *Limosina silvatica* (Meigen), *Opalimosina collini* (Richards), *O. denticulata* (Duda), *Spelobia clunipes* (Meigen), and *Telomerina pseudoleucoptera* (Duda). Of these, *Coproica vagans* and *Limosina silvatica* (fig. 527) have also been reared from human excrement and horse dung respectively.

Leptocera caenosa (Rondani) breeds in human excrement and is particularly associated with water closets where it can occur in large numbers causing a considerable nuisance and health hazard (Fredeen & Taylor, 1964). It has also been reared from wasps' nests.

Leptocera fontinalis (Fallén), *Spelobia palmata* Richards, *S. nana* (Rondani) and *S. luteilabris* (Rondani) have been reared from dead snails. *Spelobia parapusio* (Dahl) (fig. 528) has been reared from fungi. *Apteromyia claviventris* (Strobl) and *Minilimosina fungicola* (Haliday) have occurred in a nest of the ant *Lasius fuliginosus* (L.). The former species has been found in roots of rhubarb and, along with *Pullimosina heteroneura* (Haliday), has also been reared from damaged narcissus bulbs. *Kimosina empirica* (Hutton) has been reared from a dead seal, rabbit corpses, a dead human and in sewage disposal tanks.

Terrilimosina racovitzai (Bezzi) is a cave-dwelling species that may also occur indoors in cellars and has bred in a blocked drain (see introductory section on caves).

Thoracochaeta zosterae (Haliday) (figs 529–530) breeds in seaweed as do other members of the genus; Egglishaw (1961) describes the immature stages in detail.

Pallopteridae

(Figs: larvae 531–538, puparium 1194)

This is a small poorly studied family of only 44 species contained in 8 genera of which 11 species in 2 genera occur in Britain.

The immature stages of *Palloptera usta* (Meigen) and *P. ustulata* Fallén (figs 531–535) were described by Morge (1956) from larvae found under the bark of dead coniferous and deciduous trees in Europe where they were preying upon the larvae of Cerambycidae and Scolytidae (Coleoptera). Morge (1967) has found that the larvae may exert a considerable control of mass outbreaks of bark beetles, especially in mountain forests. Larvae of a North American species have also been reported from the galleries of scolytid beetles and those of a Canadian species prey upon cecidomyiid larvae in Douglas fir cones (Teskey 1976).

Smith (1957a) found larvae of *P. ustulata* under poplar bark and puparia of *P. quinquemaculata* Macquart (figs 536–538) in soil under fool's parsley (*Aethusa cynapium* L.) and dandelion (*Taraxacum*).

Nye (1958) found third instar larvae of *Palloptera quinquemaculata* overwintering in basal tillers of *Arrhenatherum elatius* (L.) (Gramineae) and Stubbs (1969) records rearing and adult associations with Compositae and Umbelliferae.

Nothing is known of the life-history of the rare *Eurygnathomyia bicolor* (Zetterstedt), so far recorded only from Yorkshire.

Lonchaeidae

(Figs: larvae 539–547, cover, egg 1043, puparia 1195–1196)

Some 300 species in 10 genera representing the two subfamilies of this family have been described from all forested regions of the world except New Zealand. Of these, 29 species in 3 genera in two subfamilies occur in Britain. They are not well known in the immature stages but Smith (1957b), Morge (1963) and Mamaev *et al.* (1977) illustrate some of the species occurring in Britain.

Dasiopinae. The larvae of some *Dasiops* species live in galls formed on grasses and others are found under the bark of dead or dying trees, but no British species appear to have been reared.

Lonchaeinae. *Earomyia schistopyga* Collin feeds on the seeds of conifers and some continental species are important pests. Other continental species of *Earomyia* live in male cones of spruce or in floscules of *Cirsium*. The lonchaeid larva recorded by Redfern (1968) from *Cirsium vulgare* heads may belong to this genus, though it was apparently predaceous.

Most *Lonchaea* species (figs 539–547, cover) develop under the bark of dead and dying trees or in decomposed wood: e.g. *L. britteni* Collin, beech; *L. fugax* Becker, poplar; *L. limatula* Collin, beech; *L. palposa* Zetterstedt (figs 540–542), birch, hawthorn, poplar; *L. sylvatica* Beling, poplar. Some species appear to be more or less specifically associated with particular tree species, e.g. *L. collini* Hackman (figs 543–544) is usually found on pines and is a facultative predator of scolytid beetles; *L. peregrina* Becker occurs under bark of *Salix* and poplars. *Lonchaea chorea* (F.) (=*flavidipennis* Zetterstedt) is a synanthropic species which develops in various decaying organic matter and it has been recorded from beetroot, but it is possible that only diseased plants (e.g. eelworm infested) are attacked and that the larvae are introduced in 'manure' (Farsky, 1879; Cameron, 1913). I have also seen *L. chorea* reared from 'stratified *Rosa canina* seed' (K. M. Harris).

Setisquamalonchaea fumosa Egger has been reared from parsnips, turnips, and from the stems of parsley and henbane.

Piophilidae

(Figs: larvae 548–563, egg 1044, puparia 1197–1199)

The family Piophilidae as now understood (McAlpine, 1977) includes the former families Neottiophilidae and Thyreophoridae and contains 67 world species in 23 genera and 2 subfamilies. Thirteen species representing 4 genera and both subfamilies occur in Britain. The subfamilies are separated in the key to families (p. 71).

Neottiophilinae. Only two British species of this subfamily are known, the Palaearctic *Neottiophilum praeustum* (Meigen) and the Holarctic *Actenoptera hilarella* (Zetterstedt).

Keilin (1924a), Tate (1954) and Zumpt (1965) describe the larva of *N. praeustum* (figs 548–551) which is an ectoparasitic bloodsucker on nestlings, usually of the smaller passerine birds forming more open nests e.g. greenfinch, chaffinch, linnet, blackbird, song-thrush, carrion-crow, etc. (with one record from a falconiform, the sparrow-hawk). Unlike *Protocalliphora* which also attacks nestlings, *Neottiophilum* is entirely dependent on blood to complete its development and if present in sufficient numbers may kill the nestlings.

The life-history of *Actenoptera* is unknown.

Piophilinae. *Centrophlebomyia furcata* (F.) (figs 560–563) has not been recorded in Britain since 1910 when Yerbury found adults at Porthcawl, Glamorgan. Previously he had found adults on a dead donkey, Mt Edgcumbe Park, Cornwall in April 1889. In Europe other 'Thyreophoridae' are associated with large skeletons, e.g. horses, donkeys, mules and more rarely on dogs but none had been seen since 1850, in spite of two World Wars, and were thought to be extinct. However, as the flies usually appeared on carcases at cold times of the year as the snows melted, it was thought the entomologists, not normally in the field then, may have overlooked them. This may well be the case as Freidberg (1981) has rediscovered *C. furcata* in Israel on the carcases of goats, cows and sheep during November to January. Eggs are laid on bones and the larvae feed and develop in the marrow. Freidberg has proposed the name 'bone-skipper' for this species since the larvae have the same skipping habit as *Piophila*. Other species have since been discovered in Kashmir and Russia.

The larva of *Piophila casei* (L.) (figs 552–554) is the well-known 'cheese-skipper', a common stored product pest on cheese, ham and bacon and consequently of cosmopolitan distribution. The common name refers to the habits of its skipping escape mechanism which the larva effects by arching its body and grasping the small anal papillae with its mouthparts. When the grip is released the larva is flung into air to a height of 2 or 3 inches and may cover a horizontal distance of several inches. Several species of *Piophila* (including *casei*) feed on carrion in the larval stages and are usually late arrivals in the faunal succession. However this may vary with the species and site of the corpse and can give the larvae a forensic significance (Smith, 1986b). The species most frequently associated with human corpses is *P. foveolata* Meigen (=*nigriceps* Meigen) which is usually found in slaughter-houses, meat factories and poultry farms. *P. vulgaris* Fallén (fig. 559) feeds on dead snails.

There may have been some confusion of the species of *Piophila* associated with carrion in the early literature and it is worth identifying and recording any Piophilidae found on carrion especially if the time of demise of the corpse can be established. A key to larvae is provided by Brindle (1965c) and Smith (1986b) but the anterior spiracles (figs 554–558) afford a ready means of identifying the most common species. However, as always, it is best to rear samples through to the more readily identifiable adult stage during research projects.

Opomyzidae

(Figs: larvae 564–577, eggs 1045–1046, puparia 1200–1201)

A small family of over 40 species mostly found in the temperate regions of the northern hemisphere with a few species in East and South Africa. Fourteen species in two genera occur in Britain. Some larvae and life-histories are described by Thomas (1933–1938) and Nye (1958). The known larvae live in the stems of Gramineae.

Of the eight British species of *Geomyza* three are known in the immature stages. Larvae of *G. balachowskyi* Mesnil (figs 567–568) overwinter in the basal tillers of *Holcus lanatus* L. and *H. mollis* L.; they pupate in April and adults emerge in May and there is probably a second generation. *Geomyza tripunctata* Fallén larvae (figs 564–566) overwinter in the basal tillers of *Lolium multiflorum* Lamarck and to a lesser extent in *L. perenne* L., *Dactylis glomerata* L., *Poa trivialis* L., *P. annua* L. and wheat. They pupate in March, emerge in April and oviposit in early May. A second generation emerges in July, oviposits in August, giving rise to the overwintering larvae. *Geomyza venusta* (Meigen) is found in *Bromus*.

Larvae of three of the six species of *Opomyza* have been reared. *Opomyza petrei* Mesnil (figs 569–571) overwinters in *Holcus lanatus* and *Anthoxanthum odoratum* L.; *O. florum* (F.) (figs 572–575) can be a serious pest of cereals, particularly winter wheat (especially in Russia). It differs from other members of the family in overwintering in the egg stage which hatches at the end of March and the larva bores into wheat tillers. Pupation occurs during May and the adult emerges in early June. Oviposition occurs again in October and early November. Eggs are laid on the soil close to the winter wheat. The wild hosts are not known. *Opomyza germinationis* (L.) (figs 576–577) overwinters as a third instar larva in the basal tillers of *Festuca, Lolium, Poa, Agrostis, Phleum, Alopecurus, Phalaris* and, to a lesser extent, in *Holcus*.

Clusiidae

(Figs: larva, 578, puparia 1202–1205)

Over 200 species of Clusiidae have been described from most regions of the world. Ten species representing 4 genera occur in the British Isles. Little is known of the immature stages which all appear to develop in rotting wood. The larvae are said to be able to skip in a manner similar to Piophilidae.

Clusia flava (Meigen) has been reared from a dry beech stump (Smith, 1950). There are also two puparia in the British Museum (Nat. Hist.) from a rotten birch stump. Unfortunately, the caps containing the mouthparts have not survived from any of the puparia available so I am unable to figure them. The characteristic 'horned' puparium is illustrated (fig. 1202).

Clusiodes albimana (Meigen) (figs 1203, 1205) has been reared several times from old logs and mossy tree stumps but in the puparia examined the ventral part of the cap, with the mouthparts, has been missing.

There is a specimen of *Clusiodes gentilis* (Collin) with a puparium, 'bred from a log' by H. Oldroyd in the British Museum (Nat. Hist.), but the half of the puparial cap with the mouthparts is missing. However, Séguy (1934) gives an outline of the mouthparts which are illustrated here (fig. 578). Also in the BM (NH) collections is a specimen of *Clusiodes (Columbiella) verticalis* (Collin) with a puparium (fig. 1204), from 'old grass heap, back cottage garden'.

Odiniidae

(Figs: larvae 579–585, puparium 1206)

Some 63 species in 10 genera of Odiniidae are known throughout the world. Of these the larval habits of only 10 species are known and all are associated with wounded, dead or dying trees. These have mostly been associated with the galleries of wood boring beetles (Buprestidae, Curculionidae, Scolytidae, Tenebrionidae, Oedemeridae), but some occur in the galleries of Diptera larvae (Hesperinidae, Pachyneuridae) and Lepidoptera (Cossidae, Gelechiidae). Most are considered to be saprophagous, or possibly feed on frass or dead insects. An American species (*Odinia conspicua* Sabrosky) is apparently predaceous on Tenebrionidae (Col.) in decayed poplar. The Asian species *Turanodinia coccidarum* Stackelberg was reported to have been reared from egg-masses of *Pseudococcus comstocki* Kuwana.

Seven species occur in Britain, all belonging to the genus *Odinia*, four of which have been reared.

The larva of *Odinia xanthocera* Collin (figs 582–585), described by Vos de Wilde (1935), is associated in Europe and North America with the weevil *Cryptorhynchus lapathi* (L.), which mines twigs of *Alnus, Salix* and *Populus*. *Odinia meijerei* Collin (figs 579–581) is found on diseased elm trees in the tunnels of *Scolytus* (Lewis, 1979). Larvae of *O. pomona* Cogan have been found under bark on apple. *Odinia ornata* Zetterstedt occurs in beetle galleries on spruce in the USSR. *Odinia hendeli* Collin occurs in elm with larvae of Oedomeridae (Col.). *Odinia maculata* (Meigen) has been found in oak infested with *Cossus* (goat moth) larvae.

Krivosheina (1981) reviews the systematics and biology of the Palaearctic species.

Carnidae

(Figs: larvae 586–589, egg 1047, puparia 1207–1208)

Some 70 species of Carnidae have so far been described and include some of the smallest Acalyptrates. They are mainly Palaearctic or Nearctic, some Holarctic in distribution with very few occurring in other regions. The larvae live in birds' nests where they are saprophagous to semi-parasitic (*Carnus*, 1 British species) or saprophagous (*Meoneura*, 12 British species). Very little is known of the immature stages.

The larvae of *Carnus hemapterus* Nitzsch are found in the nest debris of a number of birds including starling, hedge-sparrow, blackbird, kestrel and great spotted woodpecker. The tiny adults are blood sucking parasites of birds and break off their own wings after settling down in the plumage of nestling birds. De Meijere (1912a) and Engel (1930) give partial descriptions of the immature stages (figs 1047, 1207).

Meoneura species are associated with birds' nests as follows: *M. lamellata* Collin (crow, great tit, magpie, sand-martin, starling, 'thrush', etc.); *M. neottiophila* Collin (kestrel, sparrow-hawk, stock-dove, wren); *M. obscurella* (Fallén) (blackbird, sand-martin, 'finch', 'thrush'); *M. lacteipennis* (Fallén) and *M. vagans* (Fallén) (sand-martin); *M. seducta* Collin (herring-gull).

Meoneura species are also believed to develop in animal excrement and carrion on which adults are sometimes found. In France *M. exigua* Collin has been reared from a damaged puparium of *Sarcophaga*.

Acartophthalmidae

Only three species in one genus (*Acartophthalmus*) of this family are known, two Holarctic and one Palaearctic. The two Holarctic species occur in Britain. Adults have been found on decaying fungi, dung and carrion. Ozerov (1987) found eggs on carrion and reared larvae on meat in the laboratory.

Periscelididae

(Fig. 593, larva)

About 20 species of Periscelididae are known from the Nearctic, Palaearctic and Neotropical regions. Four species of *Periscelis* occur in Britain.

The life-histories and immature stages were unknown until very recently, when it was established that the larvae develop in the sap of tree wounds. The larva superficially resembles a *Fannia* (Fanniidae) and is illustrated (fig. 593) here from a figure appearing in Teskey (1976). Dr Tony Irwin has found larvae of *Microperiscelis annulata* (Fallén) in ash seepage in Norwich.

Aulacigastridae

(Figs: larva 590–591, egg 1048, puparium, 1210)

This is a small and little-known family of about 4 species in 3 genera represented in the major zoogeographical regions except the Australian and Pacific. Only one species occurs in Britain.

The larvae of *Aulacigaster leucopeza* (Meigen) develop in sap fluxes exuded from tree wounds. Robinson, I. (1953) describes the immature stages. At pupation the prothoracic spiracles are completely everted and protrude from the surface of the slime flux in which the puparium is submerged.

Stenomicridae

(Figs: larva 592, egg 1049, puparium 1209)

The problematic and little-known genus *Stenomicra* has recently been given family status in the Palaearctic Catalogue. The genus contains some 20 described species and is represented in all the major zoogeographical regions. Only one British species was known until Irwin (1982) described a second from Wales. Irwin also discusses the taxonomic peregrinations of the genus. Nothing is known of the life-history or immature stages of the five Palaearctic species. Williams (1939) records larvae in water-holding leaf bases of Gramineae (Poaceae) and other plants in Hawaii (fig. 592).

Anthomyzidae

(Figs: larvae 594–606)

The family Anthomyzidae is represented in all zoogeographical regions by a total of about 60 species. Sixteen species in 4 genera occur in Britain.

The larvae develop between the closely fitting leaf sheaths of water-loving Gramineae and occur in the galls formed by *Lipara* (Chloropidae). One species has been reared from fungi.

The larvae of *Anthomyza* (= *Stiphrosoma*) *sabulosa* (Haliday) (figs 594–597) feed between the leaf sheaths of tillers of *Arrhenatherum elatius* L. and *Lolium perenne* L., but do not sever the central shoot and cause little damage. They overwinter in the third instar and pupate towards the end of April. Third instar larvae have also been found in July so there are probably two generations per year. The larvae of *A. gracilis* Fallén (figs 598–602), *A. sordidella* (Zetterstedt) and *A. bifasciata* Wood have been found between the leaves of *Phragmites* and *Typha*. *Anthomyza albimana* (Meigen) has been reared from fungi (Agaricales). Other species have been reared from birds' nests (presumably from grasses used in their construction), e.g. *A. cingulata* Haliday (rook) and *A. neglecta* Collin (coot) (Collin, 1944).

Paranthomyza nitida (Meigen) (figs 603–606) has been recorded from *Melandrium rubrum* (Wiegel) (de Meijere 1944).

Anagnota bicolor (Meigen) has been reared from a mole's nest (Collin, 1944), presumably from grasses used in nesting material.

Asteiidae

Some 130 species in 10 genera of Asteiidae have been described and the family is represented in all of the major zoogeographical regions. Seven species in 3 genera occur in Britain (Chandler, 1978). The immature stages have not been described.

Asteia amoena Meigen is said to develop in wood detritus, in hollow trees, etc., but *A. concinna* Meigen adults are associated with marshes, fens, dune slacks and *Phragmites* beds.

Adults of *Astiosoma rufifrons* Duda are attracted to cold wood ash and smouldering bonfires of elm branches, etc., but the life-history is unknown.

Leiomyza species have been reared from fungi: *L. dudai* Sabrosky and *L. scatophagina* (Fallén) (several agarics, chiefly lignicolous, and the latter also *Polyporus squamosus*

Fries); *L. laevigata* (Meigen) (*Pleurotus cornucopiae* L.). Larvae of *L. scatophagina* have also been recorded from dried stems of the common reed (*Phragmites*) together with *Lipara* (Chloropidae) (Colyer & Hammond, 1968).

