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TEPHRITID FLIES

DIPTERA: TEPHRITIDAE

I. M. White

ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

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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.

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Contents

Introduction

Most species of Tephritidae (= Trypetidae, Trupaneidae, Euribiidae) are phytophagous and have prominently patterned wings. There is no British common name, although the Tephritoidea, which also includes such families as Platystomatidae and Otitidae, are known as picture winged flies. Elsewhere, tephritids are often called fruit flies, because most species inhabit the fruit or other seed bearing organs of flowering plants; however, British entomologists generally use this term for the Drosophilidae. A few tephritids are leaf-miners, e.g. the celery fly, *Euleia heracleii* in various umbellifers (Apiaceae or Umbelliferae); some species are stem-borers, e.g. *Cerajocera plagiata* in *Centaurea scabiosa*; others live in roots, e.g. *Dithryca guttularis* in *Achillea millefolium,* and *Euphranta toxoneura* is a predator and brood parasite in sawfly galls. Most British

tephritids are associated with composite plants (Asteraceae or Compositae), and many of these form galls in the capitulum (= flower head or seed head), stem or root system. The only tephritids known to be non-phytophagous are a few Australian and Papuan species associated with the green bark of freshly dead trees, decaying fruit and termite nests (Kapoor *et al.*, 1980). There are about 4000 described species of Tephritidae in about 300 genera, of which almost 800 species and about 140 genera are Palaearctic.

The first major work on the Palaearctic fauna was *Die europäischen Bohrfliegen* by Loew (1862), which contained postcard size photographs of the wing patterns of many species. In the series *Die Fliegen der palaearktischen Region* Hendel (1927) keyed and described 300 species and 72 genera, and included wing photographs of 200 of these species. For the western Palaearctic the subsequent regional faunas were largely based on Hendel (1927) and they covered the following countries: Bulgaria (Drensky, 1943), France (Séguy, 1934), Holland (Kabos, 1959; Kabos & Aartsen, 1984), Hungary (Mihályi, 1960) and European U.S.S.R. (Rikhter, 1970). Large numbers of eastern Palaearctic species have been described in the regional faunas for China (Zia & Chen, 1938), Japan (Shiraki, 1933; Ito, 1983; 1984a–d) and Korea (Kwon, 1985). Major faunistic papers discuss the tephritids of many Palaearctic areas, e.g., the Balkans (Dirlbek & Dirlbek, 1972), the Canary Islands (Dirlbek & Dirlbek, 1969), Crete (Neuenschwander & Freidberg, 1983), Cyprus (Dirlbek, 1974), Israel (Kugler & Freidberg, 1975), and Mongolia (Kandybina, 1972). Since Hendel (1927), it has been E. M. Hering who has contributed most to the list of described species. Best known for his work on leaf-miners, Hering also wrote 77 papers on tephritids (between 1927 and 1961, see references in Hering, 1968) describing about 400 nominal species, 140 of which are Palaearctic.

To identify our 73 species of Tephritidae, British dipterists have relied on the combined use of a key to British genera by Collin (1947), the wing photographs of Hendel (1927) and Séguy (1934), and various diagnostic notes by Andrews (1939; 1941; 1946), Collin (1910; 1915; 1937; 1940; 1943; 1946; 1950), Colyer & Hammond (1968), Parmenter (1952) and Redfern (1983). However, in some species groups wing pattern is of no diagnostic value, e.g. some *Urophora* species can only be separated by the shape of the aculeus (ovipositor piercer). For the benefit of the inexperienced dipterist, the wing photographs in this handbook are arranged according to type of pattern (see p. 13 for a guide to their use) and they may be used for approximate identification. This work also contains both a simplified key to genera and conventional keys following the taxonomic hierarchy. Unusual specimens that do not fit the key characters sometimes occur, e.g. specimens with extra setae may not run correctly to genus; also very small examples of normally large species, and specimens with abnormal wing patterns are common. To facilitate the identification of abnormal specimens, diagnostic features of the male and female genitalia are illustrated for each species. These illustrations will also be of value to confirm the identity of species belonging to some difficult species groups of *Paroxyna, Tephritis* and *Urophora*.

There have been several faunistic notes about the British tephritid fauna discussing such areas as Ireland (Chandler & Speight, 1982), the Isle of Wight (Saunt, 1947), and Yorkshire (Hincks, 1946). By far the largest contributor to our knowledge of the biology and host-plant relationships of the British Tephritidae was M. Niblett (25 papers between 1931 and 1957). Papers describing the biology and larval stages of each species are listed in Appendix I together with the known hosts of each species. Appendix II lists the tephritid species associated with each British host-plant genus, and life-cycles are tabulated in Appendix III.

Biology

Most tephritid larvae develop in fruit, leaf-mines or within the flower-heads of

Asteraceae (= Compositae). All of these three life systems include pests, and many species associated with the capitula (flower-bud, flower or seed-head) of composites (Asteraceae) are potential weed biocontrol agents. Consequently, the biology of the group has been rigorously studied and most of the information given here was found by reference to major review articles by Bateman (1972), Christenson & Foote (1960), Zwölfer (1983) and Freidberg (1984).

Three life system strategies are recognized by Zwölfer (1983), as follows:

I. Broad host-range exploiters of fruit usually lay 800 to over 3000 eggs; larvae develop in 5 to 25 days; pupate in soil for 7 to 18 days; have several generations per year; long adult life possible, up to 460 days in laboratory; adult food, e.g. honeydew and nectar important. This strategy is typical of the polyphagous fruit pest species belonging to genera such as *Anastrepha, Ceratitis* and *Dacus,* and it does not apply to our native fauna.

II. Specialized exploiters of fruit usually lay 50 to 400 eggs; larvae develop in 15 to 30 days; pupate in soil for 30 to 330 days; adults live 30 to 50 days. Most species of *Dacus* and the frugivorous trypetines use this strategy.

III. Exploiters of vegetative structures and inflorescences usually lay 50 to 150 eggs; larvae develop in 20 to 40 days; usually pupate in host; the univoltine species may remain associated with the host for more than 300 days; adults usually short lived, 25 to 30 days, except for species which overwinter as adults, e.g. *Tephritis* species; some hibernate as larvae and have a short pupal period of 15 to 25 days, others overwinter as pupae. The leaf-mining Trypetini, and the Myopitinae and Tephritinae use this strategy, although there are many exceptions to all of these rather general rules.

Strategy II species live in a short term resource and they must abandon the host fruit to pupate in the soil before frugivorous vertebrates eat them. When the new fruiting season arrives, adult emergence must be perfectly synchronized with host fruiting. Some individuals of *Rhagoletis* species may stay in the pupal stage over two or even three winters thus avoiding the risk of a population collapse caused by the host failing to fruit in some years. The adult fly finds its host by visual and odour stimuli, and the fly is then encouraged to stay by the fruit's contact arrestant chemicals. The mating site is close to the host fruits. *Rhagoletis alternata* and some other species are known to use oviposition deterring pheromones to mark fruits in which they oviposit and this reduces the number of eggs laid by other females (Bauer, *in litt.,* in Zwölfer, 1983). Where fruit density is low, a rose hip (*Rosa* spp.) may receive more than one *R. alternata* egg, but the first larva to hatch eliminates competition by eating the other eggs. The female pheromone thus helps spread the eggs throughout the available fruit crop and larval behaviour adjusts larval density towards the ideal situation of one larva per fruit.

Most British tephritids are strategy III species and most are associated with the capitula (flower or seed heads) of composite plants. The host resource is long lived and so pupation can usually take place within the host tissue, for example in dry seed heads which exist throughout the winter. Conversely, most of the leaf-miners drop to the ground to pupate, presumably because the resource is short lived and pupae in leaf-mines would be very vulnerable to parasite attack. Curiously, *Cerajocera ceratocera* usually leaves the capitulum of *Centaurea scabiosa* to pupate in the soil (Persson, 1963) and the reason for this behaviour remains unknown.

Mating behaviour and resource partitioning have been studied for a wide range of European composite-associated Tephritinae and Myopitinae. Typically, it is the male which first selects the individual capitulum for subsequent mating and oviposition. Zwölfer (1974a) discusses this 'meeting point principle' as both a communication strategy and species isolating mechanism.