Camillidae

Eleven species of Camillidae are known, all contained in the genus *Camilla* and represented in only the Palaearctic (9), Nearctic (1) and Afrotropical regions (3).

No immature stages of this family have been described. Collin (1933) notes that E. B. Basden found adults of *C. fuscipes* Collin at the entrance of rabbit burrows and has reared *C. atripes* Duda (as *acutipennis* Loew) from nests of the short-tailed field vole. Baumann (1977) found adults of *C. atripes* (as *C. atrimana* Strobl) in the nests of voles in Germany. Dr A. G. Irwin (pers. comm.) has reared a species from soil derived from feral pigeon guano.

Ephydridae

(Figs: larvae 610–624, eggs 1050–1056, puparia 1211–1218, leaf-mine 1304)

Over 1,500 species of Ephydridae (shore flies) are known from all the major zoogeographical regions. Some 130 species in 39 genera and 4 subfamilies occur in Britain.

The larvae are mainly aquatic or semi-aquatic and over the world are found in a very wide range of habitats including some of the harshest in which Diptera are known to develop, e.g. hot springs (some *Ephydra, Scatella, Paracoenia*), petroleum pools (*Halaeomyia*), brine (*Ephydra*), egg-pods of locusts (*Actocetor*), scavengers in terrestrial snail shells (*Discomyza*), in spider egg-cases (*Trimerina*), in carrion and faeces (*Allotrichoma, Hecamede*), in nests of ants (*Rhyncopsilopa*) and birds (*Nostima*), as serious pests of rice (*Hydrellia*) and of beet (*Clanoneurum*).

All stages may be present (adults 'graze' algae on mud surfaces, stones, etc.) in very large numbers and may thus provide an important food source for marsh and shore frequenting birds and even man (American Indians).

In spite of all this the immature stages and ecology of these highly successful and adaptable flies remain poorly known. R. Dahl (1959) provides a pioneer ecological study for Scandinavia. A valuable symposium volume on Ephydridae (Deonier, 1979) includes much biological and ecological information.

The larvae of only 25 of the British species in 14 genera have been described, mostly by continental or American authors. The early literature on the immature stages is summarised, with illustrations, by R. Dahl (1969) and Hennig (1943a). Other useful works are listed below. Genera not mentioned below may be assumed to be unknown in the immature stages.

Psilopinae. *Psilopa leucostoma* (Meigen) has been reared from mines in *Chenopodium* (Oldroyd, 1964); the larva of the Nearctic *P. petrolei* Coquillett (now referred to *Halaeomyia*) is unique in that it lives, swims and feeds (on the bodies of trapped insects) in pools of crude petroleum in California (Thorpe, 1930).

Discocerina obscurella (Fallén) (figs 611, 612, 1050, 1211) probably feeds on micro-organisms (Foote & Eastin, 1974).

Discomyza incurva (Fallén) (fig. 610) has been reared from a decaying snail (*Helix pomatia* L.).

Larvae of *Clanoneurum cimiciforme* (Haliday) mine *Salicornia stricta* Dum (glasswort).

The larvae of *Trimerina madizans* (Fallén) feed as parasitoids within the egg cases of marsh-dwelling spiders (*Miryphantes*).

Notiphilinae. *Notiphila brunnipes* Robineau-Desvoidy lays eggs on the flowers of the white water-lily. The flowers close at sunset and withdraw below the water surface, reappearing at sunrise. The eggs are thus alternately immersed and exposed. The larvae live in the stems. The larvae (fig. 615) of most species of *Notophila* however live in the soil at the bottom of lakes, ponds and streams and obtain their oxygen from the intercellular spaces in the roots of aquatic plants by means of sharp hollow terminal spines (figs 616, 1213) (see Varley, 1937; Keilin, 1944; Houlihan, 1969; and compare *Chrysogaster*, Syrphidae; *Erioptera*, Tipulidae).

All *Hydrellia* larvae are phytophagous. Most species mine the leaves and stems of aquatic plants but others attack terrestrial plants, especially grasses (including rice). *H. chrysostoma* (Meigen) lives on *Potamogeton* as do many other European and Nearctic species. *H. nasturtii* Collin (figs 613, 1304) mines the stems of watercress (Taylor, 1928) and can be of economic importance (compare *Scaptomyza*, Drosophilidae). The larva of *H. modesta* Loew (fig. 614) mines and overwinters in the basal part of the leaf blade and leaf sheath of grasses (*Holcus, Anthoxanthum*) but does not penetrate to the central shoot (Nye, 1958). *H. griseola* (Fallén) (some records of which may refer to the previous species) does similar damage to cereals. Attacked leaves turn yellow, starting at the tip, and wither away. *H. griseola*, when very common in any locality, is said to break its normal habit of mining in only monocotyledonous plants by mining in dicotyledons of considerable diversity, e.g. *Lychnis, Trifolium* and many others (Hering, 1951).

Parydrinae. The larva of *Parydra pusilla* (Meigen) was found in wet moss and in mud at the bottom of a lake in Iceland (Nielsen, P. *et al.*, 1954).

Vimmer (1925) briefly describes the larva of *Pelina aenescens* Stenhammer found in a quiet stream.

First and second instar larvae of the Holarctic *Ochthera mantis* (De Geer) (fig. 618) are obligate predators of larval Chironomidae but third instars will feed on other aquatic insect larvae and can be cannibalistic in the absence of prey (Simpson, 1975). Three species are now known to occur in Britain (Irwin, 1985b).

Ephydrinae. The larva of *Ephydra riparia* Fallén has well developed abdominal prolegs with claw-like spines (crochets) an adaptation for life on aquatic plants beneath the water surface in saltmarshes. The puparium is adapted for attaching itself to plants by a curious excision of the posterior segments; the posterior spiracles are situated at the ends of the branches of a long forked posterior appendage (fig. 1214). Beyer (1939) describes the larvae of *E. riparia*, *Setacera micans* (Haliday) (fig. 617) and *Paracoenia fumosa* (Stenhammer). The larva of the abundant *Scatella stagnalis* (Fallén) feeds on a wide variety of algae. *S. silacea* Loew (figs 619–621) breeds in sewage filter beds (Terry, 1952). According to Bollwig (1940) the larvae of *Scatophila unicornis* Czerny cover their bodies with small stones or faecal pellets.

Teichomyza fusca Macquart, because of its unsavoury habits, now enjoys a cosmopolitan distribution. The fly appears wherever there are cesspits, urine soaked woodwork or other materials, or cadavers at the stage when nutritious liquids ooze from collapsing tissues. The larvae (figs 622–624) are very gregarious and may assemble in such masses as to block drains and septic tanks. Sometimes larvae are swallowed in foul water and have been reported in cases of urinary and rectal myiasis (Zumpt, 1965). The puparia (fig. 1218) are often encountered in numbers during archaeological excavations and indicate the location of middens and cesspits.

Oldroyd (1964) aptly summarized the biological versatility of this family— "Evidently we are seeing in the Ephydridae a family of flies in the full flower of its evolution, and as such they offer attractive material for study, not only to the dipterist, but also to students of insect physiology and behaviour".

Diastatidae

(Figs: larva 607–609)

Some 33 species of Diastatidae are known from the major zoo-geographical regions (except the Australo-Pacific). In Britain two species of *Campichoeta* and six of *Diastata* occur. Almost nothing is known of their life-histories, but they are probably spent in decaying wood. Hennig (1952) illustrates what he believes to be *Campichoeta basalis* (Meigen) (=*punctum* (Meigen)) (figs 607–609).

Drosophilidae

(Figs: larvae 625–638, eggs 1057–1063, puparia 1219–1229, leaf-mines 1296–1298)

Over 2,500 species of Drosophilidae have so far been described throughout the world. The particular association of the family with decaying and fermenting fruits and vegetables, wine, beer, etc. have earned them several common names, e.g. fruit-flies, pomace-flies, vinegar-flies, etc. Lesser fruit-flies has been used to distinguish Drosophilidae from Tephritidae, the true fruit-flies. This association has also ensured a cosmopolitan distribution via commerce for several species. Other substances in which larvae develop include fungi, slime fluxes, dung, carrion and many are general scavengers. Some mine the leaves and stems of plants, some are symbionts of bees, and others are predators of small Homoptera.

Because of their rapid rate of development and ease of culture on artificial media many *Drosophila* species (e.g. *D. melanogaster* Meigen) have become important laboratory animals in research on genetics, cytology, physiology and ethology. Consequent upon this the immature stages and laboratory life-histories of many species have become well known. However, our knowledge of the life-histories and ecology of Drosophilidae in field conditions is not extensive, and there is much scope for research. The adults are attracted to a far greater range of apparently suitable breeding media than that which actually proves suitable for development.

Okada (1968) gives a very useful account of the immature stages of the family and Ashburner (1981) reviews the life-histories of 'bizarre' Drosophilidae. Shorrocks (1972) provides a valuable introduction to all aspects of the biology of the genus *Drosophila* and Basden (1954) is useful. Laboratory workers will find the *Drosophila Information Service* (DIS) (Department of Biology, University of Oregon, Eugene, Oregon, USA) invaluable for annual updating of knowledge on *Drosophila* mutants, species maintained in cultures throughout the world, research notes and techniques in culturing.

Some 52 species in 10 genera and two subfamilies occur in Britain. The classification below follows Bächli & Pité (in Soós & Papp, 1984), which differs from the *Handbook* Check List. Genera and species not mentioned may be assumed to be unknown in the immature stages.

Steganinae. The larva of *Steganina coleoptrata* (Scopoli) (figs 625–627) feeds on sap under the bark of birch and *Prunus* (Morge, 1956) and has also been reared from fungi (*Hypoxylon fragiforme*). *Acletoxenus formosus* (Loew) is predaceous on *Siphoninus immaculatus* (Heeger) (on ivy) in Britain and other species of Aleyrodidae (Homoptera) (on hawthorn and *Viburnum*) abroad. The larva is orange at first becoming green in the third instar and is covered in a mucilagenous slime which collects debris, including egg-shells of their whitefly prey. The puparia (fig. 1220) are whitish and flattened ventrally where they are firmly glued to the old ivy (*Hedera helix*) leaves on which they occur. The

Acletoxenus larva may consume 30–40 whitefly 'puparia' during its development but attempts at biological control against whitefly have not been successful (Ashburner, 1981; Clausen & Berry, 1932).

Cacoxenus indagator Loew (figs 628–631) is a nest parasite of many species of solitary bees (*Anthophora, Chalicodoma, Osmia*) (Julliard, 1947; de Meijere, 1944). The larva eats supplies provided for the bee progeny. It appears that both bee and drosophilid larva can survive in the same cell if enough food is provided, but if not the *Cacoxenus* may eat the host larva, possibly after it dies of starvation. Careful research is needed on the detail of this life-history. I have had larvae of *Cacoxenus* sent in to me from behind door knobs in a school; clearly solitary bees had been nesting in the old style mortice locks. Larvae have also been found in sash window-frames along with bee (?*Osmia*) larvae and *Ptinus* beetles.

Amiota (Amiota) alboguttata (Wahlberg) has been reared from fungi (*Daldinia concentrica*, Pyrenomycetae). Abroad, some *Amiota* species are predaceous on Homoptera (Pseudococcidae, Delphacidae) on sugarcane, and one species is found in the burrows of an ambrosia-beetle pest on tea where it may feed on fungi with which the beetle lives in symbiotic association (Ashburner, 1981). *Amiota (Phortica) variegata* (Fallén) (fig. 632) larvae feed on sap bleeding from oak, chestnut and willow. The three British species, as yet unknown in the immature stages, may therefore be found to have unusual or interesting life-histories.

Leucophenga maculata (Dufour) has been reared from several fungi (agarics, boleti and polypores).

Drosophilinae. *Scaptomyza* species (figs 633–634, 1296–1298) are leaf-miners in the following plants: *S. flava* (Fallén) (Cruciferae (Brassicaceae), including *Brassica*); *S. graminum* (Fallén) (*Atriplex, Brassica, Chenopodium, Lychnis, Melandrium, Silene, Stellaria, Viscaria*, also stems of watercress): *S. pallida* (Zetterstedt) (?clover) and *S. disticha* Duda (*Allium*).

Many species of *Drosophila* (figs 635–638) develop in rotting fruit and vegetable matter and fermenting substances. *D. repleta* Wollaston is a cosmopolitan species that has become a nuisance in restaurants, kitchens, canteens and taverns, where it breeds in nearby decomposing vegetables, including onions and cabbages. The common ferment-loving species include *D. (D.) funebris* (F.), *D. fenestratum* Fallén, *D. fasciata* Meigen and *D. obscura* Fallén. Species reared from fungi include *D. busckii* Coquillett, *D. cameraria* Haliday, *D. confusa* Staeger, *D. funebris* (F.), *D. histrio* Meigen, *D. kuntzei* Duda, *D. melanogaster* Meigen, *D. phalerata* Meigen, *D. obscura* Fallén, *D. repleta* Wollaston, *D. subobscura* Collin and *D. transversa* Fallén. Chandler (in Stubbs & Chandler, 1978) lists the species of host fungi. *Drosophila* reared from sap exudates on trees include *D. littoralis* Meigen, *D. obscura* and *D. subobscura*. *D. ananassae* Doleschall and *D. funebris* have been reared from excrement. *D. busckii* has been reared from carrion.

Puparia of *D. busckii* (fig. 1225) and *D. funebris* (fig. 1226) are frequently found in milk bottles where they are so firmly stuck to the glass they come through the washing process intact (though killed by it). Some may float off into the milk when the bottles are refilled and be brought to the notice of environmental health officers (see also *Spiniphora bergenstammi*, Phoridae).

The puparia and eggs of *Drosophila* species are very distinctive because of their long respiratory processes and a range of commonly encountered species is shown (figs 1059–1063, 1225–1229).

A key to drosophilid larvae is provided by Okada (1968) but because of the rapid development rate it is frequently more convenient to rear living larvae through to adults for identification purposes using the keys of Fonseca (1965) or Basden (1954). Shorrocks (1972) provides a key to adults of the common species of *Drosophila*.

Milichiidae

(Figs: larvae 639–644, puparia 1230–1231)

Some 245 species of Milichiidae are known throughout the world. The larvae are coprophagous or saprophagous and have been reared from excrement, kitchen refuse, plant detritus, birds' nests and ants' nests. Eleven species in 5 genera and 2 subfamiles occur in Britain.

Madazinae. The immature stages of the two British species of *Madiza* are unknown but adults of *M. glabra* Fallén are associated with primitive sanitary arrangements in country areas and sometimes occur in large numbers indoors. Adults have also been found on cadavers during 'caseic' or protein fermentation especially if putrid liquids exude.

Leptometopa and *Desmometopa* are known to breed in human excrement. Hennig (1956) has described the immature stages of *Leptometopa* (figs 639–644).

Phyllomyza formicae Schmitz and *P. securicornis* Fallén have been found in ants' nests (*Formica rufa* L.) (Donisthorpe, 1927) and Hennig (1937) figures the puparia (figs 1230–1231).

Milichiinae. The immature stages of *Milichia ludens* (Wahlberg) have not been described but the species is associated with the ant *Lasius fuliginosus* (Latreille) according to Donisthorpe (1927), who further states that the larvae of an African species covers itself with excreta and wanders about in ant runs.

The larva of an American milichiid feeds on exhausted fungus garden substrates and refuse in ants' nests (Moser & Neff, 1971).

Tethinidae

Ninety-two species of Tethinidae are known throughout the world, of which 10 species in 2 genera occur in Britain.

The immature stages and life-histories are unknown but the adults are found in coastal regions, on fore-shores or dunes, and in saline meadows and lagoons.

Canacidae

(Figs: larvae 645–646, puparia 1233)

Ninety-one species of Canacidae are known throughout the world. Two species in 2 genera occur in Britain.

The larva of *Canace nasica* Haliday feeds on *Enteromorpha* (Algae) in the coastal intertidal zone. The puparium (fig. 1233) is described by Hinton (1967a) who established its possession of plastron bearing spiracular gills in common with a number of other intertidal Diptera. The larval stages of an American *Canace* (figs 645–646) have also been found to feed on blue-green algae in the intertidal zone (Teskey & Valiela, 1977). The immature stages and life-history of *Xanthocanace ranula* (Loew) are unknown.

Braulidae

(Figs: larvae 647–649, egg 1064, puparia 1232)

Only 8 species of Braulidae, contained in two genera, *Braula* and *Megabraula*, are known. The tiny, wingless mite-like adults feed on pollen in the nests of honey-bees, often attached to the bees. The larvae feed on pollen in the bees' brood combs. Not surprisingly, the distribution of these flies largely coincides with the distribution of apiculture throughout the world.

One species, *Braula coeca* Nitzsch (figs 647–649), occurs in Britain, the immature stages and life-history of which have been described by several authors including Skaife (1921) and Imms (1942).

Agromyzidae

(Figs: larvae 650–668, eggs 1065–1067, puparia 1234–1240, leaf-mines 1299–1303)

Over 2,000 species of Agromyzidae have been described throughout the world, about half that number occurring in the Palaearctic region. Some 320 species in 18 genera and 2 subfamilies occur in Britain.

The larvae feed on plant tissues, the majority (75%) as leaf miners, others as stem borers, a few in roots, some developing in twigs on trees with some causing galls. About 160 of the world species may have some economic importance (Spencer, 1973b).

Most Agromyzidae are limited in their choice of host to a single plant species or, more often, several species within the same plant genus; others feed on a number of genera within a single plant family or on several related families of the same order; a few species are truly polyphagous on a wide range of unrelated hosts.

The form of the mine can be of considerable help in the identification of Agromyzidae. The main types of mine are linear or serpentine (figs 1299, 1302–1303) or form a blotch (fig. 1300). The part of the leaf that is mined may also be taxonomically important as may the arrangement of frass within the mine. It should also be borne in mind that some members of other families of Diptera also form mines (figs 1287–1298, 1304–1308), and see under Sciaridae, Chironomidae, Dolichopodidae, Syrphidae, Scathophagidae, Tephritidae, Lauxaniidae, Psilidae, Anthomyzidae, Drosophilidae, Ephydridae, Chloropidae and Anthomyiidae.

Eggs are laid on the plants, beneath the epidermis. Pupation normally takes place on the ground but a few species pupate at the end of the mine.

Knowledge of the general biology of Agromyzidae is summarised by Hering (1951) and Spencer (1972, 1976). Spencer (1973b) deals with the species of economic importance. De Meijere (1925–1955) has described the larvae of many Agromyzidae and P. Allen (1956–1958) describes the larvae of several British species. Although the host plants of many species are known, detailed studies of the life-histories or morphology of the immature stages are still few and there is plenty of scope for further research. To facilitate such research Griffiths (1962) provides useful information on rearing Agromyzidae and their parasites. Hering (1957) gives a useful account of mines, with keys.

Third instar larvae of the two subfamilies may be distinguished as follows:

1 Cephalopharyngeal skeleton with each dorsal cornu divided into two (figs 651–652) . . . . **Agromyzinae**

— Dorsal cornua not divided (figs 654, 661–662, 668) . . . . **Phytomyzinae**

Agromyzinae. The British species of *Hexomyza* all cause twig galls: *H. simplicoides* (Hendel) on *Salix* (especially *S. caprea* L.); *H. sarothamni* (Hendel) on *Sarothamnus scoparius* (L.) and *H. schineri* (Giraud) on *Populus nigra* L. and *P. tremula* L.

Nine of the 13 British species of *Melanagromyza* (figs 650–651) are internal stem-borers; *M. cunctans* (Meigen) forms slender stem galls on *Lotus; M. symphyti* Griffiths feeds in the thick leaf stalks of *Symphytum officinale* L. The hosts of 4 species are unknown.

Of the 23 British species of *Ophiomyia* (fig. 652) 13 feed as external stem-miners and one (*O. melandryi* de Meijere) forms an internal stem mine. Five are leaf miners but mostly inside the midrib with only one species (*O. maura* (Meigen)) forming a typical mine in the leaf blade. The life histories of 4 species are unknown. *Ophiomyia simplex* (Loew) (the asparagus miner) is recorded as an occasional stem mining pest of asparagus (H. F. Barnes, 1937; Spencer, 1973b) though the primary cause of damage may be a fungus (Spencer, 1976).

Forty-three of the 46 British species of *Agromyza* are leaf miners (15 on Gramineae (=Poaceae) 12 on Papilionacae, the rest on various families) with one stem miner (*A. marionae* Griffiths), one stem gall causer (*A. erythrocephala* Hendel) (both on *Vicia cracca* L.) and one unknown (*A. rubiginosa* Griffiths). Several species of *Agromyza* attack cereals (fig. 1300) but rarely cause much damage in Britain, though they can be serious pests abroad.

Phytomyzinae. The larvae of all the *Phytobia* species so far known feed on the cambium of the twigs or trunks of trees. The larvae (fig. 656) can be as long as 2 cm, quite unlike the usual agromyzid, and may do permanent damage to the wood. *P. cerasiferae* (Kangas) has been found on *Prunus cerasifera* Ehrendorfer; *P. carbonaria* (Zetterstedt) is found on Rosaceae, *Crataegus* and *Malus*; *P. cambii* (Hendel) (figs 653–656, 1065, 1235, 1301) occurs on *Salix* spp. and *Populus tremula* (Barnes, H.F., 1933); the host of the only other British species (*P. errans* Meigen) is unknown.

The two British species of *Calycomyza* are leaf (blotch) miners. *C. humeralis* (Roser) on Compositae (Asteraceae) especially *Aster, Bellis* and *Erigeron*; *C. artemesiae* (Kaltenbach) on *Artemisia* and *Eupatorium.*

The genus *Amauromyza* (8 British species) contains leaf (blotch) miners and stem-borers (s.g. *Cephalomyza*).

Of the 41 species of *Liriomyza* (figs 657–658) 34 are leaf miners; two (*L. virgo* (Zetterstedt), *L. flavopicta* Hendel) are stem-feeders, one feeds on flowerheads and the hosts of 4 species are unknown. *L. bryoniae* (Kaltenbach) is probably an introduced species which forms an irregular linear mine (fig. 1299) and is a common pest of tomato (*Lycopersicon esculentum* Miller) in glasshouses and also occurs on cucumbers (*Cucumis sativus* L.). *L. pisivora* Hering mines the leaves of peas (*Pisum sativum* L.) and *L. congesta* (Becker) mines the leaves of peas and beans (*Vicia faba* L.) but their damage is negligible (Spencer 1973b).

Pteridomyza hilarella (Zetterstedt) is a leaf miner on the ferns *Pteridium aquilinum* (L.) and *Polypodium vulgare* L.

Of the four species of *Metopomyza* three are known to be leaf-miners (two on *Carex*, one on *Viola*). The hosts of *M. flavonotata* (Haliday) are probably Gramineae among which adults are not uncommon.

The hosts of three of the 5 British species of *Phytoliriomyza* are known: *P. melampyga* (Loew) (formerly in *Liriomyza*), a blotch leaf-miner on *Impatiens*; *P. arctica* (Lundbeck), an external stem-miner on *Sonchus* and probably other Compositae; and *P. pteridii* Spencer (1973a) on *Pteridium aquilinum.*

No hosts are known for the three British *Lemurimyza* but the single British *Nemorimyza, N. posticata* (Meigen), forms large blotch mines on *Solidago.*

Of the 15 species of *Paraphytomyza* nine feed as leaf or external stem-miners on Rubiaceae (*Galium*), Dipsacaceae (*Knautia*) and Caprifoliceae (*Lonicera, Symphoricarpus*) and six are leaf-miners on Salicaceae.

Napomyza species are primarily internal stem-borers, pupating in the stem. The European *N. carotae* Spencer has not yet been recorded in Britain but the larvae cause damage to carrots superficially resembling that of the carrot fly (*Psila rosae*) and it could easily be overlooked (Spencer, 1973b). *N. lateralis* (Fallén) (figs 659–661) is common in Compositae.

Pseudonapomyza atra (Meigen) is a leaf miner on Gramineae (*Avena, Lolium, Phalaris, Poa*, etc) and the only other British species, *P. lacteipennis* (Malloch) is certainly also a grass-feeder but as yet its hosts are unknown.

Phytomyza (figs 664–667) is the largest genus of Agromyzidae in Britain. Eighty of its British species are leaf-miners, five feed mainly in the mid-rib, four are internal stem borers, six feed in seed heads and the biology of 11 species is unknown. Of the leaf-mining species *P. syngenesiae* (Hardy) and *P. horticola* Goureau are probably the best known. These two common species were formally confused under the name *P. atricornis* (of authors) until Griffiths (1967) revised this complex. Horticulturalists knew this name for the chrysanthemum leaf-miner (fig. 1303) which causes serious commercial losses to growers in Europe and the United States. This pest species is *P. syngenesiae* (figs 662–663, 1066, 1237) and in addition to chrysanthemums can cause serious damage to lettuces and is found on a wide range of Compositae and is perhaps mostly readily seen on *Sonchus* (though another 8 species in 4 genera of agromyzids also occur on *Sonchus*!). *P. horticola* is more widely polyphagous than *P. atricornis* on Compositae and many other families and is an occasional pest on peas but in Britain has no serious effect on the crop. *P. ilicis* Curtis (the holly leaf-miner) (figs 1067, 1238) is another familiar species which produces blotch-mines on the leaves of *Ilex aquifolium* L.

P. rufipes Meigen is a large species which feeds inside the stem or midrib of the larger leaves of Cruciferae, especially *Brassica* spp. on which it can be of some economic importance.

Cerodontha is another large genus, the larvae of which feed exclusively on monocotyledons. The hosts of the 34 British species are as follows: 12 on Gramineae, seven on Cyperaceae, two on Iridaceae, one on Juncaceae and 12 are unknown. *C. (Dizygomyza) iridis* (Hendel) is an abundant species which mines *Iris foetidissima* L. and another common species, *C. (D.) ireos* (Goureau), mines *Iris pseudacorus* L. (figs 668, 1302).

Chloropidae

(Figs: larvae 669–682, eggs 1068–1069, puparia 1241–1242, galls 1305–1306)

Over 2,000 species of Chloropidae are known throughout the world but the family is poorly worked and many new species and genera undoubtedly await discovery and description and many life-histories require elucidation. The larvae of many species are phytophagous, especially on Gramineae and several species are important pests of cereals, such as frit flies (*Oscinella*) and gout flies (*Chlorops*). Some form galls and others are saprophagous or even parasitic. Larvae of the Australian genus *Batrachomyia* live in perforated swellings under the skin of frogs. Some are predators on root aphids, rice boring moth larvae, Thysanoptera, egg capsules of grasshoppers and egg sacs of spiders.

Some 243 species in 39 genera and two subfamilies occur in Britain. Nye (1958) has described the larvae of several species living in Gramineae and provides a key, other papers on immature stages are cited below. Balachowsky & Mesnil (1935) is useful for chloropine larvae, especially the pest species. Viviparity has been shown to occur in some African Chloropidae (Spencer, 1985). General summaries of the biology of the family in Europe are provided by Balachowsky & Mesnil (1935) and Wendt (1968). Valley, Wearsch & Foote (1969) discuss larval feeding habits of North American species.

Oscinellinae. The three British species of *Lipara* cause galls (fig. 1305) in the common reed (*Phragmites communis* Trinius) and an account of their systematics, morphology, behaviour and ecology for all stages is given by Chvála *et al.* (1974). Other dipterous larvae are found in *Lipara* galls, including Cecidomyiidae and other Chloropidae (noted below), some of which appear to be regular inquilines (Blair, 1932, 1944a, 1944b).

Collin (1946) records that *Calamoncosis minima* (Strobl) 'appears freely when breeding out *Lipara lucens* Meigen' and that *C. glyceriae* Nartshuk (as *laminiformis* (Becker)) feeds gregariously on the ensheathed inflorescence of the grass *Glyceria aquatica* (L.).

Adults of *Siphonella oscinina* (Fallén) have been swept from conifers but the immature stages are unknown. Collin (1946) has reared *Polyodaspis ruficornis* (Macquart) from walnuts (probably imported). The immature stages of the two British *Goniopsita* species appear to be unknown. Collin (1946) has reared *Lasiamba baliola* (Collin) from 'material taken from an ulcerous elm tree'.

Nye (1958) found the larvae of *Conioscinella mimula* Collin and *C. frontella* (Fallén) overwintering in the basal tillers of *Anthoxanthum odoratum* L. and *Holcus lanatus* L. respectively. The adults of *C. gallarum* (Duda) appear to be associated with oak (Collin, 1946).

Speccafrons halophila Duda has been reared from spiders' eggs.

Gaurax niger (Czerny) has been reared from the nest of a dormouse by E. B. Basden (Collin, 1946). Larval and puparial characters of *Gaurax dubius* (Macquart) (figs 669–670) have been described (Smith, 1965) from puparia found in *Polyporus betulinus* Fries. *G. fascipes* Becker has been reared from nests of blackbird and linnet by E. B. Basden, but C. H. W. Pugh reared it from under bark in a dead branch and Smith (1967) casts doubt upon birds' nests as a usual habitat. Collin (1946) has reared *Incertella zuercheri* Duda from galls of both *Lipara lucens* and *L. similis* Schiner.

Oscinella frit (L.) (figs 671–676, 1068, 1241) (frit fly) is a serious pest of cereals, especially oats in Europe and mainly wheat in North America. It is a highly polyphagous species and is found in a wide variety of Gramineae. Steel (1931) and Nye (1958) describe the larvae of *O. frit*, the latter including morphological variants in different hosts, and other closely related species in various Gramineae. Nartshuk's (1956) paper on *Oscinella* larvae should also be studied.

Hapleginella laevifrons (Loew) has been reared from larch cones (D. Fergusson, in the British Museum (Nat. Hist.) collections).

The larva of *Elachiptera cornuta* (Fallén) overwinters in the decaying leaves of *Typha* and is a follower of *Oscinella frit* in infested cereal fields (Jepson & Southwood, 1960). Adults of *E. megaspis* (Loew) are found among watercress (Collin, 1946).

Nothing appears to be known of the immature stages of the following Oscinelline genera occurring in Britain: *Aphanotrigonum, Dicraeus, Eribolus, Gampsocera, Lioscinella, Melanochaeta, Oscinomorpha, Oscinosoma, Siphunculina, Trachysiphonella, Tricimba.* Anyone rearing adults in these genera would do well to establish at least the identity of the host plants if possible.

Chloropinae. The agile larvae of *Camarota curvipennis* (Latreille) feed in the ears of rye, wheat and barley (Balachowsky & Mesnil, 1935; Nye, 1958).

Larvae of *Platycephala planifrons* (F.) develop in the stems of reed (*Phragmites*) (Wandolleck, 1899; Wendt, 1968).

The large genus *Meromyza* contains at least 16 British species (seven were listed in the Check List, Smith 1976). The larvae of few species have been described (Fedoseeva, 1966, gives a key, but in Russian) and few host plants are known but are probably included among those from which adults are commonly swept. With Ismay's (1981) key to adults a little careful field work should soon amend this situation. The larvae of *Meromyza femorata* Macquart and *M. variegata* Meigen (figs 677–678) have been reared from *Dactylis glomerata* L. *M. saltatrix* (L.) is associated with a variety of grasses and is a pest of wheat on the continent; *M. pratorum* Meigen has been reared from marram grass (*Ammophila*).

Cryptonevra flavitarsis (Meigen) has been reared from *Lipara* galls (Blair, 1944b) but hosts of the other three species are unknown.

The larvae of *Lasiosina cinctipes* (Meigen) is said to develop in barley following attacks by *Chlorops pumilionis* (Bjerkander).

Larvae of *Cetema neglecta* Tonnoir overwinter in the basal tillers of *Lolium perenne* L., *Festuca pratensis* Huds., *Poa trivialis* L. and *Agrostis* spp. The similar *C. elongata* (Meigen) larva overwinters in *Agrostis* spp. and *C. myopina* Loew has been recorded from spring oats (probably from a ploughed-in ley) (Nye, 1958).

According to Balachowsky & Mesnil (1935) the larva of *Chlorops strigula* (F.) overwinters in species of *Brachypodium* and *Agropyron*. *Chlorops pumilionis* (Bjerkander) (= *taeniopus* Meigen) (gout fly) (figs 679–682, 1069, 1242) can be a serious pest of cereals, particularly on the Continent. The larvae overwinter in the basal tillers of wheat, barley, rye and *Agropyron repens* L. In this and other species of the genus the larvae stimulate the plant to hypertrophy and a swollen 'gouted' shoot is formed. Larvae of other species of *Chlorops* may be found in the following Gramineae: *C. brevimana* Loew in *Phalaris arundinacea* L.; *C. interrupta* Meigen in *Agropyron* spp.; and *C. speciosa* Meigen in *Deschampsia caespitosa* L.

The larva of *Chloropisca glabra* Meigen is predaceous on root-feeding aphids and the same habit is shared by *Thaumatomyia notata* (Meigen), which feeds on the root aphid *Pemphigus bursarius* (L.) and may be an important agent in biological control.

No hosts appear to be known for the following chloropine genera occurring in Britain: *Diplotoxa, Epichlorops, Eurina, Eutropha, Melanum.*

Calyptratae

Oestridae

(Figs: larvae 683–692, puparium 1243)

The family Oestridae contains 34 species in 9 genera and 2 sub-families found mainly in the Afrotropical and Palaearctic Regions. Four species in 3 genera representing both subfamilies occur in Britain.

Larvae of Oestridae develop in the head cavities (nasal or pharyngeal) of species of mammals in several groups (Marsupialia, Proboscidea, Artiodactyla and Perissodactyla). The female flies deposit live first instar larvae (as many as 400–900) into the nostrils of their hosts, which include several species of domestic animals, e.g. sheep, horse, goat and camel, and game animals. The three larval instars may differ markedly in appearance and as earlier instars are more likely to be involved in enquiries, they are included in the illustrations (in this and the two following families). Zumpt (1965) gives a good general account of the life histories and morphology of Oestridae and includes many references to other works. Papavero (1977) discusses the classification of the family.

Oestrinae. The first instar larvae (fig. 684) of *Oestrus ovis* L. (sheep nostril fly or sheep bot fly) are squirted in flight at the nostrils of sheep (also goats and dogs) where they crawl into the frontal sinuses. Here they attach themselves by their mouthhooks to the mucous membrane and feed. They remain there for some 9 months when the fully fed larvae (fig. 683) relinquish their hold on the membrane and are sneezed out by the sheep onto the ground where they pupate (fig. 1243) under stones or tufts of grass. Usually only a few larvae are present in each animal, but they may cause a serious loss of condition. Occasionally large numbers may be found (up to 350 in one animal) and high mortality may occur (especially among lambs), usually during dry years.

Occasionally (rarely in Britain) larvae may be deposited in the eye, mouth, nostrils or outer ear of man (especially people associated with sheep). Fortunately (unlike *Hypoderma*, see below), the larvae do not survive beyond the first instar but may cause what is usually diagnosed as acute catarrhal conjunctivitis (more correctly ophthalmomyiasis) for as long as 10 days. As many as 50 larvae have been removed from the conjunctival sac of a single patient (Zumpt, 1965; Keiser, 1948). Although the larvae are very tiny, transparent, and easily overlooked, in these cases the sclerotized mouthparts (fig. 686) are readily visible and identifiable even on rough slides or photographs submitted for identification from hospitals. Cases occur in Britain but are rarely recorded in the literature and appear to occur in particular 'good' years (e.g. the dry summer of 1976 brought several cases).

Cephenemyiinae. The main host of *Cephenemyia auribarbis* (Meigen) (the deer nostril fly) (figs 689–690) is the red deer (*Cervus elaphus* L.), and very occasionally the fallow deer (*Dama dama* (L.)) is infested. *C. trompe* (Modeer) (fig. 691) is found in the reindeer (*Rangifer tarandus* (L.)) and has been introduced with this host into Scotland.

Pharyngomyia picta (Meigen) (fig. 692) is a parasite of red deer and is regarded as extinct in Britain but as there are said to be more deer in Britain now than for centuries it may well reappear (Smith, 1974a).

Hypodermatidae

(Figs: larvae 693–702, eggs 1070–1072, puparium 1244)

The family Hypodermatidae (warble-flies) contains 32 species in 11 genera and 2 subfamilies, 29 of which occur in the Palaearctic Region. The family also occurs in the Afrotropical and Nearctic Regions. In the *Check-list* (Smith *et al.*, 1976) the Hypodermatidae is treated as a subfamily of the Oestridae but is now usually given family rank. One genus containing three species occurs in Britain.

The larvae are specific parasites of mammals (Rodentia, Lagomorpha and Artiodactyla). The tiny eggs (figs 1070–1072) (of which 300–800 may be laid) are glued to the hairs of the host. The first stage larvae penetrate the skin of the host usually by a hair follicle, and wander, either through the connective tissue (subfamily Oestromyiinae — non-British) or internal organs (subfamily Hypodermatinae). The second and third stage larvae finally settle under the skin of the host and form cysts (warbles) with a hole to which they apply their spiracles for respiration and through which the mature larva eventually escapes. Larval feeding causes the host pain and discomfort which affect health and condition; the warbles damage the hide and thus give the family considerable economic importance when domestic animals are involved. Zumpt (1965) gives a good general account of the biology of warble flies.

Hypoderma bovis (L.) (ox warble fly) (figs 693–696) attacks cattle and occasionally horses. Eggs (figs 1071–1072) are attached singly to the base of body hairs. Man is also sometimes attacked, both in the normal way when larvae are found in skin tumours and more seriously in the eye causing a malignant ophthalmomyiasis (see following species).