The adult male waits on or near the capitulum. This is usually only a flower-bud at this stage, whose shape and odour presumably trigger the territorial behaviour which can easily be watched in many species. The female then finds (rendezvous with) the male and a mating 'dance' takes place. The form of the dance differs between genera and the patterned wings appear to be an important part of the display, which is usually the same for both sexes. For example: *Chaetorellia* species hold their wings out to the sides of the body and twisted into a vertical plane, and shake both wings up and down simultaneously; *Tephritis* species hold their wings flat and open each wing alternately; *Urophora* species hold their wings out flat and open and close them simultaneously; they also perform a side to side rocking movement and the females wave their ovipositors (Zwölfer, 1974b); some *Urophora* females have integumental glands on their ovipositors (Berube & Zacharuk, 1984) but their function is unknown. The males of some tephritid species present their females with a froth meal as a nuptial gift (Freidberg, 1981), but this has not been recorded for any British species. Should two males meet they may fight and this can easily be watched in the field with some of our larger British species, such as *Tephritis conura* on *Cirsium palustre*. The male of *Urophora cardui* is known to release a pheromone (Zwölfer, 1974b), but its function is unknown.

A combination of rendezvous behaviour and a genus specific recognition dance appears to be an effective isolation mechanism and Zwölfer (1974a) suggests that this allows up to five different genera to utilize the same host-plant. This implies that a chance meeting in the wrong place can lead congeners to fail to recognize their own species. Experiments with *Urophora* and *Chaetorellia* species have shown that attempted mating of different species belonging to the same genus can be induced when the rendezvous site part of the species recognition process is artificaly removed (Zwölfer, 1974a; 1974b). This can easily be observed if several *Urophora* species are placed together in one collecting tube. Following normal mating, plant shape and odour are known to provide cues for oviposition (Zwölfer, 1983).

This behaviour implies that a given host-plant in a given place may be attacked by a guild of several species each of which belongs to a different genus. Exceptions to this simple rule do occur, e.g. *U. quadrifasciata* is an oligophagous species which often utilizes the same host as other *Urophora* species. In Canada this has been used to advantage in the biological control of some *Centaurea* species, where *U. quadrifasciata* has been used in combination with *U. affinis* (Frauenfeld) (p. 11). Zwölfer (1979) notes that *U. quadrifasciata* oviposits later than other *Urophora* species with which it competes. In addition to seasonal separation there is also a display difference which allows males of *U. quadrifasciata* to distinguish their own females from those of other species (Berube & Myers, 1983). Zwölfer (1965; 1974b; 1979; 1983) summed up these observations by concluding that only species occupying different trophic subniches can coexist in a guild.

Many of the monophagous and oligophagous composite feeding tephritids form galls in the capitulum, stem or root of their host-plants, and tephritid gall formation is reviewed by Freidberg (1984). During seed development the plant's food reserves are channelled into seed production and the developing capitulum contains large amounts of meristematic tissue from which galls may be formed (Zwölfer, 1983). Furthermore, galls may act as a metabolic sink, competing for assimilates with other growing parts of the plant (Harris & Myers, 1984).

Most *Urophora* species lay their eggs between the ovaries in the immature capitulum and the young larvae form a gall of receptacle tissue (Zwölfer, 1983; Harris & Myers, 1984), which engulfs the larval chamber that is situated in the achene or the receptacle (Freidberg, 1984). Conversely, *U. quadrifasciata* forms its gall from the ovary wall (Harris & Myers, 1984) and the gall is not lignified (Varley, 1937), unlike the known galls of other *Urophora* species. The structure of the galls may be unilocular (single chambered), e.g. *U. quadrifasciata* (P. Harris, *in litt.*) or multilocular, e.g. *U. cardui*

(fig. 3) (Lalonde & Shorthouse, 1984), *U. jaceana* (Varley, 1947) and *U. stylata* (fig. 4) (Harris & Wilkinson, 1984). However, many unilocular galls can occur within a capitulum (Harris & Myers, 1984). *Urophora cardui* is remarkable in that it forms an enclosed lignified multilocular gall on the stem of its host, *Cirsium arvense* (fig. 2). The eggs of *U. cardui* are laid into lateral and terminal vegetative buds (Zwölfer, 1983). As the stem gall forms, the freshly hatched larvae form channels of callus cells which subsequently rot to form the exit routes for the adults (Lalonde & Shorthouse, 1982; 1984; Rotheray, 1986). Species of the other British genus of Myopitinae, namely *Myopites,* form galls in the receptacle; this gall includes the achenes through which the larvae entered the receptacle, and out through which the adults later emerge (Freidberg, 1980).

Gall formation does not seem to be so highly developed outside of the Myopitinae. No species of Terelliini is known to form a gall (Freidberg, 1984), although most species live in the receptacle tissue of composites. A few species of Tephritinae do induce galls; for example, root and stem-base galls are formed on *Achillea millefolium* by *Dithryca guttularis* and *Oxyna flavipennis,* and also by *O. nebulosa* on *Leucanthemum vulgare,* but little is known of their biology. *Campiglossa* species, and the closely related *Paroxyna misella,* all cause deformities of their hosts. *Campiglossa argyrocephala* forms a rosette shaped gall from the capitulum of *Achillea ptarmica* (Wahlgren, 1944) and a stem gall is induced by *C. grandinata* on *Solidago virgaurea* (Andersson, 1955). *Paroxyna misella* induces stem galls on both *Artemisia vulgaris* (Niblett, 1946a; 1955) and glasshouse *Chrysanthemum* (Hodson & Jary, 1939), and it is remarkable that its second (summer) generation does not cause stem galls, but the larvae live in the capitula of *A. vulgaris* (Uffen & Chandler, 1978). Freidberg (1984) noted that some bivoltine gall formers either change their mode of attack in this manner, or change their host-plant species between generations.

Some non-gall forming Tephritinae also cause visible damage to their host-plants. For example, the stem miner, *Oxyna parietina* may sometimes cause a stem swelling (Niblett, 1946a) and some *Tephritis* species can cause a swelling of the capitulum in which their larvae develop, e.g. *T. formosa* (Berube, 1978); Shorthouse (1980) has described this in detail for the closely related *T. dilacerata* (Loew) on *Sonchus arvensis.* The larvae of some other *Tephritis* species eat the whole inside of the capitulum, leaving only the sticky black remains of faeces and rotting plant tissue, e.g. *T. hyoscyami* in *Carduus acanthoides* (Persson, 1963). Some other non-gall formers make a cocoon out of pappus hairs, e.g. *Xyphosia miliaria* (Persson, 1963).

Leaf-miners, e.g. *Euleia heracleii,* usually pupate in the soil, and they do not fit the general plan of strategy III. The mating site for *E. heracleii* is in a tree near the umbelliferous host (Leroi, 1975) and only the female visits the actual host-plant. If a minimum of contact between adult and host-plant is normal for leaf-mining Trypetini, it may explain why many species with the ovipositor structure of leaf-miners have an unknown biology, including the British *Myoleja caesio.*

The remarkable biology of *Euphranta toxoneura* has been described by Kopelke (1984; 1985). This tephritid oviposits in young leaf galls of *Pontania* species (Hymenoptera, Tenthredinidae) on *Salix* species. When the fly larva emerges, it immediately searches the gall for the *Pontania* larva, which it slits open and sucks dry. There is also a weevil (Coleoptera, Curculionidae) which develops as a predator and brood parasite in *Pontania* galls, and the weevil larvae are also attacked by *E. toxoneura* which begins its development earlier than the weevil. After the larva of *E. toxoneura* has completed its development in the *Pontania* gall, it falls to the ground and stays in the pupal stage until the following spring.

Little is known about adult feeding by tephritids, although many species will feed on honey under laboratory conditions, and some species with long lived adults are known to feed on honeydew and nectar (Bateman, 1972). Some tephritids have long, geniculate mouthparts, namely *Ensina sonchi, Dioxyna bidentis, Goniglossum wiedemanni, Paroxyna producta, Sphenella marginata, Myopites* and *Oxyna* species; it would be

worth investigating the possibility that these are nectar feeders. Gut symbiotic bacteria have been found in some tephritids and these may be needed to overcome the protein deficiencies of a sugary diet and so provide the developing ovaries with amino acids (Hagan & Tassan, 1972). Girolami (1983) tabulates the presence or absence of symbiotes in the mid gut and in special vesicles of 31 tephritid species, including 24 British species. It is of interest that occurrence of symbiotes and type of vesicle in the gut concords with higher taxonomic groups in the family, perhaps to fit the differing life strategies of each group.