Hypoderma lineatum (Villers) (lesser ox warble fly) (figs 697–700) also attacks cattle but in addition horses are occasionally infested. The eggs are laid in regular rows of 5 to 15 per hair (fig. 1070). Most of the records of warble-flies in man are probably of this species and it is possible that infestation occurs through handling cattle, rather than or as well as by direct oviposition. The few British cases known to me are recorded by Hope (1840), Style (1924), Smart (1939) and A. Smith & Greaves (1946). The most serious cases are those involving ophthalmomyiasis as (unlike *Oestrus*) the first stage larvae (fig. 698) may, if they are not removed quickly, completely destroy the eyeball causing great pain (see Krümmel & Brauns, 1956 and comments under *Oestrus ovis*). I know of no British cases of ophthalmomyiasis involving *Hypoderma*. Again, infestation may occur through contamination (by wiping hands across eyes) after handling infested cattle rather than by direct oviposition, though the flies may possibly deposit eggs on eye-brows or lashes. The mouthparts of the first instar larvae are diagnostic and easily distinguishable from *Oestrus* by the toothed mandibles (figs 696, 698).

Hypoderma diana Brauer (deer warble-fly) (figs 701–702) develops in the roe deer but has also been found in fallow deer and has adapted to reindeer imported into Scotland (Kettle & Utsi, 1955). Ironically, an initial period of quarantine had prevented the introduction to Britain of the reindeer warble-fly (*Oedemagena tarandi* L.). As yet no records of human infestation by *H. diana* have been reported.

Gasterophilidae

(Figs: larvae 703–711, eggs 1073–1076, puparium 1245)

The family Gasterophilidae contains some 16–18 species in some 3–5 genera and two subfamilies. They are found in the Palaearctic, Afrotropical and Oriental regions but some *Gasterophilus* species have been accidentally introduced into other parts of the world. Four species, all contained in the genus *Gasterophilus*, represent the family in Britain.

The larvae are specific parasites of Perissodactyl mammals (horse and rhinoceros) and elephants (Proboscidea). Eggs (200–2500) are deposited on skin and hairs (figs 1073–1076) near the mouth, or in the grass. The larvae enter the mouth via the host's tongue during body-licking, with the food, or by their own movement. Zumpt (1965) gives a good general account of the biology of the family and much of what follows is from his work, but based on non-British data.

The normal hosts of *Gasterophilus haemorrhoidalis* (L.) (the nose bot fly) (fig. 703) are the horse and donkey (and zebra in Africa). The eggs (fig. 1073) are brownish black with a stalk-like pedicel which is a continuation of the broad chorionic flange and hollow along one side to receive the supporting hair. The first instar larvae penetrate the lips and migrate into the mouth. Second instar larvae are found in the stomach and duodenum where they moult to the third stage and eventually pass to the rectum where they re-attach themselves to the wall, often in great numbers, near the anus. Eventually they detach themselves and pass out, not necessarily with the faeces. Occasionally man may become infested with first instar larvae, usually on the face and buttocks, where they cause a 'creeping myiasis' in the skin.

G. intestinalis (De Geer) (the horse bot fly) (figs 705–708) is only known from the horse and donkey and their cross breeds. Occurrences in other animals (e.g. dogs, hyaenas, vultures) have only occurred when they have fed on infested equine intestines. Eggs hatch on the application of moisture and friction and the first instar larvae travel on the tongue and after some 24 days pass to the stomach. Here they complete their development to third instar, and are eventually excreted with the faeces and pupate in the soil. Records of 'creeping myiasis' in man may have involved other species of *Gasterophilus* but there is one probable North American record of human ophthalmomyiasis.

G. nasalis (L.) (throat bot fly) (fig. 704) infests horses and donkeys (and Burchell's zebra). Eggs are attached to the hairs of the intermaxillary space between the rami of the mandibles beneath the head. A female may lay some 300 to 500 eggs, usually one per hair (fig. 1075), but occasionally up to 5 have been found. Undisturbed a female may lay 20 eggs on a given host. The larvae hatch without the stimulation of external moisture or pressure, migrate to the lips and invade the spaces between the teeth below the gum line and behind the alveolar process of the gums. Pus pockets form, following necrosis of the tissue, which may contain as many as 12 larvae. After 18–24 days the larvae moult to the second instar and after a few more days move on to the duodenum. Here they become attached to the wall near the pylorus and moult to the third stage. The larva takes some 11 months to mature and then passes out with the faeces. Larvae are also said to occur in the stomach. There are no records of 'creeping myiasis' in humans as the first instar larvae seem to be incapable of penetrating unbroken human skin.

Normal hosts of *G. pecorum* (F.) (figs 709–711) are the horse and donkey (and Burchell's zebra). The eggs are glossy black with a fringed pedicel and are not attached to the host's hairs but are laid on plants (fig. 1076). A female lays from 1,300 to 2,500 eggs which can remain alive for many months but once in the mouth of the host the larvae hatch within 3–5 minutes and immediately penetrate the mucous membrane of the lips, gums, cheeks, tongue or hard palate. They burrow towards the root of the tongue and soft palate, where they remain for 9–10 months until attaining the third instar when they move to the stomach. They may also be swallowed with the food and settle in the walls of the pharynx, oesophagus and stomach. The fresh first stage larva (fig. 709) has a distinct crown of recurved spines on the first segment but these disappear later (fig. 710). First instar larvae can penetrate the skin within 3–5 minutes and a human infestation can be easily obtained by passing the hand over grass on which flies have oviposited.

A unique feature of the third stage larva is the arrangement of denticles on the pseudocephalon into 3 groups, 2 lying laterally and a third centrally in front of the mouthhooks (fig. 711).

This species has been much studied in Asia where it is regarded as the most pathogenic *Gasterophilus* species on horses (Zumpt, 1965).

Tachinidae

(Figs: larvae 712–755, eggs 1077–1085, puparia 1246–1251)

This may be the largest family of Diptera although at present more species of Tipulidae are actually known. Over 8000 species have been described. The classification of Tachinidae is fraught with difficulties because of the enormous number of species and the variation in taxonomic value of the many morphological characters available on the adult flies. Herting (1984) recognises 1,552 species in 398 genera, 33 tribes and 4 subfamilies for the Palaearctic Region. The British *Check List* (Smith *et al.*, 1976) listed some 236 species and the classification used here, for convenience, follows the sequence of genera of the Check List with higher taxonomic and nomenclatorial adjustments to conform with Herting's work, some faunistic additions, and to link with Emden's (1954) *Handbook* to adults.

In spite of the varied form of the adults all Tachinidae share the parasitoid habit and most larvae live as endoparasites of other insects and rarely (*Loewia* and *Eloceria*) centipedes. The main hosts are Lepidoptera and Coleoptera, but Hemiptera, Hymenoptera, Orthoptera, Mantodea, Phasmatodea, and Embioptera are also attacked. Rarely Tachinidae are parasitic in their own order, usually in their larvae (e.g. *Siphona*), but only very rarely do they attack adult flies (Smith, 1974c). However, as so few life-histories are known the possibility should always be borne in mind (see also Sarcophagidae, Miltogramminae). Some tachinid groups are highly specialized in the hosts they select, while others are polyphagous. Tachinidae may be oviparous or larviparous. Oviparous species may deposit large (macrotype) eggs (100–200) on the body of the host or small (microtype) eggs (2,000–6,000) on plants eaten by the host (see Salkeld, 1980). Larviparous species deposit first instar larvae on or near their hosts. Females of species that attack Hemiptera or adult Coleoptera may have their claspers and ovipositors specially adapted for piercing or specially modified spines for gripping the host. Some species no doubt exert a considerable control on certain agricultural pests and some have been deliberately used as biological control agents with varying success. In spite of this adequate descriptions of the immature stages are few. Hennig (1948–1952) lists references to descriptions of under 300 species or about 3% of the world fauna. For this reason, entomologists should always preserve with full data any parasites reared from the insects they are studying, including the puparial caps containing anterior spiracles and cast larval mouthparts (see Introduction) and pass them on, with full host data, to interested specialists or suitable museums and institutions. The hosts of British Tachinidae are listed by Audcent (1942), Emden (1954) and Herting (1960). Papers by Hammond & Smith (1953–1957) and Smith (1980) may be of interest to rearers of Lepidoptera and Emden (1950) to Coleopterists. For world species (as a host guide for unreared British species) see W. R. Thompson (1943–1965) continued by Herting (1971–). Some useful papers describing immature Tachinidae are J. C. Nielsen (1909, 1911–1918), Bisset (1938), Zuska (1963), and Lehrer & Plugerj (1966); other papers are mentioned below. Good accounts of the biology of Tachinidae are given by Clausen (1940) and Askew (1971). Ferrar (1987) should also be useful. Genera not mentioned may be assumed to be unknown in the immature stages. A new *Handbook* to the British Tachinidae is in active preparation by Robert Belshaw.

Phasiinae

Members of this subfamily are virtually exclusive parasites of Hemiptera-Heteroptera. The egg (figs 1077–1079) is deposited on the host or injected through the integument (*Phasia*). The mature larvae leave the host before pupation and the bug may survive for some days. The monograph of Dupius (1963) includes some immature stages.

Phasiini. Of the 3 British species of *Phasia* (= *Alophora*) the hosts of two are known: *P. pusilla* Meigen which parasitizes *Cydnus* (Cydnidae) and *Chilacis* (Lygaeidae), and *P. obesa* (F.) has been reared from *Zicrona caerulea* (L.) (Pentatomidae). *Cistogaster* species (figs 712–714) are parasites of Pentatomidae and some Cydnidae. *Subclytia rotundiventris* (Fallén) parasites *Elasmucha grisea* (L.) (Acanthosomatidae).

Cylindromyiini. *Cylindromyia brassicaria* (F.) (figs 715–716) parasitizes Pentatomidae (*Dolycoris, Holcostethus, Palomena*), but the hosts of *C. interrupta* Meigen are unknown. *Lophosia fasciata* Meigen has been reared from *Aelia* (Pentatomidae). *Hemyda (= Evibrissa) vittata* (Meigen) has been reared from the pentatomid *Arma custos* Hahn (non-British species) on the Continent. *Phania* species have been reared from Carabidae (Col.) on the Continent.

Leucostomatini. *Cinochira atra* Zetterstedt has been reared from *Eremocoris plebeius* (Fallén) (Lygaeidae). Foreign species of *Dionaea* and *Leucostoma* parasitize Coreidae and the latter some other bugs as well.

Herting (1984) includes the rare *Redtenbacheria insignis* Egger in the Phasiinae (Eutherini) although its only recorded host is *Lymantria monacha* L.; it is also recorded from a pied flycatcher's nest!

Dexiinae

Dexiini. Members of the tribe Dexiini are virtually exclusive parasites of larval Coleoptera (the few records from Lepidoptera need confirmation and may be from species living in the same habitat as 'suitable' beetle hosts). The females deposit fully incubated eggs or first stage larvae in areas frequented by beetles, especially chafers. The larvae search for a host and probably gain entry through a spiracle. The mature larva leaves the host before the latter pupates.

There are non-British records of *Dinera carinifrons* (Fallén) from larvae of Lucanidae, Melolonthinae, Cetoniinae and Cerambycidae. *D. grisescens* (Fallén) parasitises *Harpalus* (Carabidae). *Dexia* species (Bovien & Bollwig, 1939) and *Prosena siberita* (F.) parasitise Melolonthinae.

The two British species of *Trixa* are ovoviviparous and *T. oestroidea* (Robineau-Desvoidy) has been recorded from Lepidoptera (*Operophtera fagata* (Scharfenberg), Geometridae and *Hepialus lupulinus* (L.), Hepialidae). Only first instar larvae have been described (Zuska, 1962) and the genus clearly needs biological investigation.

Herting (1984) includes the tribes Dufouriini and Voriini in Dexiinae (under his system Dufouriinae is the valid name for Dexiinae) which include genera placed in the tribes Campylochaetini and Thelairini in the subfamilies Tachininae and Dufouriinae in the Check List.

Dufouriini. The larvae of the tribe Dufouriini are mostly parasitic in adult Coleoptera, e.g. *Anthomyiopsis* in *Plagiodera* (Chrysomelinae), *Microsoma* (=*Campogaster*) (figs 717–718) in *Sitona* (Curculionidae) (Müller, 1962), *Dufouria* (fig. 719) in *Cassida* (Chrysomelidae), *Freraea* in Carabidae, and *Rondania*, probably on weevils.

Voriini. Members of this tribe are mostly parasites of Lepidoptera, with a few also attacking sawflies (Hym., Symphyta).

The genera *Voria, Athrycia* and *Cyrtophleba* have been reared from Lepidoptera, mostly Noctuidae, and some species from the sawfly *Diprion pini* L.

Blepharomyia pagana (Meigen) (=*amplicornis* Zetterstedt) is parasitic on Geometridae (*Bapta, Opisthograpta, Hybernia*). *Periscepsia carbonaria* (Panzer), *Ramonda* (=*Periscepsia* in part) and *Wagneria* are parasitic on Noctuidae.

Eriothrix species have only been reared on the Continent: *E. prolixa* (Meigen) from *Pyrausta prophyralis* Schiffermüller (Pyralidae) and *E. rufomaculata* (De Geer) from *Arctia hebe* L. (Arctiidae), Noctuidae and 'Bombycids'.

Campylochaeta praecox (Meigen) is a parasite of *Crocallis elinguaria* (L.) (Geometridae), several larvae developing in one caterpillar. *C. (=Elpe) inepta* (Meigen) also parasitizes Geometridae, Sphingidae (*Hyloicus pinastri* (L.)), Notodontidae and (abroad) Arctiidae. *Thelaira nigripes* (F.) parasitizes caterpillars of larger moths, especially Arctiidae.

Tachininae

The tribal classification used here follows Herting (1984).

Microphthalmini. *Dexiosoma caninum* (F.) is a parasite of cockchafer larvae (*Melolontha*, Coleoptera).

Macquartiini. *Macquartia* species are parasites of Chrysomelidae (Col.) and are believed to deposit fully incubated eggs or newly hatched larvae in the vicinity of the hosts. The parasite sometimes emerges only after pupation of the host.

Pelatachinini. *Pelatachina tibialis* (Fallén) (figs 720–721) is a parasite of *Vanessa s.l.* (Lepidoptera), also moths (Agrotidae, Aegeriidae).

Ernestiini. The hosts of *Zophomyia temula* (Scopoli) are unknown. *Hyalurgus lucidus* (Meigen) is a sawfly parasite (*Pteronidea, Pristiphora*, Tenthredinidae). *Gymnochaeta viridis* (Fallén) parasitizes some Noctuidae, Geometridae and Lymantriidae, and *Fausta nemorum* (Meigen) has been reared from *Orthosia cruda* Denis & Schiffermüller (Lep., Noctuidae). *Ernestia* species (fig. 722) parasitize caterpillars of moths (Noctuidae, Lasiocampidae, etc.).

Eurithia species parasitize Noctuidae and other moths; *E. anthophila* (Robineau-Desvoidy) (=*radicum* auctt.) has also been reared from the peacock butterfly (*Inachis io* (L.)) and various Sphingidae.

Loewia foeda (Meigen) and *Eloceria delecta* (Meigen) are parasites of centipedes (*Lithobius*).

Minthoini. *Mintho rufiventris* (Fallén) (=*lacera* Rondani) is a parasite of *Orthopygia glaucinalis* L. (Pyralidae).

Nemoraeini. *Nemoraea pellucida* (Meigen) is a parasite of *Spilosoma lubricepida* (L.) (Arctiidae), *Biston betularia* (L.) (Geometridae) and various Noctuidae.

Leskiini. *Aphria longirostris* (Meigen) has been reared from 'cutworms' (Noctuidae larvae), and *Bithia* (=*Rhinotachina*) *modesta* (Meigen) has been reared from an unnamed Sesiidae (Lep.); the host of *B. spreta* (Meigen) is unknown. *Demoticus plebeius* (Fallén) has been reared on the continent from *Arctia hebe* (L.) (Lep. Arctiidae), *Solieria inanis* (Fallén) from *Spilosoma lutea* Hufnagel (Arctiidae) and *Orthosia incerta* Hufnagel (Noctuidae); *S. pacifica* (Meigen) from the small tortoiseshell butterfly (*Aglais urticae* (L.)). *Leskia aurea* (Fallén) is a parasite of clearwing moths (Sesiidae) and is also recorded from the codling moth (*Cydia pomonella* (L.), Tortricidae).

Linnaemyini. *Lypha dubia* (Fallén) (figs 723–725) is a parasite of the winter moth (*Operophtera brumata* (L.)) and *Agriopis marginaria* (F.), two important geometrid defoliators and other Lepidoptera. It has also been reared from the narcissus bulb fly (*Merodon equestris*, Syrphidae) (Collin, 1945). *L. ruficauda* (Zetterstedt) is a northern species which has been reared from *Notodonta phoebe* Siebert (Notodontidae) and *Hydriomena impluviata* Denis & Schiffermüller (=*coerulata* F.) (Geometridae).

Lydina aenea (Meigen) has been reared from *Panolis flammea* (Denis & Schiffermüller) (=*griseovariegata* Goeze) (Noctuidae) and *Acrobasis tumidella* (Zincken) (Pyralidae). *Linnaemya* species are also parasites of Lepidoptera, especially Noctuidae and Sphingidae, and *Chrysosomopsis auratus* (Fallén) attacks *Horisme tersata* (Denis & Schiffermüller) (Geometridae).

Tachinini. *Peleteria rubescens* Robineau-Desvoidy is a parasite of the swallowtail butterfly (*Papilio machaon* L.), various Noctuidae and the 'nun' moth, *Lymantria monacha* (L.) (Lymantriidae), which can be a serious defoliator of trees on the Continent. *Nowickia ferox* (Panzer) is a parasite of Noctuidae. The large *Tachina grossa* (L.) is parasitic on Sphingidae, Lasiocampidae and Lymantriidae, and the other (smaller) species of *Tachina* (*s.s.*) use Lymantriidae and Noctuidae as hosts. *T.* (s.g. *Servillia*) *lurida* (F.) parasitizes Noctuidae and Sphingidae, but *T. (S.) ursina* Meigen has yet to be reared, as have any species of *Germaria*.

Neaerini. On the continent *Graphogaster brunnescens* Villeneuve has been reared from *Teleiodes notatella* (Hübner) (Gelechiidae), *Evetria resinella* (L.) (Tortricidae) and *Leucoptera laburnella* (Stainton) (Lyonetiidae) (Herting, 1960). *Phytomyptera nigrina* (Meigen) (=*nitidiventris* Rondani) parasitizes Geometridae, Pterophoridae and Olethreutidae. *Elfia cingulata* (Robineau-Desvoidy) is a parasite of *Esperia sulphurella* (F.) (Oecophoridae), the corn moth *Nemapogon (=Tinea) granella* (L.), and the cork moth *N. (=T.) cloacella* (Haworth) (Tineidae), and *Neaera laticornis* (Meigen) has been reared from *Eucosma fulvana* (Stephens) (Olethreutidae).

Triarthriini. *Triarthria (=Digonochaeta) setipennis* (Fallén) (=*spinipennis* Meigen) (figs 726–727) is a parasite of the common earwig *Forficula auricularia* L. (Thompson, 1928) (see also *Ocytata*, Goniini). Records from the caterpillars of various moths and beetles may be erroneous due to earwigs finding access to rearing cages or sharing larval tunnels. Fully incubated eggs are deposited near the hosts into which the larvae burrow. The characteristic puparia (fig. 1249) may be found during winter in soil, under bark, etc.

Siphonini. This tribe was included in the subfamily Goniinae in the *Check List* (Smith *et al.* 1976). First instar larvae of the tribe are described by O'Hara (1988).

Actia species are parasitic on Tortricidae and other families of 'Microlepidoptera' including several pest species. *A. lamia* (Meigen) has been studied by Cheng (1967). *Ceranthia, Ceromya, Goniocera* and *Peribaea* species parasitize the larvae of larger moths e.g. Lasiocampidae.

Siphona species parasitize Noctuidae (including *Mamestra brassicae* (L.)), Geometridae, etc., but *S. cristata* (F.) and *S. geniculata* (De Geer) have also been reared from leatherjackets (Tipulidae larvae: *T. maxima, T. oleracea* and *T. paludosa*). *S. geniculata* (figs 728–730) has 4 slits in each of the posterior spiracles. The larva is attached to one of the main tracheal trunks by means of a chitinous sheath (Rennie & Sutherland, 1920).

Exoristinae

Blondeliini. *Admontia (=Trichopareia)* species are parasites of wood-boring leatherjackets (Tipulidae larvae: *Dictenidia, Ctenophora* and *Tanyptera*). *Belida angelicae* (Meigen) has been reared from *Tortrix viridana* L. (Tortricidae), and *Blondelia nigripes* (Fallén) is parasitic on moths (Noctuidae, Geometridae, Lymantriidae, etc.) and occasionally on sawflies (Hymenoptera: *Athalia, Pteronidea, Priophorus, Diprion*).

The common *Compsilura concinnata* (Meigen) (figs 731–732) has been reared from a greater variety of Lepidoptera than any other British tachinid; it also attacks sawfly larvae of several families. In the U.S.A. and Canada it has been introduced for use in the biological control of caterpillar defoliators including the nun moth (*Lymantria monacha*) and brown-tail moth (*Euproctis chrysorrhoea* (L.)) (Culver, 1919); it also attacks the cabbage white butterflies (*Pieris brassicae* (L.) and *P. rapae* (L.)) (Bissett, 1938).

The rare *Leiophora innoxia* (Meigen) is a parasite of adult fleabeetles (*Haltica*, Chrysomelidae), and *Ligeria angusticornis* (Loew) parasitizes plume moths (Pterophoridae). *Medina* species are parasites of adult Chrysomelidae (Coleoptera), but *M. luctuosa* (Meigen) has also been reared from some Lepidoptera.

Meigenia species are parasites of Chrysomelid larvae, but *M. mutabilis* (Fallén) (figs 733–736) has also been reared from sawfly larvae, moth larvae and *Chorthippus* (Orthoptera, Acrididae).

Oswaldia muscaria (Fallén) attacks Geometridae and Noctuidae.

Pericheta (=Policheta) unicolor (Fallén) is recorded as a parasite of sawfly larvae (*Croesus*) and adult beetles (*Chrysomela*).

Zaira cinerea (Fallén) (fig. 737) parasitizes adult Carabidae (Coleoptera).

Exoristini. *Bessa* parasitizes many families of moths and numerous sawfly larvae. *Diplostichus* is also a sawfly parasite (Diprioniidae) and is recorded from *Acronicta rumicis* (L.) (Lep., Noctuidae).

Exorista larvarum (L.) (figs 738–740) and *E. grandis* (Zetterstedt) are common parasites of a large number of families of butterflies and moths; *E. fasciata* (Fallén) occurs on Lymantriidae and Lasiocampidae but hosts are not known for the remaining British species of the genus.

Parasetigena silvestris (Robineau-Desvoidy) is an important parasite of *Lymantria monacha* and *L. dispar* (L.) (the gipsy moth); it is also recorded from other Lymantriidae and Thyatiridae. *Phorocera* species are also recorded from gipsy moth and several other families of Lepidoptera. *Chaetogena (=Stomatomyia) acuminata* (Rondani) is a moth parasite (Noctuidae) but also attacks terricolous Tenebrionidae (*Blaps, Opatrum*, etc., Coleoptera).

Winthemiini. *Nemorilla floralis* (Fallén) (figs 741–742) is a parasite of Tortricidae, Pyralidae, Oecophoridae (especially *Depressaria*), Hyponomeutidae, and many other families of moths, the peacock butterfly (*Inachis io*) and it has been recorded from a coccinellid beetle (*Epilachna*). Lehrer & Pascovici (1966) illustrate the immature stages.

Smidtia, Timavia and *Winthemia* parasitize several families of moths (e.g. Noctuidae, Geometridae, Lymantriidae, Lasiocampidae).

Goniini. Genera in this tribe are mostly parasitic on Lepidoptera, with some on sawflies.

Erycilla (= Allophorocera) ferruginea (Meigen) parasitizes *Lymantria monacha* and abroad is recorded from a noctuid (*Hypena*) and a tortricid. The rare *Brachichaeta strigata* (Meigen) has been reared from *Notodonta dromedarius* (L.) (Notodontidae). *Clemelis pullata* (Meigen) is a parasite of Pyralidae and abroad has been reared from a psychid.

Cyzenis albicans (Fallén) is the most important parasite of the winter moth (*Operophtera brumata*). The female stores as many as 2,000 minute black eggs in her greatly expanded uterus until they are ready to hatch. The eggs are then laid on leaves damaged by caterpillar feeding. Few of the eggs are in fact swallowed by winter moth caterpillars, but may be swallowed by the caterpillars of other species in which they would not hatch, but most are not swallowed at all. The few successful eggs hatch in the fore gut of the host and the larvae enter a cell of the salivary (silk) gland. Other Geometridae are also attacked by *Cyzenis*.

Elodia ambulatoria (Meigen) attacks Tineidae and Hyponomeutidae while *E. morio* (Fallén) is a parasite of the codling moth (*Cydia pomonella* (L.)), other Tortricidae and some other 'Microlepidoptera'.

Erynnia ocypterata (Fallén) (omitted from the Check List) has been reared from *Sparganothis pilleriana* (Denis & Schiffermüller) (Tortricidae).

Eumea linearicornis (Zetterstedt) (=*westermanni* (Zetterstedt)) parasitizes Noctuidae, Pyralidae, Olethreutidae and Tortricidae.

Eurysthaea scutellaris (Robineau-Desvoidy) (figs 743–745) is one of the Tachinidae with 4 slits in the posterior spiracles (see also *Siphona* and key to families); it attacks Hyponomeutidae, Tortricidae, Noctuidae and Geometridae.

The very rare *Frontina laeta* (Meigen) parasitizes Sphingidae and *Philudoria potatoria* (L.) (Lasiocampidae); *Masicera pavoniae* (Robineau-Desvoidy) also attacks these two families and is a parasite of the emperor moth (*Saturnia pavonia* (L.)) (Saturniidae). *Gonia* species mostly parasitize Noctuidae. *Hebia flavipes* Robineau-Desvoidy attacks Noctuidae and Geometridae, and *Myxexoristops blondeli* (Robineau-Desvoidy) parasitizes sawflies (Hym., Tenthrediniidae) and has also been recorded from *Euproctis chrysorrhoea* (L.) (Lymantriidae). *Ocytata pallipes* (Fallén) (= *Rhacodineura antiqua* (Meigen)) (figs 746–747) is a parasite of earwigs (Dermaptera, *Forficula* — see also *Triarthria*) and is also recorded from the gipsy moth (*Lymantria dispar*) and *Orthosia miniosa* (Denis & Schiffermüller) (Noctuidae).

Pales pavida (Meigen) is commonly reared from Noctuidae, Lymantriidae and other families of Lepidoptera including butterflies (*Inachis io, Aglais urticae*); it has also been reared from a sawfly, *Tenthredo amoena* Gravenhorst.

Phryno vetula (Meigen) attacks *Orthosia, Cosmia* (Noctuidae) and *Apocheima pilosaria* (Denis & Schiffermüller) (Geometridae) and *Lymantria monacha*. *Platymya fimbriata* (Meigen) parasitizes some Noctuidae, Geometridae, Zygaenidae and some sawflies. *Thelymorpha marmorata* (F.) attacks Lymantriidae, Lasiocampidae, Arctiidae, Noctuidae and has also been recorded from chrysomelid beetles (*Phytodecta*). *Zenillia libatrix* (Panzer) is another wide-ranging parasite of many families of Lepidoptera.

Eryciini. This tribe mostly parasitizes Lepidoptera (including several species of butterflies) and some sawflies.

Bactromyia aurulenta (Meigen) is a parasite of *Strymonidia w-album* (Knoch) (Lycaenidae) and moths of the families Notodontidae, Drepanidae, Noctuidae and Geometridae. *Cadurciella tritaeniata* (Rondani) parasitizes *Callophrys rubi* (L.) (Lycaenidae) and *Ostrinia nubilalis* (Hübner) (Pyralidae). *Carcelia* species parasitize Lymantriidae, Lasiocampidae (including the lackey moth, *Malacosoma neustria* (L.)), Arctiidae, Noctuidae, etc. and some sawflies (*Cimbex, Anantholyda*). The large eggs of *Carcelia* may be attached to the host by stalks (fig. 1085).

Senometopia species (usually considered as a subgenus of *Carcelia*) are parasites of Geometridae (including the pine-looper, *Bupalus piniaria* (L.) and *Abraxas*) and several other families of moths and (*S. exisa* (Fallén), figs 748–749) the brimstone butterfly (*Gonepteryx rhamni* (L.), Pieridae) and Sphingidae.

Thecocarcelia species are parasites of Hesperiidae and *T. acutangulata* (Macquart), recently added to the British List (Wyatt, N.P., 1986), has been reared from *Thymelicus lineola* (Ochsenheimer), the Essex skipper, in Austria (Carl, 1968). The very rare *Drino lota* (Meigen) parasitizes certain Noctuidae (*Acronicta, Xestia ashworthii* (Doubleday), *Orthosia stabilis*, (Denis & Schiffermüller)), Sphingidae, the lackey moth (*Malacosma neustria*, Lasiocampidae) and the large white butterfly (*Pieris brassicae*, Pieridae), whilst the very common *Epicampocera succincta* (Meigen) (figs 750–751) attacks the small white butterfly (*Pieris rapae*) and the emperor moth (*Saturnia pavonia*, Saturniidae). *Erycia furibunda* (Zetterstedt) is a parasite of the marsh fritillary (*Euphydryas aurinia* (Rottemburg)) and *Arctia caja* (L.) (Arctiidae). *Huebneria affinis* (Fallén) parasitizes many Arctiidae, Noctuidae, Lymantriidae, Lasiocampidae, the emperor moth (*Saturnia pavonia*) and the butterflies *Aglais urticae* (Nymphalidae) and *Callophrys rubi* (Lycaenidae).

The two very common species of *Lydella* are parasitic on a variety of Noctuidae and other families, including the economically important European corn-borer (*Ostrinia nubilalis*, Pyralidae). *Nilea hortulana* (Meigen) parasitizes Noctuidae, especially *Acronicta* species and several pest species of Lepidoptera including *Mamestra brassicae* (L.), *Pieris brassicae, Malacosoma neustria, Orgyia antiqua* (L.), etc.

Phebellia species have been reared from Lymantriidae, Arctiidae and Noctuidae, and the sawflies *Cimbex* and *Diprion*. Probably most species occurring in Britain have been confused with *P. glauca* (Meigen) and their precise host ranges need clarification.

Phryxe species (figs 752–755) have been recorded from a wide range of Lepidopterous hosts of at least 15 families (as well as earwigs and sawflies) and are probably the most commonly reared tachinids. However, there has been confusion over the identity of the British species and no doubt records for *P. vulgaris* (Fallén) and *P. nemea* (Meigen) include some for other species.

Pseudoperichaeta nigrolineata (Walker) (= *roseanae* Brauer & Bergenstamm) parasitizes Pyralidae (including *Ostrinia nubilalis*, the European corn-borer), Tortricidae, Noctuidae and *Lysandra bellargus* (Rottemburg) (Lycaenidae). *Tlephusa diligens* (Zetterstedt) has been reared from *Melanchra persicaria* (L.) (Noctuidae), and *Xylotachina diluta* (Meigen) (= *ligniperdae* Brauer & Bergenstamm) is a parasite of the goat moth *Cossus cossus* (L.)

Rhinophoridae

(Figs: larvae 756–767, eggs 1086–1087, puparium 1252)

The family Rhinophoridae (woodlouse-flies) contains 23 species in 10 genera mostly found in the Old World and best represented in the western Palaearctic Region and South Africa. Until recently the family has been variously placed as a subfamily of either Calliphoridae or Tachinidae. The larvae are parasitic in woodlice (Isopoda, Crustacea) and those of the first stage (figs 758, 764–767) are specially adapted for holding onto and penetrating the host (e.g. pseudopods, sclerotised scales, elongated pharyngeal sclerites, etc.). Eggs (figs 1086–1087) are laid freely away from the host. Some species have been recorded from spiders (Arachnida) and bugs (Hemiptera) but these associations require confirmation. Eleven species representing 8 genera occur in Britain.

Crosskey (1977) provides a taxonomic review of the family. Thompson (1934) and Bedding (1973) have described the immature stages of seven of the British species: *Phyto melanocephala* (Meigen) (figs 756–757), *P. discrepans* Pandellé, *Tricogena rubricosa* (Meigen) (figs 758–760), *Stevenia atramentaria* (Meigen) (figs 766–767), *Rhinophora lepida* (Meigen), *Paykullia maculata* (Fallén) (figs 761–762) and *Melanophora roralis* (L.) (figs 763–765).

Bedding (1973) found that *Porcellio scaber* Latreille is much more heavily parasitized (by five species) than other equally common and gregarious woodlice, e.g. *Oniscus asellus* L. (attacked by *P. maculata* and *P. discrepans*). *Armadillidium vulgare* (Latreille) is attacked by *P. melanocephala* and *Trachelipus rathkei* (Brandt) by *S. atramentaria.* No Rhinophoridae had been recorded from other British woodlice until Irwin (1985a) reared *M. roralis* from *Porcellio spinicornis* Say. Bedding found that among the species of Rhinophoridae attacking *P. scaber* specific habitats were favoured as follows: *Melanophora* on the upper shore, *Phyto discrepans* in rubbish dumps and gardens, and *Paykullia* on colonies of woodlice under loose bark.

Further research will clearly be fruitful on these parasites of woodlice and the excellent book by Sutton (1972) will facilitate identification of the hosts. There is also an active British Isopoda Study Group organised from the Institute of Terrestrial Ecology, Huntingdon.

Sarcophagidae

(Figs: larvae 768–785, eggs 1088–1090, puparia 1253–1254)

The Sarcophagidae (flesh-flies) is a large and cosmopolitan family of about 2,500 species in 5 subfamilies. Until recently the family was treated as a subfamily of the Calliphoridae. Some 56 species in 16 genera representing 4 subfamilies occur in Britain.

The reproductive habit is mostly larviparous though some lay eggs. The larvae may be parasitic on Orthoptera, Isoptera, Hymenoptera and some Diptera, or saprophagous, and they may (especially *Wohlfahrtia*) also be involved in cases of myiasis in man and animals, mostly abroad.

W. R. Thompson (1920) describes the larvae of several species, especially first instar Miltogramminae. Zumpt (1965) is useful for larvae of *Sarcophaga.* Some other references are cited below and the excellent work of Pape (1987) should be consulted.

Miltogramminae. Larvae of *Amobia signata* (Meigen) (figs 768–770) are found in the nests of wasps (Sphecidae, Vespidae) and some bees (Apidae). The adult female settles near the nest and enters as the host leaves. Inside the nest she deposits small larvae which commence feeding on the food store of the host larvae (e.g. spiders, caterpillars, etc.).

Adults of *Miltogramma* species (figs 771) shadow the host sand or digger wasp (Sphecidae) back to the nest, then dart in to lay one or two eggs on the prey, then quickly exit.

Larvae of *Senotainia conica* (Fallén) (figs 772–774) also develop in the nests of Sphecidae. Adult females apparently oviposit on the female wasps while they are carrying prey back to the nests.

Larvae of *Pterella grisea* (Meigen) have been found in *Cerceris* (Hym., Sphecidae) burrows in *Clythra* (Col., Chrysomelidae) collected by the female wasp as food for its larvae.

Metopia species (fig. 775) are apparently viviparous. The female either enters the nest (of Sphecidae, Apidae and *Pompilus*) or pounces upon the prey as it is being dragged in.

The larvae of *Oebalia* (= *Ptychoneura*) (figs 776–777) are found in the nests of Sphecidae (*Coelocrabro, Cemonus, Rhopalum, Pemphredon*). Eggs are laid on the female wasps (figs 1088–1089) (Day & Smith, 1980) and this behaviour has also been observed in North America (Sanborne, 1982).

Macronychiinae. *Macronychia striginervis* (Zetterstedt) (= *ungulans* (Pandellé)) larvae have been found in the nests of Vespidae, Sphecidae and *Bombus*. In North America P. H. Thompson (1978) has found larvae of a *Macronychia* species (near *aurata* Coquillett) in adult Tabanidae. Dipterous parasites of Diptera are very rare indeed, especially of adults (see under Tachinidae and Smith, 1974c).

The female of *Brachicoma devia* (Fallén) deposits young larvae in *Bombus* (especially *B. pascuorum* (Scopoli) (= *agrorum* (F.)) and *Vespula* nests, where they are very common. The larvae (figs 778–779) attack and kill the prepupal stage of the host and pupate in the nest material (summer pupae) or in nearby soil (hibernating pupae).

Agriinae. *Nyctia halterata* (Panzer) is parasitic in weevils (*Lixus*). Larvae of *Angiometopa falleni* Pape (= *ruralis* Fallén) are said to have been found abroad in superficial wounds of man and horse. The larvae of *Agria* species are polyphagous and frequently parasitic or predaceous on insects, especially the larvae and pupae of Lepidoptera (Tölg, 1913). *Sarcophila latifrons* (Fallén) (fig. 780) feeds on carrion, dead insects and possibly also living insects. It has been recorded from various Acrididae.

Helicobosca distinguenda Villeneuve is viviparous, producing larvae some 5 mm long which feed on dead snails. Some workers regard this genus as more correctly placed in the Calliphoridae.

Sarcophaginae. *Ravinia pernix* (Harris) is parasitic in molluscs and insects.

Blaesoxipha species are ovoviviparous; the larvae are parasitic in grasshoppers and locusts (Orthoptera, Acrididae) abroad (see Greathead, 1963 who reviews the parasites of Acrididae).