Most British tephritids are univoltine, although some species are bivoltine and a few have a variable number of generations per year. *Euleia heracleii* shows different colour morphs in each generation, adults emerging from overwintered pupae being reddish-brown and those emerging in late summer being black (Labeyrie, 1958). Similarly, *Paroxyna misella* induces a stem gall in one generation and lives in the capitulum in the next (Uffen & Chandler, 1978). In some species (*Cerajocera ceratocera, Chaetorellia jaceae, Chaetostomella cylindrica, Terellia colon* and *Trypeta zoe*) eggs laid one year may give rise to adults in the same year or in the spring of the following year. *Myopites* species have been known to delay emergence until a second winter has passed and *Terellia vectensis* has been known to pass a third winter before emergence (Niblett, 1942), but it is usually univoltine. It is possible that any normally univoltine or bivoltine species can delay emergence, and life cycle variations may help a species survive years when their host-plants become temporarily rare. Selected references to each species life-cycle are given in Appendix I and the known life-cycles are tabulated in Appendix III.

Speciation in tephritids is closely linked to host-plant and life system strategy. The classical studies on sympatric host race formation and sympatric speciation in phytophagous insects were carried out with North American *Rhagoletis* species (many papers by G. L. Bush which were reviewed by Zwölfer & Bush, 1984). *Rhagoletis* are strategy II species and they have often undergone host shifts to taxonomically unrelated plant species (Zwölfer, 1983). Relative to the total range of *Rhagoletis* species, our British *R. alternata* and *R. meigenii* are very closely related, but one feeds on *Rosa* species (Rosaceae) and the other on *Berberis* species (Berberidaceae). Zwölfer (1983) noted that pulpy fruits are often very similar in structure regardless of plant family, and this, combined with such factors as the short contact period of the fly with its host-plant, may produce a predisposition for host shifts and in some cases the formation of host races. This may explain why *Anomoia purmunda,* which is normally associated with *Crataegus* species, has also been reared from other genera of Rosaceae and *Berberis*.

Conversely, in strategy III species the host-plants of related fly species are usually related plant species. For example, *Urophora jaceana* and *U. cuspidata* larvae induce galls in the capitula of *Centaurea nigra* (species group) and *C. scabiosa* respectively. Because the immature seed head of *C. scabiosa* is very much larger than that of *C. nigra,* the associated flies had to evolve very different ovipositor lengths (Zwölfer, 1983, correlated these parameters). This speciation amongst related hosts may therefore require more adaptive changes than the speciation process used by strategy II species (Zwölfer, 1983). Shape of capitulum appears to be important as a visual cue for *Urophora, Chaetorellia* and perhaps other composite associated genera. The shape of a *Centaurea* capitulum is related not only to size, but also to the shape of the intermediate involucral bracts. For example, *C. calcitrapa* has 20 mm long spines on these bracts, but *C. nigra* and *C. scabiosa* lack these spines. Zwölfer (1983) suggested that plant genera with a high diversity of bract form, such as *Centaurea,* have a correspondingly high diversity of associated tephritids.

Only a very few strategy III species feed on more than two composite genera, for example, *Acanthiophilus helianthi, Ensina sonchi, Paroxyna producta* and *Trupanea* species. Zwölfer (1983) discussed *A. helianthi* whose larvae feed gregariously in the

receptacle and seeds of a host. This apparently unspecialized mode of attack may explain its ability to live on almost any species of Cardueae.

Parasitoids

Tephritids are attacked by a wide variety of hymenopterous parasitoids and these are an important factor in the regulation of their populations. Unfortunately, records of host associations are widely scattered through the literature and they probably include many misidentifications; a critical review is badly needed. Similarly, no summary of tephritid parasitoids exists and most of the following information was kindly provided by Dr H. C. J. Godfray (*in litt.*).

The parasitoids attacking a particular tephritid species are influenced by both taxonomic and ecological factors. Parasitoid groups that include species specific to Diptera and which attack tephritids are Alysiinae and Opiinae (both Braconidae), and Miscogasterinae (Pteromalidae); however, in northern Europe no parasitoid group has radiated solely on the Tephritidae. The larval ecology of a tephritid species is perhaps the most important factor determining its parasitoid complex. A tephritid frequently shares either the same or closely related parasitoids with hosts that have similar life-cycles, even though these may not even be dipterous. Similarly, seed head feeding tephritids and Lepidoptera are attacked by the same genera of Pteromalinae. First instar leaf-mining tephritids may be attacked by the same small ectoparasitoids (Eulophidae and Pteromalidae) which are very common on the much smaller leaf-mining Agromyzidae. By the time a tephritid enters its second instar it is big enough to be invulnerable to attack by these parasitoids; however, it may then be attacked by the same endoparasitic Alysiinae, Opiinae and Miscogasterinae as leaf-mining Anthomyiidae. Tephritids that pupate in the soil, that is leaf-miners and frugivorous species, may be attacked by *Phygadeuon* (Ichneumonidae) and possibly the parasitoid beetle *Aleochara* (Staphylinidae) which attacks many Diptera pupae in the soil.

One of the first modern studies of population dynamics was carried out by Varley (1947) with *Urophora jaceana,* and its parasitoids, on a *Centaurea* species (either *C. nigra* or *C. debeauxii*), and this remains a classic study. The potential use of para-sitoids for the biological control of tephritid pests has been investigated, for example, *Dapsilarthra apii* (Curtis) (Alysiinae) for *Euleia heracleii* in Europe, and *Opius* species (Opiinae) for tropical fruit pests. A classroom practical exercise to study the parasitism of *Urophora stylata* was described by Cameron & Redfern (1974).

Pest species

The most serious tephritid pests damage fruit crops. For example, the medfly or Mediterranean fruit fly, *Ceratitis capitata,* has been reported from most warm temper-ate and tropical countries. Also of importance are several other Ceratitini in Africa, *Dacus* species in the tropical and warm temperate Old World, *Rhagoletis* species in the New World and southern Europe, and *Anastrepha* in the New World tropics. In the Palaearctic region the most serious pests are *Rhagoletis cerasi,* which is a pest of cherries in southern Europe, and *Dacus oleae* (Gmelin), which is a very serious pest of olives. Some fruit pest species have been found in imported fruit in Britain and the major pest genera are included in the following keys.

Some British species are injurious to commercially and garden grown plants in some parts of their range; the following notes on these species were obtained from abstracts in *Review of Applied Entomology* series A and other abstracting journals (RAE was searched up to 1950 by Hennig, 1953; the author searched RAE between 1951 and

1972; subsequent abstracts were extracted from the CAB International Abstracts Database by the *Dialog* computer system).

Acanthiophilus helianthi (safflower or capsule fly) is rare in Britain, but in some areas it has been reported as a serious pest of safflower (*Carthamus tinctorius*), namely Egypt (RAE **63:** 3097), India (RAE **28:** 511, **30:** 317, **52:** 299, **62:** 208, **64:** 2080, **69:** 5049), Iraq (RAE **65:** 5033, **66:** 824, **66:** 4039), Israel (RAE **54:** 636), Romania (RAE **31:** 227) and Turkey (RAE **68:** 1311). In France, safflower was introduced as an oil crop in 1942, but was so badly damaged that production had almost ceased within ten years (RAE **49:** 656). However, some safflower varieties have now been bred for resistance to *A. helianthi* (RAE **69:** 5409, **71:** 6450, *Herb. Abstr.* **32:** 6505). In Egypt *A. helianthi* is a pest of artichoke (*Cynara scolymus*) (RAE **68:** 4350) and in Hungary it is a pest of the commercial production of cornflower seed (*Centaurea cyanus*) and sweet sultan seed (*C. moschata*) (RAE **55:** 1522). (See also RAE **51:** 516 for parasitoids).

Anomoia purmunda has been reported as injurious to ornamental garden fruit bushes, namely *Berberis, Cotoneaster* and *Pyracantha* in Britain (RAE **23:** 255), and *Pyrus baccata* in Finland (RAE **53:** 422).