Sarcophaga species (figs 781–785) are larviparous and have a wide range of larval habitats from saprophagous feeding in decaying organic matter, dung and carrion to parasitism (of molluscs, insects and spider egg sacs) and causing myiasis in man and other vertebrates, as follows:

Dung (including human excrement): *S. albiceps* Meigen, *S. argyrostoma* Robineau-Desvoidy, *S. cruentata* Meigen (= *haemorrhoidalis* (Fallén)) (figs 781–785), *S. exuberans* Pandellé, *S. incisilobata* Pandellé.

Carrion: *S. argyrostoma, S. carnaria* L., *S. cruentata*.

Myiasis: ?*S. argyrostoma*, ?*S. carnaria*, ?*S. exuberans*, *S. cruentata*.

Molluscs (*Helix*, etc.): *S. agnata* Rondani, *S. anaces* Walker (= *setipennis* Rondani), *S. argyrostoma, S. filia* Rondani, *S. haemorrhoa* Meigen, *S. hirticrus* Pandellé, *S. melanura* Meigen, *S. nigriventris* Meigen (from living *Helicella* and *Theba*) and *S. teretirostris* Pandellé.

Insects: *S. albiceps* (Lepidoptera; Scarabaeidae and *Saperda* (Col.)), *S. aratrix* Pandellé (*Lymantria monacha* (Lep.), *Prionus* (Col.), *S. argyrostoma* (locusts)), *S. caerulescens* Zetterstedt (= *scoparia* Pandellé) (*Lymantria monacha*), *S. exuberans* (Lepidoptera, *Diprion* (Hym.), Orthoptera), *S. incisilobata* (locusts), *S. nigriventris* ('locust'; *Carabus*, moribund *Nicrophorus, Blaps* (Col.)).

Spider egg sacs (*Epeira cornuta* Koch): *S. sexpunctata* F. (= *clathrata* Meigen).

The above data cover the whole zoogeographical range of the species concerned and include non-British records (especially of myiasis). However, some identifications may be suspect; for example the common *S. carnaria* has been widely reported to cause myiasis in man (e.g. James, 1947). Zumpt (1965) refutes this, citing Kirchberg's claim (1954) that *S. carnaria* is an obligate parasite of earthworms. Greenberg (1971:79) however casts doubt on Kirchberg's claim as he has reared *S. carnaria* from carrion.

Clearly, detailed study of the precise feeding habits of the larvae of our British *Sarcophaga* would be a useful undertaking providing extreme care were taken over identification (from reared adult males which should be submitted to a specialist).

Calliphoridae

(Figs: larvae 786–790, 794–828; eggs 791, 1091–1093; puparia 792–793, 1255–1256)

Over 1100 species of Calliphoridae (blow-flies) are known and the family occurs abundantly in all zoogeographical regions. The classification is difficult and the family is variously divided into 5 to 10 subfamilies by different workers. Some 32 species in 11 genera representing 4 subfamilies occur in Britain.

Calliphoridae are oviparous or larviparous. The larvae (maggots) may be omnivorous, carnivorous or parasitic on or in decaying organic matter such as carrion, excrement, foodstuffs, insects, earthworms, snails, toads, birds and mammals. They may also cause myiasis in man and other vertebrates. The nomenclature follows Schumann (in Soós & Papp, 1986) but for convenience the sequence of genera follows the British Check List (Smith 1976).

Calliphorinae. Larvae of *Calliphora* (bluebottles) occur in a variety of decaying substances, especially carrion, including human cadavers which gives them considerable forensic importance in establishing post mortem interval (time of death) (Smith 1986b). Their occurrence in human foods, especially meat products, cheese, etc. makes them easily the commonest insect larvae submitted to entomologists for identification. Usually accompanying such requests is a desire to know rate of development and temperature-tolerance (especially under refrigeration). A few comments on this may therefore be of value. *Calliphora* oviposits at night (except in slaughterhouses) and it is doubtful if eggs are laid at temperatures lower than 12°C (though oviposition on partly frozen pig carcasses when exposed to air temperatures has been observed). At temperatures below 4°C *Calliphora* eggs will not hatch but at 6–7°C hatching of eggs and larval development occurs. Up to 300 eggs may be laid, either in smaller groups or a single batch, in natural orifices, crevices in the surface or wounds. The rate of development fluctuates with temperature but at 27°C and 50% R. H. for *C. vicina* Robineau-Desvoidy (the common urban bluebottle) is recorded as follows (average in brackets): egg, 20–28 (24) hours; first stage larva, 18–34 (24) hours; second stage larva 16–28 (20) hours; third stage larva, 30–68 (48) hours; prepupa, 72–290 (128) hours; pupa, 9–15 (11) days; total immature stages 14–25 (18) days (figures after Kamal, 1958). On completion of feeding the maggots disperse from the food source up to a distance of 20 feet or more searching for pupation sites. When this occurs indoors, this may result in maggots being sent to entomologists via local health authorities. In such cases hidden sources should be sought, e.g. dead pigeons trapped behind sealed fireplaces, dead mice in attics, cellars, cupboards, etc. To facilitate identification of this very important species all the immature stages are shown (figs 786–793) on one plate and some also to illustrate the introductory sections.

C. vomitoria (L.) (the rural bluebottle) may be equally common, especially in country areas, and has a similar life-history, but appears to spend longer in each of the later stages (especially the prepupa) (see Kamal, 1958); further investigation is required.

Other *Calliphora* species share similar larval habits but are more restricted in distribution. *Calliphora* larvae may be distinguished at once from *Lucilia* species (except *L. ampullacea* Villeneuve, fig. 810) found in similar situations by the presence of the accessory oral sclerite (os) between the mandibles (best seen in ventral view).

Erzinçlioğlu (1985) provides keys to all larval instars of British species of *Calliphora* and further information on establishing their age is provided by Smith (1986b).

Melinda cognata (Meigen) and *M. gentilis* Robineau-Desvoidy (figs 795–798) are parasitic in snails (e.g. *Cernuella virgata* Da Costa, *Discus rotundatus* Müller, *Helicella itala* (L.), etc.) (Keilin, 1919; Schumann, 1973).

Larvae of *Bellardia agilis* (Meigen) (figs 799–801), *B. pandia* (Walker) (=*biseta* Kramer) and *B. pusilla* (Meigen) (fig. 802) occur diffusely in the soil of orchards, kitchen gardens, etc. and are thought to be parasites or predators of earthworms, but no specific rearings have been made (Lobanov, 1971; Schumann, 1974).

The larva of *Cynomya mortuorum* (L.) (figs 803–804) is a carrion feeder and also occurs in human excrement, but is not a myiasis producer. It shares with *Calliphora* the distinctive accessory oral sclerite (os) in the mouthparts (figs 788, 804) and is treated fully by Erzinçlioğlu (1985).

Lucilia species (greenbottles) have similar habits to *Calliphora*, i.e. are saprophagous and will breed in carrion and dung. Some may be facultative parasites and be involved in myiasis and a few are obligate parasites of Amphibia (Zumpt, 1965).

L. sericata (Meigen) (sheep maggot fly or sheep blowfly) (figs 806–809) has been known as the causal agent of sheep strike since the sixteenth century. Infested sheep do not feed properly, lose condition and death can occur within a few days (probably due to toxaemia or septicaemia). A female fly lays 2,000 to 3,000 eggs in 9–10 batches. The rates of development at 27°C and 50% R.H. (average in brackets) are: eggs, 12–38 (18) hours; first stage larva, 12–28 (20) hours; second stage larva 19–26 (12) hours; third stage larva, 24–72 (40) hours; prepupa 48–192 (90) hours; pupa, 5–11 (7) days; total immature stages, 12–15 (12) days (after Kamal, 1958). Probably bacterial activity in the fleece (wool rot) or the presence of wounds initiates oviposition but work is still required on this. Larvae in pre-existing wounds become facultative parasites and do the most damage. However on the credit side, the larvae restrict themselves to dead tissue and in fact stimulate the healing process by their excretions (Pavillard & Wright, 1957). This has led to their surgical use in the treatment of osteomyelitis and other non-healing wounds, e.g. gangrene, heat burns, X-ray burns, varicose and diabetic ulcers, etc. However, care must be taken, as if sufficient necrotic tissue is unavailable the larvae may attack living healthy tissue in order to complete their development (see also under *Phormia, Musca domestica* and introductory section on Medical and Veterinary Importance). *L. sericata* has been involved in aural myiasis in Britain (Smart, 1936). *L. caesar* (L.) and *L. illustris* (Meigen) (fig. 805) (as well as occasionally *Calliphora vicina, C. vomitoria, Protophormia terraenovae* and the muscid *Muscina prolapsa* (=*pabulorum*)) may also be involved in sheep strike in addition to their general role as carrion-feeders (Macleod, 1937).

L. ampullacea Villeneuve (fig. 810) and *L. richardsi* Collin are carrion breeders. The larva of the former has a small accessory oral sclerite similar to *Calliphora*. The larvae of *L. bufonivora* Moniez (figs 811–812) are obligate parasites of Amphibia (especially toads) and are unable to develop in carrion. Apart from *L. bufonivora* almost any *Lucilia* could have forensic importance on human cadavers (Smith, 1986b).

The biology of the Scottish *Pseudonesia puberula* (Zetterstedt) is unknown. The viviparous *Eggisops pecchiolii* Rondani is parasitic in snails.

Polleniinae. *Pollenia* (figs 813–818) species parasitize earthworms of the genus *Allolobophora*. Keilin (1915) worked out the life-history but later workers especially in America (e.g. Thomson & Davies, 1973–1975) differ in detail. Keilin claimed that only one larva developed in each host worm so that the abundance of *Pollenia rudis* (F.) (the cluster fly) may seem puzzling until one reflects that Darwin (1881) estimated that the soil population of earthworms was perhaps some 50,000 per acre!

Phormiinae. *Phormia regina* (Meigen) and *Protophormia terranovae* (Robineau-Desvoidy) (figs 819–822) are both carrion feeders and myiasis causers. Although *P. terranovae* has not been recorded as causing myiasis in man, both species have been used to clean wounds sustained by soldiers (see comments under *Lucilia sericata*). Both species may have forensic importance in human cadavers (Smith, 1986b).

The larvae of *Protocalliphora azurea* Fallén (bird blowfly) (figs 823–824) occur in the nests of birds (swallow, sparrows and other birds especially Oscine Passeriformes) where they suck the blood of nestlings by means of a suction pad on the first segment, often killing them.

Rhiniinae. *Stomorhina lunata* (F.) (figs 825–828) has only been recorded sporadically in Britain (1901, with scattered records to 1947). Abroad it lays its eggs in the egg pods of locusts (Greathead, 1963) and appears to be associated with locust swarms. It may be significant that in the two years cited there was notable insect immigration in this country, 1947 in particular yielding many records of the migratory locust (*Locusta migratoria* (L.)) (Colyer & Hammond, 1951). Perhaps it may adapt (or has adapted) to a British Acridid.

Scathophagidae

(Figs: larvae 829–854, eggs 1094–1096, puparia 1257–1262, leaf-mines 1307–1308)

Some 360 species of Scathophagidae in 66 genera are distributed mainly in the Northern Hemisphere. The larvae are mostly phytophagous but some develop in dung, possibly in carrion, and others in rotting seaweed on the coast. Fifty-three species in 22 genera and 2 subfamilies occur in Britain. British genera not mentioned may be assumed to be unknown in the immature stages.

Scathophaginae. *Norellia spinipes* (Meigen) (figs 829–832) has been found to mine the leaves of daffodils (*Narcissus*) (fig. 1308), pupating at the base of the plant and sometimes damaging the bulbs (Ciampolini, 1957, Chandler & Stubbs, 1969, 1970; de Jong, 1985; Smith & Vardy, 1988). *N.* (s.g. *Norellisoma*) *spinimana* (Fallén) (figs 833–834) mines stems of docks (*Rumex*) (Disney, 1976b) and *N.* (*N.*) *liturata* (Meigen) appears to be associated with meadowsweet (*Filipendula*).

The immature stages of *Cordilura* species develop in *Carex*, *Scirpus* and *Juncus* in the U.S.A. according to Wallace & Neff (1971) who include one Holarctic species that occurs in Britain, viz. *C. pudica* Meigen (figs 835–837). The larvae of *Cordilura* are apparently distinguished by the presence of paired bifid mouth-hooks (fig 838) which should help in searching for the 10 other British species so far unknown in this stage.

Nanna (= *Amaurosoma*) species (timothy flies) (figs 839–840) feed on the flower heads of grasses and some (*N. armillata* (Zetterstedt), *N. flavipes* (Fallén)) are pests of rye and *Phleum pratense* L. (Timothy grass) (Nye, 1958).

The larvae of *Cleigastra (= Cnemopogon) apicalis* (Meigen) occur in *Phragmites* where they were thought to be predaceous on the larvae of *Lipara* (Chloropidae) and where their puparia overwinter between the top blades of the *Lipara* galls (Chvála *et al.*, 1974). However, Groth (1969) found that the *Cleigastra* larvae feed on the excrement of caterpillars (*Archanara geminipuncta* Haworth and *Arenostola phragmitidis* Hübner, Noctuidae) in the stems.

According to Vockeroth (in Chandler & Stubbs, 1974), *Cosmetopus, Microprosopa, Pogonota, Chaetosa, Trichopalpus* and *Spaziphora* belong to a group of genera which probably have predaceous larvae living in subaquatic or aquatic situations. Of this group, only the life cycle of *Spaziphora (= Spathiphora) hydromyzina* (Fallén) (figs 841, 842) had then been fully worked out. It occurs in sewage beds and stagnant water where the larva grazes over the pebbles, on algae and fungal growth but also eats cocoons of Chironomidae and clusters of *Lumbricillus lineatus* (Müller) worms and cocoons (Graham, 1939; Lloyd *et al.*, 1940).

The genus *Acanthocnema* can now be added to this group of aquatic Scathophagidae. Females of *Acanthocnema (Clinoceroides) glaucescens* (Loew) crawl beneath the water surface of streams, down the sides of projecting stones. On the underside of the stones they lay their eggs in the egg masses of *Dixa*, other flies and Trichoptera. The larva feeds on the eggs and surrounding jelly of the host (Hinton, 1981). *Coniosternum obscurum* (Fallén) (formerly in *Scathophaga*) may now also be included in this group. The larvae feed on the egg masses of caddis flies (Trichoptera) (Berté & Wallace, 1987).

Scathophaga stercoraria (L.) (the yellow dung fly) (figs 843–847) breeds in dung (cow, sheep, horse, dog, poultry and human) where the larvae are said to be carnivorous. The larva is described by Schumann (1960). Other dung breeding *Scathophaga* include *S. furcata* (Say) (dog, human, sheep, privies; also owl pellets); *S. lutaria* (F.) (human); *S. inquinata* Meigen and *S. scybalaria* (L.) (unspecified 'dung'). *S. litorea* Fallén, *S. calida* Curtis and *Ceratinostoma ostiorum* (Curtis) breed in thick moist rotten seaweed on the sea shore.

Gimnomera tarsea (Fallén) (fig. 848) develops in the seed pods of *Pedicularis* species (Scrophulariaceae) (Chandler, 1975).

The larvae of *Hydromyza livens* (F.) (figs 849–851) mine the stems and leaves of the yellow water lilies (*Nymphaea, Nuphar*) (fig. 1307).

Delininae. *Parallelomma vittatum* (Meigen) and *Delina nigrita* (Fallén) (figs 852–854) are both leaf-miners in orchids (Meijere, 1940). The life-history of *Leptopa filiformis* Zetterstedt is unknown but the adults inhabit shady woods.

Anthomyiidae

(Figs: larvae 855–902, eggs 1097–1099, puparia 1263–1265, leaf-mines 1309–1310)

About 1,200 species in some 55 genera of Anthomyiidae are known to science but no doubt more species await description in this neglected family. The immature stages are little known; some are phytophagous and a few species are well known agricultural pests. Others live as scavengers in decaying organic matter. Some 220 species in 34 genera occur in Britain. Papers by Dušek (1969, 1970) are useful for the identification of the immature stages, especially of the economically important species. Other references are cited under each genus. The arrangement of the posterior fleshy processes is a valuable help for spot identifications among the economic species. Genera not mentioned may be assumed to be unknown in the immature stages. Reared adults should be identified using Hennig (1966–1976) who also gives a full list of rearing records and parasites. Much biological information is also included in Stubbs & Chandler (1978).

The larvae of *Chirosia* species (figs 855–857) mine the leaves of ferns (*Pteridium, Athyrium filix-femina, Thelypteris palustris*), some causing the tips of the frond to roll over (fig. 1310) (see also *Acrostilpna* below).

Fucellia species frequent seaweed on seashores. Egglishaw (1960c) describes the life-history of *Fucellia maritima* Haliday (figs 858–862), which he found mostly in the smaller wrack banks.

Chiastocheta species (figs 863–865) lay their eggs in the unripe seed-heads of *Trollius* and the larvae bore into and feed upon the seeds, eventually leaving the seed-head to pupate in the earth.

Pegohylemyia fugax (Meigen) (figs 866–868) is associated mostly with decaying vegetation. From May to October its eggs are numerous on cruciferous crops, usually on dead leaves, in cracked and broken stems, etc. Larvae have been recovered from cauliflower heads, Brussels sprouts, swedes, spring cabbages, cabbage seedlings, turnips, lettuce, beet and oat seedlings. The larvae of *P. gnava* (Meigen) (figs 869–871) (the lettuce seed fly) develop in *Lactuca* species. *P. silvatica* (Robineau-Desvoidy) has been reared from fungi (agarics, boleti, *Phallus*). *P. phrenione* (Séguy), *P. dissecta* (Meigen) and *P. laterella* Collin are all associated with the grass-fungus *Epichloe typhina* Tulasne (though they have been misidentified in the literature as *Anthomyia spreta*, e.g. Lucas, 1909; *Chortophila humerella*, etc.). The larvae of *P. seneciella* (Meade) and *P. jacobaeae* (Hardy) develop in the flower-heads of *Senecio* and have been used in Australia and New Zealand in the biological control of introduced weeds; *P. pseudomaculipes* Strobl develops in the flower-heads of *Solidago virgaurea* L.; *P. brunneilinea* (Zetterstedt) in *Centaurea* (? base of stem); *P. sonchi* (Hardy) in *Sonchus*; *P. spinosa* (Rondani) in *Achillea millefolium* (stem); *P. sanctimarci* (Czerny)? in *Allium ursinum*.

Lasiomma meadei (Kowarz) has been reared from cow and human dung and birds' nests. *L. anthomyinum* (Rondani) and *L. octoguttatum* (Zetterstedt) have also been reared from birds' nests (Collin, 1939; Hicks, 1959). Beaver (1969) has reared the latter from dead snails and a puparium has been described from an 'alluvial deposit of River Rhine near Herwen' by Stork (1936). *L. melania* and *L. infrequens* (both described by Ackland (1965)) may feed on the seeds of larch as do related species abroad.