Chaetorellia jaceae has been reported as a safflower pest in Israel (RAE **54:** 636), but this was probably a misidentification of *C. carthami* Stackelberg.

Ensina sonchi has been known to cause serious injury to rubber producing *Scorzonera tau-saghiz* and *Taraxacum* species, such as *T. kok-saghyz* in the Ukraine, U.S.S.R (RAE **23:** 339, **26:** 618).

Euleia heracleii (Celery fly) is a serious pest of celery (*Apium graveolens*) in Britain (RAE **54:** 469, **57:** 1399, **71:** 5979), France (RAE **47:** 213, **48:** 486, **62:** 596, **62:** 4500, **63:** 3209, **65:** 609, **65:** 809, **66:** 1159), Greece (RAE **58:** 848), Italy (*Hort. Abstr.* **46:** 4738) and Spain (RAE **68:** 2463). It has also been known to damage carrots (*Daucus carota*) in Spain (RAE **68:** 2463), cow parsley (*Heracleum* sp.) near Moscow (RAE **67:** 3880), and lovage (*Levisticum officinale*) and parsnip (*Pastinaca sativa*) in Czechoslovakia (RAE **53:** 628). (See also RAE **48:** 184 and **63:** 112 for parasitoids and sexing of pupae).

Paroxyna misella sometimes disfigures glasshouse *Chrysanthemum* species in Britain (RAE **27:** 519; see correction to this record in Andrews, 1941).

Paroxyna sp., reported as *P. tessellata* (Loew) and probably a misidentification of *P. producta*, has been known to injure rubber producing composites (see references with *Ensina sonchi* given above).

Platyparea poeciloptera (asparagus fly) is a serious pest of asparagus (*Asparagus officinalis*) in France (RAE **46:** 7, **47:** 110, **49:** 92, **49:** 519, **49:** 520, **51:** 59, **53:** 12), Germany (RAE **60:** 433) and Holland (RAE **48:** 355). It has been reported in Britain (Niblett, 1956c) and Dingler (1934) provided a detailed account of its morphology and bionomics. (See also RAE **48:** 184, **59:** 2850.)

Rhagoletis alternata is a pest of rose hips (*Rosa* spp.) in Germany (RAE **23:** 506), Norway (RAE **68:** 5013), Poland (RAE **66:** 1940), Sweden (RAE **31:** 322) and the U.S.S.R. (RAE **12:** 358, **60:** 4272). In Britain it has been reported as injurious to garden roses (RAE **19:** 246, **23:** 255).

Trupanea amoena has been known to injure lettuce (*Lactuca sativa*) in Hungary (RAE **25:** 538), Italy (RAE **53:** 271) and Turkey (RAE **68:** 1311). It has also been reported as a pest of commercially grown marigold flowers (*Calendula officinalis*) in India (RAE **39:** 28).

Trupanea stellata has caused serious injury to rubber producing *Taraxacum kok-sagyz* in the Ukraine, U.S.S.R. (RAE **26:** 618) and to marigold flowers in India (RAE **32:** 408).

Trypeta artemisiae has been known to mine the leaves of glasshouse *Chrysanthemum* species in Britain (Andrews, 1941; RAE **27:** 519) and Norway (RAE **42:** 238).

Trypeta zoe has been reported mining the leaves of nursery grown *Chrysanthemum* species in Britain (RAE **63:** 4249).

Urophora jaceana, U. quadrifasciata and *U. stylata* have been reported from some crop plants in Turkey (RAE **68:** 1311), but these were probably misidentifications.

Biological control of weeds

Composite feeding tephritids often reduce the seed production of their host-plants, and many of their hosts grow amongst crops, or in pasture or rangelands where tephritids sometimes help in the natural control of these weeds. Many composites have been accidentally introduced to areas where they have no natural control agents and some of these plants have become serious rangeland weeds. Some tephritids now play an important role as introduced biological control agents of some of these weeds; a catalogue of both the successes and failures in weed biocontrol has been compiled by Julien (1982). In some cases European tephritids which have been introduced into North America have reached population densities 12 to 18 times as high as they typically reach in Europe where natural enemies control their numbers (Zwölfer, 1983). The following British species of Tephritidae have been used experimentally, and in some cases successfully, for weed control outside of Europe:

Urophora cardui has been released in both western and eastern Canada for the control of *Cirsium arvense*. However, *U. cardui* died out in the west, and in the east it failed to reduce the infested areas of *C. arvense* (Harris, 1984; Peschken, 1984).

Urophora quadrifasciata has been successfully established on *Centaurea diffusa* and *C. biebersteineii* (= *C. maculosa* auctt: N. America) in western Canada. Used in combination with *U. affinis* (Frauenfeld), also introduced from Europe, seed production of these knapweeds has been reduced and in some areas the total plant biomass has now declined (Harris, 1984; Harris & Myers, 1984).

Urophora stylata has been established on *Cirsium vulgare,* in British Columbia, where seed production was substantially reduced. It was also released in Quebec, but it died out there after the release site was mowed (Harris, 1984; Harris & Wilkinson, 1984).

Rhagoletis alternata was tested as a potential biocontrol agent of *Rosa rubiginosa* in New Zealand, but it was not subsequently introduced (RAE **56:** 1735).

The following British tephritids have become accidentally established outside of what is believed to be their native range: *Ensina sonchi* has been reported from Hawaii (Hardy & Delfinado, 1980) and Peru (Steyskal, 1971); *Terellia ruficauda* is found on *Cirsium arvense* in the USA and was first reported in 1893 (Wasbauer, 1972); *Urophora jaceana* is established on *Centaurea nigra* in eastern Canada and was first found there in 1923 (Shewell, 1961); the British Museum (Natural History) collections contain single specimens of *U. quadrifasciata* and *U. stylata* which were collected in New South Wales, Australia, in 1967 and these species appear to have arrived there by accident.

Collecting and rearing

The composite feeding Tephritinae and Myopitinae can be swept from their host-plants during the summer months and some Tephritini, which overwinter as adults, can be found by general sweeping at almost any time of the year. Conversely, many of the leaf-mining and fruit feeding Trypetinae spend very little time on their larval host-plants and are usually found by general sweeping during the summer; many of these

species are easier to find by rearing from their host-plants than by sweeping. A general account of collecting Diptera is given by Irwin (1978a).

If immature stages are collected while the larvae are still feeding, it is necessary to keep the plant material turgid until pupation, or until hibernation in the case of the species which overwinter as larvae. If plant material containing active larvae is allowed to dry out the larvae will usually die; however, *Acanthiophilus helianthi* and perhaps other species, will be induced to pupate before the larvae are fully developed and the result is abnormally small adults.

Species which pupate within the seed heads and stems of composites are the easiest species to rear. The seed heads should be collected in the autumn, winter or spring after the flowers have dried and gone to seed and the larvae are fully grown. Seed heads or stems should be placed in a porous container such as an empty margarine tub with a muslin top, an old stocking or a glass tube with a muslin top. The glass tube method allows seed heads to be stored individually so that the empty puparia can be stored with their resulting series of adults. Alternatively, each puparium can be removed from the plant material and placed in a gelatine capsule, so that the emerging fly can be kept with its own puparium for future study. It is advisable only to treat puparia in this manner shortly before emergence time, generally May or June, otherwise desiccation may occur. It should also be noted that species which develop in seed head galls, namely *Myopites* and *Urophora* species, are enclosed by lignified plant tissue and are easily damaged if one tries to remove them. Plant material containing larvae or puparia should be stored in a sheltered area which maintains roughly outdoor temperature, for example a garage.

Mined leaves containing larvae have to be kept turgid until pupation occurs, and to do this the leaves should be kept attached to a portion of the stem and placed in a polythene bag (Spencer, 1972). The larvae will usually leave the leaf to pupate and puparia should be kept in damp sand in glass tubes, and stored in a garage or similar place. The sand should be dampened every few days using a plant spray, but excess moisture should be removed from the glass walls of the tube, so that mould is not encouraged and emerging flies are not damaged. A detailed account of leaf-miner rearing was given by Spencer & Stegmaier (1973).

Fruit believed to contain tephritid larvae should be placed in a muslin topped container that has sand in its base. Frugivorous species leave their host fruit to pupate and the sand will become the pupation medium. It is important that fruit juices do not wet the sand because that may provide a medium for mould growth. After pupation, the remains of the fruit should be removed and the sand kept damp with a plant spray, taking care to remove excess moisture. An account of rearing tropical fruit feeding larvae was given by Drew (1982b), but this differs from the method needed for the long pupal period of our temperate species.

In all cases adults should not be killed until about four days after emergence, so as to allow the wing and body colours to develop fully. Empty puparia may be placed in gelatine capsules and kept with the adults that emerged from them. When an individual puparium can be matched to its own adult the gelatine capsule containing the puparium should be staged on the same pin as the adult (fig. 6).

The only method of determining the host of a tephritid that is within the scope of this handbook is rearing; however, it is of interest to note that trace element analysis has been used to determine the larval host of individual adults of some *Rhagoletis* species (Diehl & Bush, 1983).

Methods of study

Preparation of specimens

The following keys are primarily designed for use with dry mounted specimens, but

most of the characters used will also be visible on spirit (70–80% ethanol or industrial methylated spirit) preserved material. Specimens to be dry mounted should be killed with ethyl acetate vapour.

Dry mounted specimens may be side pinned with A-1 size micropins; larger micropins, such as D-2 size, may be used for the very large species. There is no right or wrong way to orientate a side pinned specimen, but for direct comparison with the figures in this handbook the head should be placed to the left (fig. 5). The micropin is inserted just behind the left wing base at such an angle that it emerges just in front of the right wing base. The specimen is then pinned to a piece of plastazote sheet (9 mm or 12 mm thickness) with the wings raised and, if necessary, held in place with another micropin (fig. 5). If the specimen has geniculate mouthparts these are then pulled into an extended position and held in place with a micropin (fig. 5). When pinning females belonging to genera such as *Tephritis* and *Urophora* it is advisable to extrude the aculeus by gently squeezing abdominal segments 5 and 6 with a pair of fine forceps; the aculeus tip can then either be examined in situ or removed for detailed examination without the need to remove the whole abdomen. After a few days the wing and mouthpart positioning pins may be removed and the specimen staged on a strip of plastazote measuring 4 × 4 × 15 mm (fig. 6). A general account of curating a Diptera collection is given by Irwin (1978b).

The plastazote stage is then mounted on a continental size pin (size 5 is ideal) together with a locality label, a host label if the specimen was reared, and a determination label (fig. 6). Note that the collection and emergence dates are given separately. The possible host of non-reared specimens should be clearly differentiated from that of reared specimens; for example, 'ON CENTAUREA NIGRA', would refer to a specimen swept from *C. nigra,* as opposed to 'EX CENTAUREA NIGRA' for a reared specimen. Other items which may have to be mounted on the same pin are a gelatine capsule containing the empty puparium (fig. 6) and a terminalia preparation.

Identification and use of keys
This handbook is designed to allow the combined use of four different approaches to identification; namely, comparison with wing plates, a simplified key to genera, specialist keys and terminalia characters. All of the external characters used can be observed with a good stereo or dissection microscope equipped with top or incident light; a Wild M5APO with fibre optic ring illumination was used in the production of this work, but many cheaper microscopes will suffice. To see wing pattern detail a white background is necessary, and this can be supplied either by using a white microscope base plate or by using a transmitted light base. Terminalia dissections are ideally examined with a compound microscope, but most of the important characters can be seen with a good stereo microscope equipped with a transmitted light base; a Leitz Laborlux compound microscope was used for this study.

Inexperienced dipterists may look firstly at the wing plates to make a tentative identification and then use the keys in reverse to check the determination. In this way an understanding of the important characters will be gained, so that eventually the keys can be used properly; this method also allows a study of tephritids to be used as an introduction to acalyptrate Diptera in general. To facilitate identification by wing pattern, the wing photographs are arranged in an ordered progression of pattern type rather than by taxonomic hierarchy (figs 223–286).

The wing of at least one representative species from each genus is shown, but it must be stressed that many species cannot be identified purely by wing pattern and in these cases only one representative from a group of similar looking species is illustrated. Groups of similarly patterned species are indicated in the legend of each plate and identification of these species must be completed using the keys.

A simplified key to genera is presented which uses a combination of wing pattern and other characters such as chaetotaxy.

For the benefit of the specialist reader, genera are also keyed via the taxonomic hierarchy of subfamily and tribe. It is not possible to produce a simple key to sub-families and tribes because exceptions to general character sets are found in every group. Furthermore, the precise content of each subfamily and tribe is still far from agreed and no world classification has been produced in recent years. With experience, the tribe to which a species belongs will be instantly recognizable and then only the keys to genera and species will be needed.

The keys to species and the confirmatory descriptions contain far more information than will be needed for most determinations. These details should help in the identifi-cation of aberrant individuals and reduce the possibility of additional species being overlooked. The confirmatory characters are given in parenthesis and they refer to an illustration of the aculeus and usually the distiphallus, as well as wing length (WL) and aculeus length measurements.

The illustrations (p. 78) include scale lines against the distiphallus drawings because their size is not indicated in the text. The aculeus drawings for any given genus are to a uniform scale, and the head and thorax drawings are to one scale. The wing photo-graphs are to a variety of scales and the keys should be consulted for wing and aculeus length measurements.

No attempt has been made to gather comprehensive distribution data; most of the British distribution data were compiled from the collections of the British Museum (Natural History), supplemented by data from other collections, published records and some unpublished distribution maps compiled by L. Clemons (the term 'old record' means pre-1960). It is hoped that the following keys will now allow accurate identifi-cations to be made so that a Biological Records Centre mapping scheme becomes a practicality. Non-British distribution data were based on Foote (1984). The keys also include a summary of the British host-plants of each species; for a detailed host-plant list see Appendix I.

Dissection of terminalia
To dissect the terminalia, first break off the abdomen (removal of only the tip of the abdomen may result in the loss of the distiphallus or of the base of the aculeus) and place it in absolute alcohol (ethanol or propan-2-ol), to which an equal volume of 10% KOH (potassium hydroxide) is then added. If the aculeus was completely extruded when the specimen was pinned, it is possible to remove only the aculeus from the dry mounted specimen and leave the rest of the abdomen intact. After leaving the abdomen overnight in alcoholic KOH at room temperature (or 20 minutes at 95°C if a hot plate is available to stand the preparation on), transfer the abdomen to glacial acetic acid at room temperature. If a permanent slide is being made, remove a wing from the speci-men and place it in the glacial acetic acid with the abdomen, so that the wing is cleaned and softened. After a period of at least 15 minutes, the abdomen is removed from glacial acetic acid and transferred to the mountant via the appropriate intermediate steps; details are given at the end of this section. The dissection should be done on a microscope slide and two fine dissection needles are required, each of which can be made by fixing a micropin to the end of a matchstick with an epoxy resin glue.

When dissecting a female, begin by breaking the abdomen between segment 6 and the oviscape (fig. 13). By gently squeezing the oviscape with one pin it is possible to telescope the aculeus out of the oviscape. It is usually necessary to finish removal of the aculeus by holding the oviscape with one pin and pulling the aculeus out with the other; take great care not to damage the tip of the aculeus when doing this. If all else fails the oviscape will have to be torn open to remove the aculeus. If making a permanent slide the spermathecae should be removed from the abdomen (in the Myopitinae they are not sclerotized and usually cannot be found) so that they are clearly displayed on the slide; eggs, if present, should also be squeezed from the abdomen and displayed.

With a male, begin by holding the abdomen with one pin, and with the other pin, pull

the epandrium from the abdomen; the rest of the terminalia should come out of the abdomen with the epandrium (fig. 14). If making a permanent slide the hypandrium should be broken from the epandrium and arranged to show either a lateral or a posterior view of the epandrium and the associated surstyli. The basiphallus is broken just below where it joins the distiphallus and, to produce comparable views of the distiphallus, the distiphallus should be placed so that the broken piece of basiphallus attached to it points to the right from the bottom of the distiphallus, e.g. figs 178–183. An exception to this rule is that Terelliini distiphalli should be arranged so that the accessory sclerite is to one side of the distiphallus apex and to its upper left, e.g. figs 82, 83. It is very difficult to produce comparable views of the distiphallus of some species, e.g. *Paroxyna misella* may be mounted as fig. 176, but its distiphallus will usually rotate before the mountant has set, so that it looks like fig. 177. Luckily, most of the species that are likely to have to be dissected do not have this annoying habit and their distiphalli stay where they are put.