Hydrophoria lancifer (Harris) (= *conica* (Wiedemann)) breeds in human dung. There is a specimen of *H. linogrisea* Meigen in the British Museum (Nat. Hist.) labelled 'round *Andrena* burrows', but no association between *Hydrophoria* and bees is known.

Larvae of *Acrostilpna latipennis* (Zetterstedt) occur in the leaf-stem of the fern, *Athyrium filix-femina*.

According to Stork (1936) larvae of *Craspedochoeta pullula* (Zetterstedt) have been recorded as injurious to *Iris* and *Gladiolus* by eating the flowers, leaves and stems, but I know of no recent (or British) records of this. Hammond & Smith (1953) record a specimen of *C. pullula* which had emerged in a tin containing seedling lettuce leaves and sterilized peat and leaf-mould provided as pabulum for a caterpillar of *Agrotis segetum* (Lep., Noctuidae). The caterpillar died and parasitism was thus suspected but seemed hardly likely. However there are two specimens of *C. cannabina* Stein in the British Museum (Nat. Hist.) ex coll. W. Rait-Smith (a Lepidopterist but also a careful recorder of their parasites, e.g. see Morley & Rait-Smith, 1933), labelled 'Dip. parasite of *Tinea lapella* Hübner'. At least we were not alone in our mistake if such it proves to be (see also comments under rearing Tachinidae; and Smith, 1974b). These records seem doubtful or possibly chance occurrences. Both *C. cannabina* and *T. lapella* occur in birds' nests! Beaver (1969) has reared *C. pullula* from dead snails (pupating in the soil) and suggests that it probably breeds in decaying animal matter.

Anthomyia species have been reared from fungi: *A. pluvialis* (L.) from several agarics, boleti and *Phallus*; *A. procellaris* Rondani (figs 872–874) from *Pleurotus ostreatus* Quélet. Both species have also been reared from birds' nests (Hicks, 1959–1971), where Keilin (1924b) claims they feed on 'various decomposed organic substances including greasy scales and down left by the birds'.

The larvae of *Phorbia securis* (Tiensuu) (=*genitalis* auctt.) (figs 875–877) and *P. sepia* (Meigen) (late-wheat shoot-flies) attach the shoots of wheat and occasionally other cereals.

The larvae of some *Leucophora* species live upon the pollen masses stored by bees or have otherwise been associated with Aculeate Hymenoptera as follows: *L. grisella* Hennig (*Panurgus calcaratus* (Scopoli), *Cerceris arenaria* (L.)); *L. cinerea* Robineau-Desvoidy (*Halictus nitidiusculus* (Kirby); *L. obtusa* (Zetterstedt) (*Andrena fulva* (Müller in Allioni)); *L. personata* (Collin) (*Andrena labialis* (Kirby), *A. nigroanenea* (Kirby) and *A. trimmerana* (Kirby)); *L. sericea* Robineau-Desvoidy (*Andrena haemorrhoa* (F.) (= *albicans* misident), *A. fulva*) (Collin, 1921).

Eustalomyia species (figs 878) are similarly associated with Aculeate Hymenoptera (Smith, 1971), especially the burrows of Sphecidae.

The genus *Delia* (=*Erioischia, Leptohylemyia*) contains several species which are well known agricultural and horticultural pests. *D. antiqua* (Meigen) (onion fly) (figs 879–881) attacks young onion plants, leeks and shallots in gardens and market gardens especially in the Midlands and East Anglia; it kills young plants outright and also tunnels in onion and tulip bulbs. *D. radicum* (L.) (=*brassicae* (Hoffmannsegg in Wiedemann)) (cabbage root fly) (figs 882–886) inflicts most damage on early cauliflowers and summer cabbages but radishes, turnips and swedes are also attacked. The larvae are mostly root feeders but also tunnel the stems. The larvae of *D. cardui* (Meigen) (carnation fly) attack carnations and sweet williams, first mining the leaves then later burrowing down into the stem and devouring the pith. *D. coarctata* (Fallén) (wheat bulb fly) (figs 887–890) attacks winter wheat, barley and rye; its known wild host is couch grass (*Agropyron repens* (L.)). The larvae in the central shoot kill the growing point, then move to another plant. *D. echinata* (Séguy) (spinach stem fly) (figs 891–893) attacks seedlings of spinach forming small blotch mines in the leaves, then tunnelling via the veins or midribs into the stem (Miles, 1953). *D. floralis* (Fallén) (turnip root fly) attacks turnips, especially in Scotland, making wounds which admit pathogens causing the swollen roots to rot; it may also cause severe damage to seedlings and newly transplanted crops of onions and leeks (Miles, 1953). *D. platura* (Meigen) (=*cilicrura* Rondani) (bean seed fly) (figs 894–897) is widely polyphagous and attacks French and runner beans, broad beans, onions, *Brassica*, lettuce, and occasionally winter cereals. Other known associations of *Delia* species with higher plants (not all are British rearing records) are as follows: *D. coronariae* (Hendel), *Lychnis flos-cuculi* L. (stem); *D. flavifrons* (Zetterstedt), *Silene cucubalus* Wibel (seed); *D. florilega* (Zetterstedt) (=*trichodactyla* Rondani), *Raphanus sativus* L., *Armoracia rusticana* Gaertner, *Brassica* spp., *Cichorium intybus* L. (root); *D. planipalpis* (Stein), *Brassica napus* L., *B. rapa* L. (in turnip roots); *D. quadripila* (Stein), *Honckenya peploides* (L.) (leaf-miner). Further information on this important genus is given in Hennig (1966–1976) and Stubbs & Chandler (1978). Some species of *Delia* have been reared from fungi as follows: *D. albula* (Fallén), from *Psathyrella*; *D. antiqua*, several agarics (*Russula, Amanita, Tricholoma, Armillaria*) but the precise association with fungi requires investigation, see above); *D. frontella* (Zetterstedt) from *Suillus bovinus* (L.); the widely polyphagous *D. platura* (see also above) from young plasmodium of *Fuligo*.

Subhylemyia longula (Fallén) has been reared from dead snails (*Cepaea nemoralis* (L.)); it pupates in the soil (Beaver, 1969).

The larvae of some species of *Hylemya* occur in cow dung as follows: *H. nigrimana* (Meigen), *H. vagans* (Panzer) (=*strigosa* (F.)) and *H. variata* (Fallén). Adults of these and other species have been seen on dung (including human) but not reared from it. *H. latifrons* Schnabl & Dziedzicki has been reared from fungi (*Boletus subtomentosus* L.).

Heterostylodes species have been reared from flower-heads of Compositae (*Hieracium, Picris, Leontodon* and *Hypochoeris*). *Paregle audacula* (Harris) (=*radicum* of authors) breeds in cow, human and dog dung; *P. cinerella* (Fallén) is recorded from the dung of hedgehog, dog and cow/horse manure. The larvae of all *Egle* species develop in the catkins of *Salix* and *Populus tremula* L.

Calythea nigricans (Robineau-Desvoidy) occurs in pig dung and *Nupedia aestiva* (Meigen) breeds in cow dung but the life-histories of the other common species in these two genera appear to be little known. *Paradelia palliceps* (Zetterstedt) (=*Pseudonupedia setinerva* Ringdahl) has been reared from fungi (*Suillus granulatus* (L.)), and *Emmesomyia* species probably breed in excrement; adults have been seen on human and horse dung.

The habits of the large genus *Pegomya* (42 British species) are about evenly divided between feeding on fungi and the higher plants. Full host lists are provided by Hennig (1966–1976) and Stubbs & Chandler (1978), but here the fungus feeders are listed first and selected plant feeders are treated below.

Fungus feeding *Pegomya*: *calyptrata* (Zetterstedt), *deprimata* (Zetterstedt), *fulgens* (Meigen), *furva* Ringdahl, *geniculata* Bouché, *incisiva* Stein, *maculata* Stein, *pallidoscutellata* (Zetterstedt), *pulchripes* (Loew), *rufina* (Fallén), *tabida* (Meigen), *tenera* (Zetterstedt), *transversa* (Fallén), *ulmaria* Rondani, *vittigera* (Zetterstedt) and *zonata* (Zetterstedt).

The larvae of *Pegomya hyoscami* (Panzer) (beet or mangold fly or beet leaf miner) (figs 898–902) form blister mines on beet and mangolds. Most damage occurs on late sown plants which have little leaf area developed when the first brood of flies appears. *P. rubivora* (Coquillett) (loganberry cane fly) attacks stems of *Rubus idaeus* L. and *Filipendula*.

Mycophaga testacea Gimmerthal has been reported as having carnivorous larvae in many fungi but this seems very doubtful. Adults occur near fungi and may have been confused with similar adult Muscidae which do have carnivorous larvae (see also Muscidae).

Fanniidae

(Figs: larvae 903–908, egg 1100, puparium 1266)

There are some 265 species of Fanniidae contained in 4 genera. The family is best represented in the Palaearctic (107 species) and Nearctic (105, of which 29 are Holarctic) regions. There are 59 British species representing two genera. Larval Fanniidae are very characteristic with a thickened coarse cuticle and the body is dorso-ventrally flattened with a number of fleshy dorsal and lateral processes, which may be plumed, pubescent or simple. The eggs have flange-like processes (fig. 1100). The immature stages develop in a wide range of decaying organic matter usually of vegetable origin but also in excrement and in carrion. Some occur in fungi or the burrows and nests of mammals, birds and insects (social Hymenoptera) and a few are of medical or veterinary importance in cases of myiasis. The larvae of only 16 of the British species are known (Lyneborg, 1970) but rearing data for a further 12 species are available.

Piezura species have been reared from fungi; *P. boletorum* (Rondani) from an unidentified fungus and *P. graminicola* (Zetterstedt) from *Coprinus micaceus* Fries.

Fannia aequilineata Ringdahl has been reared from a blackbird's nest, wood detritus and the fungi *Inonotus dryadeus* and *Daldinia concentrica*; the adults are associated with sap runs. Other fungus-feeding *Fannia* include *F. canicularis* (L.) (many decaying fungi and other media, see below), *F. difficilis* (Stein) (*Lactarius*, *Boletus*), *F. immutica* Collin (indet. fungus), *F. incisurata* (Zetterstedt) (indet. fungus), *F. manicata* (Meigen) (*Amanita*, *Laetiporus*, boleti), *F. melania* (Dufour) (several boleti, *Armillaria*, *Lactarius*, *Tricholoma*, *Phallus*), *F. monilis* (Haliday) (*Pleurotus*, *Polyporus*), *F. lepida* (Wiedemann) (= *mutica* (Zetterstedt)) (indet. fungus), *F. scalaris* (F.) (*Boletus*, *Polyporus*, *Laetiporus*, other media, see below).

Species reared from birds' nests (hosts of the apprarently more specific species are cited) include: *F. canicularis*, *F. clara* Collin (little owl, heron), *F. coracina* (Loew), *F. difficilis*, *F. hirundinis* Ringdahl (sand martins), *F. incisurata*, *F. manicata*, *F. monilis*, *F. nidica* Collin, *F. parva* (Stein) (house martin), *F. rondanii* Strobl (house martin), *F. scalaris*, *F. vespertilionis* Ringdahl (starling), *F. lineata* Stein (heron).

Fannia canicularis, *F. fuscula* (Fallén) (fig. 908), *F. coracina*, *F. scalaris* and *F. vesparia* (Meade) have all been reared from the nests of wasps or bees.

F. vespertilionis has been reared from droppings of the noctule bat and *F. canicularis* has also been associated with bats.

Some other species have been reared from wood detritus, litter or woodland soil, e.g. *F. gotlandica* Ringdahl, *F. umbrosa* (Stein), *F. minutipalpis* Stein, *F. polychaeta* (Stein), *F. postica* (Stein), and *F. speciosa* (Villeneuve). *F. genualis* (Stein) has been found in leaf litter.

Clearly the examination of fungi, old nests and the droppings of smaller mammals (especially bats) yields the rarer species of *Fannia* and should help elucidate our knowledge of the life-histories and immature stages.

Some of the commoner species of *Fannia* mentioned above have a wide range of habits which may bring them into a closer involvement with man and give them a considerable medical importance. *Fannia canicularis* (figs 903–905) is the lesser house-fly, a common domestic species with a cosmopolitan distribution. The larvae develop in a variety of media including rotting vegetables and apples, large accumulations of faeces (e.g. on poultry farms) and in carrion. *F. scalaris* (fig. 907), the latrine fly, is essentially an outdoor species associated with primitive lavatories and cesspits. Optimum conditions occur in semi-liquid masses of faeces, especially pigs', but also of other animals, including man. Both species have been involved in cases of urogenital and intestinal myiasis and may occur in urine soaked babies' napkins and cot blankets (Zumpt, 1965). These species may also have an importance in forensic investigations (Smith, 1986b). *F. manicata* (fig. 906) has also been implicated in myiasis and forensic cases but is normally found in decaying vegetable matter such as garden refuse, putrid cabbage leaves, etc. and has also been reared from rabbit excrement and a dead gull.

Muscidae

(Figs: larvae 909–966, eggs 1101–1108, cover, puparia 1267–1281, cocoon 1272)

There are some 3,900 species of Muscidae in some 170 genera and the family occurs abundantly in all the major zoogeographical regions. Six subfamilies are usually recognised and 5 of these, including 280 species in 44 genera, occur in Britain.

Larval Muscidae develop in a wide range of substances from decaying vegetable matter, wood, fungi and living plants, the nests and burrows of birds, mammals and insects, to rot-holes, water margins and running water. A few species cause myiasis in man and animals. Many larvae are carnivorous at least in the later instars and associated with this habit is a longer incubation period in the egg which may hatch as second or even third instar larvae. The females of some species deposit third stage larvae. Some species form cocoons (fig. 1272) prior to pupariation (Ferrar, 1980).

Skidmore (1985) describes, keys and illustrates the known larvae of Muscidae, amounting to 440 of the world species. He defines them according to their habits as trimorphic (3 instars) saprophages, facultative carnivores, to monomorphic (one instar, the last) carnivores.

The relationship between the morphology and biology of the larvae and puparia of Muscidae may be summarised (after Skidmore, 1985) as follows (figure numbers refer to the present *Handbook*):

1. A sieving mechanism (fig. 911, sm) occurs in all known trimorphic larvae and in some dimorphic ones. Micro-sectioning of the pharyngeal floor of a wide range of monomorphic and dimorphic forms is desirable to ascertain if these structures occur widely. The structure is described in detail by Keilin (1917).
2. All known carnivorous species have well-developed oral bars (fig. 911, ob) and anterior ribbons (axillary rods) (fig. 911, ar), but in some species these are apparently being lost due to reversal to non-carnvivorous diet.
3. Massive posterior spiracles indicate trimorphism.
4. Minute posterior spiracles indicate reduced number of instars, the smallest being probably monomorphic.
5. Obligative carnivores found in dung do not have gut discoloured by the dung.
6. Dung-frequenting larvae with dung in gut are coprophagous or facultative carnivores.

7. Most wholly aquatic larvae have false legs and often long anal spiracular processes.

8. Obligate phytophages have oral bars (fig. 911, ob), the hypopharyngeal sclerite (fig. 911, hs) massively enlarged and the pharyngeal sclerite (fig. 911, ps) often fused to it.

Other useful works are Keilin (1917), Keilin & Tate (1930) and Skidmore (1973).

Larvae of the subfamilies of Muscidae occurring in Britain may be separated in the third instar as follows (simplified after Skidmore (1985) who recognises 10 subfamilies (8 British)).

1 Pharyngeal sclerite (ps) of mouthparts with a distinct atrial angle (at) (fig. 919) . . 2
— Atrial angle absent or if present (some *Spilogona, Phaonia*) then weak and obtuse . 5
2 Posterior spiracles with slits straight, sinuate or curved; parallel convergent or radiate (figs 925, 930) (never serpentine or tortuous) 3
— Posterior spiracular slits serpentine to tortuous, peripheral or encircling (figs 910, 913, 916) 4
3 Posterior spiracles on dorsal surface of last segment; in wasps' nests . **Achanthipterinae**
— Posterior spiracles otherwise; usually in dung, carrion or soil . . . . **Azeliinae**
4 Lower half (ventral cornu, vc) of pharyngeal sclerite (ps) with a strong 'tooth' (posterior projection, pp) (figs 788, 919, pp) . . . . **Muscinae**
— At most only a small weak pharyngeal tooth present (figs 958, 962, 966) . **Stomoxyinae**
5 Posterior spiracles with slits convergent, straight to tortuous (fig. 934). Mouthparts with sieving mechanisms (fig. 911, sm). Body never with false legs or caudal processes . . . . **Reinwardtiinae**
— Slits of posterior spiracles parallel to radiate, straight to curved or angular, never tortuous (figs 936, 940). Body sometimes with long false legs or caudal processes (e.g. *Limnophora*) (figs 938, 949) . . . . **Mydaeinae, Coenosiinae, Phaoniinae**

The classification used mainly follows Skidmore (1985) but as far as possible follows the sequence of genera in the *Check List* (Smith *et al.*, 1976). For nomenclature see Pont (in Soós & Papp, 1986).

Achanthipterinae. The larvae of *Achanthiptera rohrelliformis* (Robineau-Desvoidy) (fig. 909) feed on decaying matter in wasps' nests (*Vespula*).

Muscinae. The larvae of this subfamily are trimorphic and saprophagous or (*Mesembrina*) faculatative carnivores.

Polietes species (figs 910–912) are found in cow dung or (*P. domitor* (Harris) (= *albolineata* Fallén) and *P. steinii* Ringdahl) in horse dung. They become carnivorous in the third instar, though there is no evidence of this yet for *P. lardaria* (F.).

Mesembrina meridiana (L.) (figs 913–915) breeds in cow dung and less frequently in horse dung. Occasionally the first stage is spent entirely within the egg and a second instar larva hatches. Even normally development is very rapid and within 24 hours of hatching from the egg the larva will reach the third instar and the whole life-history takes only a week in summer. Two adults in the B.M. (N.H.) are labelled 'bred from half-grown larvae which destroyed 40 larvae, large and small, of *Musca corvina*'.

The immature stages of the British *Pyrellia* are unknown, but the only known larval pabulum is the dung of cattle and horses.

Eudasyphora cyanella (Meigen) and *E. cyanicolor* (Zetterstedt) have been reared from sheep dung. *Neomyia* (= *Orthellia*) and *Morellia* species breed mostly in cow dung.