If a terminalia preparation is to be kept with the dry mounted specimen a number of methods are available. The simplest technique is to place the dissected abdomen in a drop of glycerol in a microvial through which the mounting pin may be passed. It is possible to either use glass microvials which have cork tops like miniature collecting tubes (Irwin, 1978b) or to make microvials from fine plastic tubing which can be plugged with plastic rod equal in diameter to the bore of the tube. Some specialists mount terminalia in a permanent mountant between small coverslips placed either side of a punctured slip of card. To do this a piece of card the size of a normal data label is perforated with a stationery punch and a 10 mm diameter coverslip is glued across the underside of the hole. A spot of mountant, e.g. Canada balsam is added. When the dissection is completed a second coverslip may be added on top; if a second coverslip is not added it facilitates reorientation of the dissected parts by softening the balsam with xylene. Uncovered mounts become pitted and wrinkled, but this can be cured by adding a drop of xylene to the mount when it is being re-examined.

If a permanent slide is being made the tergites and sternites of the abdomen should be separated so that any abdominal characters can still be examined. To do this, one pin is slid into the abdomen and the pleural membrane is torn with the other pin (some specialists cut the pleural membrane with spring dissection scissors of the type used by eye surgeons). With large specimens both pins may be slid into the abdomen so that the pleural membranes can be torn by stretching the sides of the abdomen with the pins. If successful, the dorsal and ventral sides of the abdomen can be laid open on the slide so that the shape of each sternite and tergite is visible; in particular, the shape of the male 5th sternite is a useful character in some groups. Another drop of mountant is then added to another area of the slide and the wing is taken from glacial acetic acid and carefully placed in this second drop of mountant (after passing through other stages if Canada balsam or euparal are used).

If a 75×25 mm slide is used, there is room for two 13 mm coverslips to be used providing the abdomen and wing preparations are placed in diagonally opposite areas of the central 25 mm square area on the slide; this leaves room for two 25 mm square labels. Slides should be given a number corresponding to a number on the remaining dry mounted specimen, e.g. IMW-999. Examples of suitable mountants and the processes needed before their use, are as follows:

1. Berlese fluid — This is one of the many gum arabic based water soluble mountants and it is very easy to use; however, its permanence is in doubt and it should not be used to make slides of valuable specimens. Specimens should be transferred directly from glacial acetic acid to the Berlese fluid. When the dissection is complete, leave the slide to set for at least a day at room temperature before adding a further drop of Berlese fluid and the coverslip. This period of initial drying minimizes the tendency for parts of the preparation to move and roll when the coverslip is added. The slide must then be kept

flat for a few weeks to dry at room temperature before being ringed with *Glyceel* (which is acetone soluble). Some microscopists ring Berlese mounts with *Euparal,* but it is essential that the Berlese is absolutely dry before doing this, otherwise a chemical reaction occurs which damages the slide. Before ringing, excess mountant must be chipped away from around the coverslip. A method for making Berlese fluid is given by K. M. Harris (*in litt.,* in Freeman & Lane, 1985) and other gum arabic based water soluble mountants are *Hoyer's, Faure's* and *Andre's.* Unlike Euparal and *Canada balsam,* these media will clear very small insects, but it is still essential to clear tephritid abdomens in KOH before dissection.

2. Euparal — This mountant is soluble in absolute alcohol and *Euparal essence;* it is believed to be permanent and it does not need ringing. Specimens should be transferred from glacial acetic acid to absolute alcohol; after a few minutes they may be placed in the Euparal. The completed slide should then be kept flat for several weeks to dry at room temperature, or placed in a hot air cabinet at 35–40°C for at least two weeks. There is no need to ring a slide made with Euparal.

3. Canada balsam — This is a permanent mountant with a long established usage; it is soluble in *xylene* and *clove oil.* Specimens should be transferred from glacial acetic acid to absolute alcohol for several minutes; they should then be placed in either xylene or clove oil for several minutes before being transferred to the Canada balsam. When the dissection is complete a coverslip is added and the slide should be kept flat for at least six weeks in a hot air cabinet at 40–45°C, longer for thick mounts. It is not advisable to store Canada balsam slides vertically unless they have been dried for a long period and ringed with Glyceel or a similar ringing compound.

Absolute alcohol can be either absolute *ethanol* (ethyl alcohol) or *propan-2-ol* (isopropyl alcohol or iso-propanol). Ethanol is very expensive because it is heavily taxed; conversely, propan-2-ol is very cheap, has no tax on it, and has the advantage that it is considerably less hygroscopic than ethanol; ethanol absorbs water from the air and becomes diluted very quickly so that it is no longer of any use for slide preparation work. Most standard textbooks on insect collecting give a more detailed account of slide making, e.g. Oldroyd (1970b).

Advanced techniques
The modern taxonomist is now aware that almost any so-called species may one day be shown to be a complex of morphologically inseparable species, i.e. many of our currently recognized species may only be *morphospecies* consisting of more than one genetically distinct species. If we are lucky it may be possible to separate the true species by some previously overlooked morphological feature, e.g. two of our species of *Cerajocera* can only be separated in the larval and pupal stages. Similarly, some *Dacus* species can only be separated by a stereoscan examination of the eversible ovipositor sheath (Drew & Hardy, 1981). In some cases multivariate statistical methods may help to identify ways of separating species morphologically with discriminant functions.

Several tephritids are now known to have host races and some of these may in reality be separate species, e.g. *Tephritis formosa* larvae can only develop on the *Sonchus* species from which their parents were reared (Berube, 1978). In Central Europe *T. conura* lives on *Cirsium oleraceum* at low altitudes and *C. helenioides* at high altitudes. This observation, combined with the fact that each population of the fly also differs in phenology, prompted Seitz & Komma (1984) to see if gel electrophoresis showed any differences between specimens from each host, and they found iso-enzyme differences implying that *T. conura* is really a species complex. Niblett (1947) suggested that *Sphenella marginata* might also have host races, but this has never been investigated.

Even populations on the same host can in reality belong to separate species in some cases, e.g. *Rhagoletis cerasi* populations north and south of the River Danube are separated by a sterility barrier (Boller *et al.*, 1976).

In North America gel electrophoresis has been used to construct a key to nine species of *Rhagoletis* and this key can be applied to any life cycle stage (Berlocher, 1980). Serological techniques have not been seriously applied to tephritids, although the immunological distances between a few representatives of each tribe were measured by Kitto (1983). Such advanced techniques are beyond the scope of this handbook, but their importance to the study of tephritids is likely to increase in the near future.

Morphology and recognition

Terminology

This handbook uses the recently proposed terminology of McAlpine (1981), with modifications of relevance to tephritids by Freidberg & Mathis (1986). Equivalent terms used by Oldroyd (1970a) and others are given in the annotated alphabetical list of key characters at the end of this section.

Recognition of Tephritidae

Tephritids vary in wing length from about 2 mm to 8 mm (up to 25 mm in some tropical species) and most species have patterned wings. They may be distinguished from other picture-winged Acalyptratae by the right-angled bend near the end of vein Sc (fig. 10), just before Sc becomes faint and joins C (the costa), and by the presence of frontal setae. Other important features are: vibrissae absent (not to be confused with genal setae); wing with both H and Sc breaks; R_1 with dorsal setulae; R_{4+5} often with dorsal and/or ventral setulae; cell cu*p* usually with a pointed extension (fig. 10); ovipositor telescopic (fig. 13); distiphallus at the end of a long coiled basiphallus (fig. 14).