Musca domestica L. (figs 916–919) is the ubiquitous house fly, a truly synanthropic species that has followed man around the world, breeds in his refuse and is a major mechanical transmitter of disease organisms in the adult stage. Up to 2,500 eggs may be laid and as many as 18 broods a year may be reared. It is perhaps fortunate that many predaceous muscid larvae (*Muscina, Myospila, Hydrotaea*) attack the larvae of *M. domestica* (and other *Musca* species) and that the fungus *Entomophthora muscae* Cohn also plays a part in controlling its numbers. In natural conditions in rural areas eggs are laid on horse dung but human, cow and poultry dung or material contaminated with excrement, decaying vegetable matter, garbage, decomposing foodstuffs, meat and carcases may all provide suitable food for the larvae, which can also complete their development on urine alone. *M. domestica* is one of the few Diptera to have an individual monograph (West, 1951) and a bibliography (West & Peters, 1973) devoted to it; Bollwig (1946) gives a detailed study of the larval sense organs. *Musca autumnalis* De Geer is known as the face fly because adults cause irritation to cattle by feeding on their body secretions, especially around the eyes and muzzle. They are also vectors of *Thelazia* (parasitic eye worm). The larvae develop in cow and horse dung and occasionally in carrion.

Azeliinae. The larvae of this subfamily are trimorphic facultative to dimorphic (or monomorphic) obligate carnivores.

The larvae of *Azelia* (figs 920–921) occur in horse and cow dung, where, in their final instar, they prey upon small nematocerous and acalyptrate larvae.

Thricops larvae have been found in the soil under logs, leaf litter and wet moss where they are presumed to be carnivorous.

Alloeostylus larvae have been found in decayed logs and have minute posterior spiracles which suggests that they hatch in the final instar and are probably obligate carnivores (Skidmore, 1985).

Larvae of *Drymeia* (=*Trichopticoides, Pogonomyia*) species are probably soil dwellers in deep leaf litter in woodland but *D. vicana* (Harris) (=*decolor* Fallén) (fig. 922) occurs in old cow pats and is probably an obligate carnivore.

The larva of *Potamia* (=*Dendrophaonia*) *littoralis* Robineau-Desvoidy (=*querceti* Bouché) (figs 923–924) is a facultative carnivore and has been reared from bat droppings, rabbit dung, human faeces, rotten wood, nests of birds and social insects, liquid substrates in rubbish dumps, cess pits, privies and fungi.

Ophyra capensis (Wiedemann) (fig. 1270) has been reared from human faeces, carrion, dead locusts, and the nests of birds and mammals. This species was rare until recently, but changed methods of poultry farming favour its development and it is now common in poultry battery farms where it breeds with *O. ignava, Musca domestica, Muscina stabulans* and *Fannia canicularis* (Conway, 1970). *O. ignava* (Harris) (=*leucostoma* Wiedemann) (figs 925–928) breeds in dung, carrion, birds' nests and rotting foodstuffs. It appears to be strongly attracted to ammonia resulting from decaying matter. *Ophyra* is often of value in forensic investigations, especially when corpses have been concealed and not therefore exposed to the normal blowfly fauna (Smith, 1986b).

Hydrotaea species (adults of some species are sweat flies) lay relatively few eggs and the larvae usually hatch in the second instar which lasts only a few hours. They are carnivorous in the third instar. The majority of species breed only in the dung of herbivores or in humus soil. *H. basdeni* Collin and *H. nidicola* Malloch are known only from birds' nests and *H. floccosa* Macquart (=*armipes* of authors) has been reared from rotting compost, seaweed, sheep carcases, dead snails and fungi. Graham-Smith (1916) claims that *H. dentipes* (F.) (figs 929–931) is the most important species with carnivorous larvae and destroys enormous numbers of larvae of other flies. It occurs on carrion and in fungi and so does *H. armipes* (Fallén) (=*occulta* (Meigen)); both species are occasionally of forensic importance (Smith, 1986b). Females of *H. irritans* (Fallén) (fig. 932) (the sheep head fly) are a considerable nuisance to man, cattle and sheep in late autumn. The species was formerly thought to belong to the true cow dung community but is now known to develop in mostly pasture soil under long grass or along the edges of woodland where the density of mature larvae may be *c.* 15,000 per acre (Robinson, J. & Luff, 1976; Skidmore, 1986). Lobanov (1970a) provides a useful paper on *Hydrotaea*.

Reinwardtiinae. *Muscina levida* (Harris) (= *assimilis* Fallén) develops in a wide range of fungi; it also occurs in the excrement of man and domestic animals. *Muscina prolapsa* (Harris) (= *pabulorum* Fallén) develops in carrion, especially of larger carcases, where it is saprophagous until the third instar when it becomes a facultative carnivore. The larvae of *M. stabulans* (Fallén) (figs 933–934) are found in rotting fungi, fruits, broken eggs, excrement and carrion where they become carnivorous and even cannibalistic in the later instars; in birds' nests they will attack and kill nestlings and have been found in the dead bodies of other insects. All three species have been reared from nests of the wasp *Vespula vulgaris* (L.).

Phaoniinae. The larvae of this subfamily are dimorphic or monomorphic obligate carnivores.

The immature stages of *Lophosceles* are unknown.

Phaonia is the largest British genus of Muscidae with 45 species. *Phaonia* (= *Dialytina*) *atriceps* (Loew) occurs under the loose outer sheaths and in the workings of other insects in the plants *Typha latifolia* L., *Phragmites*, etc. Most *Phaonia* species appear to hatch from the egg in the third instar as obligate carnivores. Development occurs in a wide range of habitats but groups of species appear to favour particular media (Skidmore, 1985). *P. exoleta* (Meigen) (figs 935–938) develops in water holes in old foliferous trees (*Ulmus, Fraxinus, Aesculus, Acer*); its larva swims actively and feeds voraciously on culicid larvae. A single *P. exoleta* larva may consume 100 mosquito larvae. Keilin (1917) and Tate (1935) describe three groups of long mobile hairs on the ventral surface of the thoracic segments but these appear to be absent in the specimen of *P. exoleta* (in the B.M. (N.H.)) illustrated by Oldroyd (1964). I have combined the features of Oldroyd's and Tate's illustrations to include these hairs (fig. 938). The larva of *P. gobertii* (Mik) is found under sodden bark (especially on *Ulmus, Populus*), where it preys on lonchaeid and clusiid larvae; it also develops in woodland leaf-litter and fungi. *P. laeta* (Fallén) (= *trigonalis* (Meigen), *laetabilis* Collin) has been reared from tree rot-holes. *P. palpata* (Stein) has been reared from dead trees. The following *Phaonia* species have been reared from fungi: *P. canescens* Stein (also under bark and in rotten wood etc.), *P. gobertii, P. pallida* (F.), *P. rufiventris* (Scopoli) (= *populi* Meigen) (and dead or sickly trees), *P. subventa* (Harris) (= *variegata* Meigen) (also rotten trees, under bark, dung, carrion and compost).

Species reared from humus soil, under moss, etc include *P. valida* (Harris) (= *viarum* Robineau-Desvoidy), *P. errans* (Meigen) (also dung and compost), *P. tuguriorum* (Scopoli) (= *signata* Meigen), *P. angelicae* (Scopoli) (= *basalis* Zetterstedt), *P. incana* (Wiedemann). *P. villana* Robineau-Desvoidy (= *mystica* of authors) has been reared from dense cushions of moss on soil, rocks or tree trunks in woods on calcareous basic igneous rocks. *P. cincta* (Zetterstedt) develops in sap runs of broad-leaved trees (especially *Ulmus*) where larvae prey upon those of lonchaeids, clusiids and *Mycetobia pallipes* Meigen (Anisopodidae). *P. trimaculata* (Bouché) (fig. 939) is primarily associated with herbaceous plants (especially larger Cruciferae) where its larvae prey upon those of various anthomyiids (including *Delia brassicae*) and Coleoptera.

The genus *Helina* has 38 British species which mostly develop in moss of humus soil, though some may invade adjacent materials (e.g. cow dung). Variations from this habit are mentioned below. They are obligate monomorphic carnivores. *H. quadrum* (F.) appears to be predaceous on larvae of the beetle *Phyllopertha horticola* (L.) (the garden chafer) in grassland (Smith, 1983). The larvae of *H. pertusa* (Meigen) (figs 940–941) are found behind loose bark on dead or dying trees where they prey on the larvae of Lonchaeidae, Clusiidae, Mycetophilidae, Sciaridae and Ceratopogonidae; it is also found in birds' nests. The larva spins a frail silken cocoon which incorporates particles of debris. Larvae of *H. vicina* (Czerny) have been found under moss on tree trunks and rocks in hilly areas and I found larvae of *H. reversio* (Harris) (=*duplicata* Meigen) under moss on the Wrekin in Shropshire (Smith, 1954). The latter species has also been recorded from a hornets' nest and a tree stump in Denmark (Michelsen, 1977). The female of *H. protuberans* (Zetterstedt) oviposits in sand dunes and has an ovipositor reminiscent of Asilidae but the larval habits and prey are unknown. *H. sexmaculata* (Preyssler) (=*punctata* Robineau-Desvoidy) has been reared from a swallow's nest and *H. pulchella* Ringdahl from the nest of a tawny owl (Smith, 1960).

Brontaea humilis Zetterstedt has been reared from horse dung.

Mydaeinae. Larvae of this subfamily are dimorphic or monomorphic obligate carnivores. The eggs (fig. 1105) have respiratory horns of varying length.

Hebecnema species develop in humus soil, and cow and horse dung; *H. umbratica* (Meigen) also occurs under garden compost.

The larvae of several species of *Mydaea* develop primarily in fungi: *M. affinis* Meade (=*discimana* Malloch) in *Suillus bovinus; M. electa* (Zetterstedt) agarics, Boletaceae, *Phallus*; *M. humeralis* Robineau-Desvoidy (=*tincta* Zetterstedt) in agarics, boleti, *Morchella*; *M. maculiventris* (Zetterstedt) in *Polyporus squamosus*; *M. orthonevra* (Macquart) (=*detrita* Zetterstedt), in *Boletus, Suillus, Lactarius, Amanita*; *M. setifemur* Ringdahl, indet. fungus. *M. urbana* (Meigen) and *M. ancilla* (Meigen) have also been reared from fungi but *urbana* is found mainly in cow dung and *ancilla* is also recorded from human faeces, dog and cattle dung and rotten elm wood. *M. corni* (Scopoli) (=*scutellaris* Robineau-Desvoidy) breeds in cow dung.

Myospila meditabunda (F.) breeds mainly in cow dung and sometimes in sheep dung; it has also been recorded from dog dung and human faeces.

Coenosiinae. Larvae of *Graphomya maculata* (Scopoli) (figs 942–945) were found in putrid black mud in shallow pools (in France) by Keilin (1917). They were in company with larvae of tipulids, *Ptychoptera*, tabanids, *Eristalis* and scathophagids upon which they were preying. Early authors have recorded larvae of this species from dung and carrion. It has also been found in tree rot-holes (preying on *Myathropa*, Syrphidae) and in rotting vegetable matter beside ponds and land drains (Skidmore, 1985). The larvae have retractile pseudopods on segments 2–7 and anal papillae.

Most species of *Spilogona* develop in damp soil and moss cushions from which some have invaded drier situations whilst others have become entirely aquatic.

The larva of *Villeneuvia aestuum* (Villeneuve) (figs 946–948) occurs under stones (Mercier, 1921) and in wet sand in the tidal zone, sometimes in association with and probably predatory upon *Balanus* and possibly other littoral animals. The cephalopharyngeal skeleton apparently has the pharyngeal sclerite pigmented only anteriorly (fig. 946).

The immature stages of *Neolimnophora* are unknown.

Many of the larvae of *Limnophora* (figs 949–950) are aquatic and have caudal processes which help anchor them to dense mosses or liverworts in running water. They prey mainly on oligochaetes and small insect larvae (Psychodidae, Ceratopogonidae, etc.). *L. riparia* (Fallén) is common in running water and preys on larval Simuliidae. Some non-British species are known to develop in dung or decaying plant and animal matter.

The larvae of all known *Lispe* species develop in wet sand or mud (including saline situations) with a high organic content. They are obligate carnivores, probably dimorphic and usually have the posterior spiracles strongly exserted (figs 951–955). Vaillant (1953) found that larvae of *L. consanguinea* Loew fed voraciously on tipulid, chironomid and dolichopodid larvae in the laboratory.

Pseudocoenosia abnormis Stein has been reared from wet *Sphagnum* moss.

The immature stages of *Limnospila, Orchisia* and *Spanochaeta* are unknown.

Caricea (= *Lispocephala*) species have not been reared in Britain, but the structure of Hawaiian larvae suggests affinities with *Spilogona* (Skidmore, 1985). British species are likely to be aquatic or subaquatic.

Schoenomyza litorella (Fallén) has been reared from puparia 'ex *Carex* sand' in Sweden.

Macrorchis meditata (Fallén) has been reared from soil around bulbs imported from Holland to New Zealand.

Larvae of *Allognota agromyzina* (Fallén) were found among wet leaf litter with numerous tiny oligochaetes on which they were feeding and in company with *Ula sylvatica* (Meigen) (= *macroptera* (Macquart)) larvae (Tipulidae).

Puparia of *Dexiopsis lacteipennis* (Zetterstedt) have been found amongst seaweed and those of *D. minutalis* (Zetterstedt) under the angiosperm *Honckenya peploides*, both on sandy beaches.

Coenosia larvae are obligate carnivores and develop in humus and in plants already infested with other Diptera larvae. *C. tigrina* (F.) is regarded as an important predator on *Delia antiqua* (onion fly) with which it is frequently found in humus soil near plant roots. The larva of *C. campestris* (Robineau-Desvoidy) (= *sexnotata* of authors) is described by Lobanov (1970b), but he gives no biological data. In Austria *C. dubiosa* Hennig larvae have been found in noctuid moth larval burrows in stems of *Typha latifolia*, where they preyed on nematocerous larvae (Sciaridae, Ceratopogonidae and Scatopsidae).

Stomoxyinae. The larvae of this subfamily are trimorphic and saprophagous.

Stomoxys calcitrans (L.) (stable fly or biting house fly) (figs 956–959) develops in cow-dung. It is another important muscid species with a large literature, mainly because of the importance of the blood sucking adult (which attacks man and his domestic animals) and its disease-carrying potential. The larvae move very rapidly but feign death if alarmed (Ferrar, 1979).

Haematobia irritans (L.) (horn fly) (adults sit in clusters around the horns of cattle) (figs 960–963) and *Haematobosca stimulans* (Meigen) (cattle biting fly) (figs 964–966) develop in fresh cow dung and the adults suck the blood of cattle (*H. stimulans* also attacks man).

Greenberg (1971, 1973) gives a good assessment of the medical and veterinary importance of the Stomoxyinae, and also of other Muscidae and Diptera in general.

Hippoboscidae

(Figs: larva 967, puparia 1282–1285)

There are about 200 species of Hippoboscidae, which mostly occur in the Old World tropics, but about 35 species are found in the western Palaearctic region. Thirteen species are recorded from Britain, but five of these are not resident. Adults of about 75% of the known species occur as ectoparasites of birds and are commonly known as 'keds'. Hippoboscidae are larviparous, producing a single larva (fig. 967) which develops internally (3–8 days), is then released as a prepupa which immediately starts to pupariate. The larvae may be extruded on the bird, in or around the nest or away from the nest. The pupae (figs 1282–1285) are shiny dark brown to black, rather round and seed-like. Hutson (1984) gives a general account of the biology, keys the adults, and discusses species likely to occur in Britain but not yet recorded. Bequaert (1953–1957) treats the world species.

Ornithomyinae. Adults of this subfamily are all ectoparasitic on birds.

There is only one British record of *Ornithophila metallica* (Schiner) (from the whitethroat) and no details of the life-history or immatures stages are known.

Ornithomya species are associated with birds as follows: *O. avicularia* (L.) (fig. 1282) on larger passerines (e.g. thrush, starling size upwards), Ciconiiformes, Anseriformes, Accipitriformes, Falconiformes, Galliformes, Gruiformes, Charadriformes, Columbiformes, Cuculiformes, Strigiformes, Caprimulgiformes, Piciformes; *O. fringillina* Curtis on small Passeriformes up to size of greenfinch particularly Motacillidae, Prunellidae, Turdidae, Muscicapidae, Fringillinidae, Embezeridae; *O. chloropus* Bergroth (*lagopodis* Sharp) (the grouse fly) (fig. 1283) on birds of open habitat particularly Accipitriformes, Falconiformes, Galliformes, Charadriformes, Cuculiformes, some Passeriformes; *O. biloba* Dufour is on swallows. Hill has studied the pupae (1962) and life-histories (1963) of *Ornithomya*.

Crataerina species are associated with birds as follows: *C. hirundinis* (L.) (house martin, occasionally sand-martin, swallow and swift), *C. pallida* (Latreille) (swift, occasionally hirundines or other passerines). Overwintering pupae may be found in the nests while the birds are away from Britain.

Icosta is the largest genus of the family (56 species) of which only two occur (rarely) in Britain associated with birds as follows: *I. ardeae* (Macquart) on Ardeidae (in Britain on purple heron, bittern and little bittern); *I. minor* Bigot (tree pipit and corncrake, both on Fair Isle).

Olfersia spinifera (Leach) (fig. 1284) is known from only one specimen recorded in Britain on a frigate bird. Guimarães (1944) describes the larva and Bequaert (1957) figures the puparium.

Hippoboscinae. Adults of this subfamily are ectoparasites of mammals.

Hippobosca equina L. (forest fly) is on horses and occasionally cattle, man and dogs.

Lipopteninae. *Lipoptena cervi* (L.) (deer fly) (fig. 1285) occurs principally on roe deer, and red deer; also on fallow deer, sika deer and reindeer with stray records from badger, man and dog.

Melophagus ovinus (L.) (known variously as skeep-ked, sheep-fly, sheep-louse, sheep-tick) occurs on sheep where the larva sticks to the fleece of the host and the whole life history is passed there.

Nycteribiidae

(Fig: puparium 1286)

There are over 250 species of Nycteribiidae (bat-flies), most of which are found in the Old World, especially in the Oriental and Pacific areas. About 12 species occur in Europe of which three have been recorded in Britain. Females leave the host bat to deposit the fully grown larva (as a non-feeding prepupa) on beams, walls, etc. near the bat colony. The larva is hemiovoid. Sticky secretions, helped by a narrow marginal 'skirt', secure the flat ventral surface firmly to the substrate. In addition, peristalsis of the freshly deposited larva ensures an airtight seal in which the female assists by backing over it and pressing down with her body. The freshly deposited larva is white and soft but soon hardens to a dark reddish-brown puparium (fig. 1286). Hutson (1984) gives a general account of the biology and keys the adults. Immature stages are described by H. Scott (1934), Ryberg (1939) and Schultz (1938).

Nycteribia kolenatii Theodor & Moscona is mostly restricted to Daubenton's bat (*Myotis daubentoni* (Kuhl).

Phthiridium biarticulata (Hermann) occurs mainly on horse-shoe bats (*Rhinolophus* spp.) but also occur on long-eared bats (*Plecotus* spp.).

Basilia nana Theodor & Moscona is found on the rare Bechstein's bat (*Myotis bechsteini* Kuhl)).

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