Head

The major features of the head are shown in figs 7–9, with the following abbreviations:

ar — arista
comp eye — compound eye
fc — face
flgm 1 — first flagellomere
fr — frons
fr s — frontal setae
fr slae — frontal setulae
gn — gena (pleural: genae)
gn grv — genal groove
gn s — genal seta
i vt s — inner vertical seta
lbl — labellum
lun — lunule
oc — ocellus
oc s — ocellar seta
o vt s — outer vertical seta
orb s — orbital setae
pafc — parafacial area
plp — palpus
ped — pedicel
poc s — postocellar seta
pocl s — postocular setae
ptil fis — ptilinal fissure
rst — rostrum

scp — scape
vrt — vertex

Thorax
The features of the thorax are shown in figs 11, 12.

a npl s — anterior notopleural seta
a sctl s — apical scutellar seta
a spal s — anterior supra-alar seta
a spr — anterior spiracle
anatg — anatergite
anepm — anepimeron
anepst — anepisternum
b sctl s — basal scutellar seta
cx — coxa
dc s — dorsocentral seta
hlt — haltere
ial s — intra-alar seta
kepst — katepisternum
kepst s — katepisternal seta
ktg — katatergite
mr — meron
npl — notopleuron
p npl s — posterior notopleural seta
p spal s — posterior supra-alar seta
p spr — posterior spiracle
pal cal — postalar callus
pprn lb — postpronotal lobe
pprn s — postpronotal seta
prepst — proepisternum
presut area — presutural area
presut dc s — presutural dorsocentral seta
presut spal s — presutural supra-alar seta
psctl acr s — prescutellar acrostichal seta
psut sct — postsutural scutum
sctl — scutellum
subsctl — subscutellum
trn sut — transverse suture
u anepst s — upper anepisternal seta

Wing
Features of the wing are shown in fig. 10. Full names of wing veins and cells are not used in the following keys and are therefore not listed here; the full names of the veins and cells are given by McAlpine (1981).

ap cb — apical crossband
cg bk — costagial break
cu*p* ex — extension to cell cu*p*
ds cb — discal crossband
h bk — humeral break
prap cb — preapical crossband
sc bk — subcostal break
subbs cb — subbasal crossband

Abdomen
Features of the abdomen and female terminalia are shown in fig. 13.

acul — aculeus
ev ovp sh — eversible ovipositor sheath

ovsc — oviscape
st — sternite (numbered 1–6 in the ♀ and 1–5 in the ♂)
tg — tergite (1 + 2 fused, followed by 3–6 in the ♀ and 3–5 in the ♂)

Features of the main terminalia are shown in fig. 14.

ac scl — accessory sclerite
aed apod — aedeagal apodeme
bph — basiphallus
bph microt — basiphallic microtrichia
distiph — distiphallus
ej apod — ejaculatory apodeme
epand — epandrium
hypd — hypandrium
i sur — inner surstylus
o sur — outer surstylus
prens — prensiseta
proct — proctiger (cerci & anus)

Annotated list of key characters

Morphological features and other terms used in the keys are explained in the following alphabetical list; simple terms that can be found in any general introduction to entomology and terms that are easily explained by figs 7–14 are omitted.

1st FLAGELLOMERE — This is the 3rd segment of the antenna (fig. 7).

ACCESSORY SCLERITE — British species of Terelliini all have a small sclerite attached by a membrane to the apical part of the distiphallus. The function of this sclerite is unknown and its shape is usually very variable. Its only taxonomic value is as a point of reference so that the distiphallus can be positioned in such a way as to produce comparable views, e.g. figs 82, 83, 116.

ACROSTICHALS — see prescutellar acrostichals.

ACULEUS — This is the piercing part of the female ovipositor which is normally retracted into the oviscape (fig. 13). Given a partly extended aculeus and a very good high power stereomicroscope, about × 100, it is sometimes possible to see the shape of the aculeus without dissection. Usually, the aculeus will have to be dissected, slide mounted, and then examined with a compound microscope if its shape is critical. With some *Urophora* species it is essential to dissect the aculeus; see p. 14 for method. Some authors call this structure the gynium, ovipositor piercer or ovipositor. The method by which a tephritid extrudes its aculeus was described by Berube & Zacharuk (1983).

ANATERGITE — This sclerite is just below the scutellum and just above the haltere (fig. 12). The Euphrantini are differentiated from other tephritids by the long pale coloured hairs on the anatergite; however, these are sometimes difficult to see and our only species, *Euphranta toxoneura*, is more easily recognized by its wing pattern. The anatergite and the katatergite together form the laterotergite, which is the pleurotergite of many authors.

ANEPISTERNUM — A large pleural sclerite of the thorax (fig. 12). Many tephritids have a vertical suture just anterior to the series of setae along the posterior edge of the anepisternum; this suture is well developed in the Trypetinae and Terelliini, but reduced or absent in other groups; it is not a reliable diagnostic character. The colour of the uppermost anepisternal seta is used as a character to split *Paroxyna* into species groups. The anepisternum is the mesopleuron of many authors.

ARISTA — Style or seta-like part of the antenna attached near the base of the 1st flagellomere (fig. 7). Most tephritids have a micropubescent arista, i.e. it is covered in a microscopic downy pile. A few species, e.g. *Myoleja caesio*, have a long pubescent covering to the arista.

APICAL CROSSSBANDS — see crossbands.

BASIPHALLUS — This is the long tubular basal part of the male aedeagus or penis (fig. 14). Some genera, e.g. *Paroxyna, Campiglossa* and *Oxyna*, have microtrichia just prior to the apex of this organ, before it joins the distiphallus (figs 142, 156, 175–183).

BIOVOLTINE — Having two generations per year.

CAPITULA (singular: capitulum) — A botanical term meaning the flower bud, flower or seed head of a composite (Asteraceae). The term is used here where it would otherwise be necessary to say flower buds, flowers and seed heads.

CELL cu*p* — A basal wing cell bounded anteriorly and apically by vein CuA_2 and posteriorly by vein A_1 (fig. 10). In the Myopitinae this cell is closed by a convex vein CuA_2. In other groups Vein CuA_2 is concave across the apical side of cell cu*p*, forming an acute extension which may be very small, e.g. *Ensina sonchi* (fig. 184), or long, e.g. *Orellia falcata* (fig. 251).

CELL sc — The cell distal to the faint part of vein Sc, bounded anteriorly by C and enclosed by R_1 both posteriorly and distally (fig. 10).

CONVERGENT SETAE — Any setae which lean towards the mid-line of the fly. The Terelliini, *Xyphosia miliaria* and *Vidalia cornuta* have the posterior pair of orbital setae converging in this manner.

COSTAL EDGE — The leading (anterior) wing edge along which vein C runs (fig. 10).

CROSSBANDS — The system of named wing crossbands used here follows Steyskal (1979); it was devised for use with *Urophora* but is here applied to other genera when appropriate. *Urophora* species have up to 4 crossbands, namely: subbasal, through the basal cells bm and cu*p*; discal, through cell sc, the r–m crossvein and the middle of cell dm; preapical, through the dm–cu crossvein; apical, at the wing apex (fig. 10).

CROSSVEIN r–m — This links veins R_{4+5} and M, joining M part way along cell dm (fig. 10). In some keys the position of r–m is described in relation to the end of vein R_1, i.e. where R_1 joins C. In some other keys, reference is made to the position of r–m relative to an imaginary point half way along the top of cell dm, i.e. is r–m before or beyond the middle of dm?

DISCAL CROSSBAND — see crossbands.

DISTIPHALLUS — This is the apical part of the male aedeagus or penis (fig. 14). In the tephritids this is a very complex structure which was first used for species diagnosis by Munro (1947). The structure of the distiphallus is very uniform in some genera, e.g. *Tephritis* and *Urophora*; however, it is often of considerable value, especially in *Paroxyna* (figs 175–183). Names have recently been given to some of the internal structures of the distiphallus by Munro (1984) and Korneev (1985).

DORSOCENTRAL SETAE — Tephritids usually have at most 1 pair of postsutural dorsocentral setae; a term here contracted to dorsocentral setae (fig. 11). The relative position of these setae to the anterior supra-alar setae is of some interest to the higher classification; in Tephritini the dorsocentrals are usually placed in front of an imaginary line between the anterior supra-alar setae; in the Trypetinae and Terelliini they are usually on or behind this line; however, this is not a definitive character. The Dacinae lack dorsocentral setae. The dorsocentrals should not be confused with the prescutellar acrostichal setae. See also presutural dorsocentral setae.

FEMUR (setae on) — *Rhagoletis* species have one or more setae near the apex of the hind femur, which are placed subapically in an anteroventral position, i.e. on the curve between the front and underside of the femur. *Paroxyna* species have one or more setae near the apex of the hind femur, which are placed dorsally (fig. 160).

FLAGELLOMERE — see 1st flagellomere.

FRONS — The anterodorsal area of the head, bounded laterally by the eyes, posteriorly by the ocellar triangle, and anteriorly by the lunule (fig. 7). In *Vidalia cornuta* the males have extensions of the frons which bear enlarged frontal setae, so forming antler-like structures (fig. 46).

FRONTAL SETAE — The row of setae next to each eye in the lower part of the frons (fig. 7). Most British tephritids have between 1 and 3 pairs, i.e. 1–3 setae next to each eye. They are usually incurved and many authors call them inferior or lower fronto-orbitals. In males of *Vidalia* species the frontals are abnormally well developed, sometimes forming antler-like structures (fig. 46). In *Oxyna* species there is usually only one pair of frontals; freak specimens with extra frontal setae are common and the genus is then differentiated from other Tephritini by the upper frontal setae being no higher on the frons than the top of the lunule (fig. 139).

FRUGIVOROUS — A species whose larvae feed on fruit.

GENAL SETAE — *Chaetostomella* species have a series of long setae along each gena (fig. 89).

GENICULATE MOUTHPARTS — Long elbowed mouthparts; found in *Ensina sonchi, Dioxyna bidentis, Goniglossum wiedemanni, Myopites* species, *Oxyna* species, *Sphenella marginata* and *Paroxyna producta* (fig. 9).

HIND FEMUR — see femur.

HYALINE WING — A wing with no markings.

INTRA-ALAR SETAE — A series of setae between the dorsocentral and supra-alar series; tephritids only have one pair of intra-alars, placed level with the prescutellar acrostichal setae (fig. 11).

KATEPISTERNUM — The triangular sclerite between the coxae of the fore and mid legs (fig. 12). Most species have a well developed seta near the posterior corner, but this is absent in some leaf and stem mining Trypetini. It is the sternopleuron of many authors.

LOWER FACIAL MARGIN — The lower anterior part of the head, below the face and above or in front of the mouth opening. In *Myopites* the long geniculate mouthparts protrude in front of the lower facial margin even when folded (fig. 27). The lower facial margin is the epistome of many authors.

LUNULE — The semicircular plate above the antennal bases and below the ptilinal fissure (fig. 7).

MONOPHAGOUS — A species whose host-plant range is confined to a single species-group of plants (this is a modified definition designed to suit application to the Tephritidae).

NOTOPLEURAL SETAE — The notopleuron (fig. 12) is a lateral thoracic sclerite, which has an anterior and a posterior setal position. In *Paroxyna,* the posterior notopleural seta is either white or black, and this helps split the genus into species groups (figs 169–171).

OCELLAR TRIANGLE — The subtriangular area that encloses the 3 ocelli, which are themselves arranged as a triangle.

OLIGOPHAGOUS — A species whose host-plant range is broader than a single species group, but confined to a single family of plants.

ORBITAL SETAE — The setae in the upper part of the frons which usually form a series of 1–3 reclinate setae near the upper part of each eye (fig. 7). Most species have 2 pairs, i.e. 2 setae next to each eye. Most Tephritini have a black anterior pair and a white posterior pair. *Ensina, Euphranta, Vidalia* and the Myopitinae have only a single pair. Strictly, these setae are 'reclinate orbital setae' and they are the superior or upper fronto-orbitals of many authors. The prefix 'reclinate' is superfluous because tephritids lack proclinate orbitals. Furthermore, the Terelliini, *Vidalia cornuta* and *Xyphosia miliaria* have the posterior pair of orbitals convergent rather than reclinate (figs 99, 136).

PARAFACIAL SETAE — *Chetostoma curvinerve* has a series of well developed flattened setae along each side of the lower part of the face (fig. 37).

PEDICEL — The second segment of the antenna. In some male *Cerajocera* species the pedicel is greatly enlarged and protrudes from the head at least as far as the apex of the 1st flagellomere (fig. 96).

PLEURA (singular: PLEURON) — The lateral sclerites of the thorax (fig. 12).

PLEURAL MEMBRANE — The lateral membrane of the abdomen.

POLYPHAGOUS — A species whose range of host-plants are not confined to one plant family.

POSTGENAL SETAE — Setae at the back of the genae which are used as secondary characters of some *Trypeta* and *Vidalia* species.

POSTOCULAR SETAE — The row of small setae behind each eye (fig. 7). These are usually thin and black, but in the Tephritini at least some of these setae are white and scale-like.

PREAPICAL CROSSBANDS — see crossbands.

PRESCUTELLAR ACROSTICHAL SETAE — The acrostichal setae are the setae nearest to the mid-line of the scutum; tephritids have at most one pair and they are placed just in front of the scutellum (fig. 11). Consequently, some authors call them the prescutellar setae.

PRESUTURAL DORSOCENTRAL SETAE — This is a pair of dorsocentrals in front of the suture, and they are absent from most tephritids (fig. 11). Their presence is an important distinguishing feature of *Chaetorellia* species, *Dithryca guttularis* and *Oxyna flavipennis*.

PROCLINATE SETAE — Any setae which lean forwards.

PTILINAL FISSURE — The inverted 'U' or 'V' shaped slit which runs over the antennal bases, ending in the genal grooves (fig. 7).

RECLINATE SETAE — Any setae which lean back.

SCUTUM — The scutum and scutellum form the dorsal part of the thorax. The scutum includes both the pre- and postsutural areas (fig. 11). The scutum is the mesonotum of many authors.

SPERMATHECAE — Female internal organs used to store sperm until needed to fertilize eggs; these can be found in segment 6 when an aculeus is being dissected. British Tephritinae have 2 spermathecae; in the Myopitinae they are very poorly sclerotized and cannot be found in preserved specimens, but they appear to have 2 (A. Freidberg, pers. comm.); *Euphranta toxoneura* and most Trypetini have 3; Trypetini with only 2 spermathecae are *Cryptaciura rotundiventris, Platyparea poeciloptera, Rhagoletis alternata* and *R. meigenii*. As the shape of spermathecae may vary between pre- and post-mated, and post-oviposition females, spermathecal shape is not used as a character in this handbook.

STERNITES — The shape of sternite 5 of the male is sometimes a useful character, but it can only be reliably interpreted from a dissected specimen. *Paroxyna* and *Campiglossa* can be separated from *Dioxyna* (fig. 166) by the presence of a broad membraneous extension to sternite 5 (figs 167, 168). Furthermore, some *Paroxyna* and *Campiglossa* species have a 'V' shaped posterior margin to sternite 5, namely *C. argyrocephala, P. loewiana, P. plantaginis, P. producta* and *P. solidaginis*; however, the character is very variable in some of these species and it is not used for their separation.

SUBBASAL CROSSBAND — see crossbands.

SUPRA-ALAR SETAE — Tephritids have up to 3 pairs of supra-alar setae, as follows: presutural; anterior postsutural, a term usually reduced to anterior; posterior postsutural, a term usually reduced to posterior (fig. 11).

SURSTYLI (singular: SURSTYLUS) — The outer and inner pairs of surstyli derive from the epandrium (fig. 14) and in some groups of tephritids their shape can be used for species diagnosis, e.g. *Trypeta* species (Rikhter, 1985). However, it is often difficult to orientate these structures to produce comparable views and the only species covered by this *Handbook* whose distiphalli were very similar, but could be separated by surstyli characters were *Terellia longicauda* and *T. serratulae* (figs 108, 109); consequently, the surstyli of other species are not illustrated. Korneev (1979) reviews surstylus form throughout the family.

TENERAL — A freshly emerged adult with a soft pale coloured body and poorly formed wing markings. Reared specimens should always be kept alive for a few days to allow their bodies to harden and colours to develop before being killed.

TERGITES $1+2$ — In the higher Diptera the first visible dorsal abdominal sclerite is formed by the fusion of tergites 1 and 2, sometimes called syntergite $1+2$ (fig. 13).

TOMENTOSE/TOMENTOSITY/TOMENTUM — A covering of ultramicroscopic pubescence on any part of the body, so that the body surface is matt; pollinose/pollinosity of many authors. As a general rule the Tephritini are more tomentose than other groups.

TRANSVERSE SUTURE — Calyptrate Diptera have a distinct suture across the scutum, between the notopleura. In the Acalyptratae, e.g. the Tephritidae, this suture is absent across the central part of the scutum and is only represented by vestiges of the suture next to each notopleuron (fig. 11). Even so, this vestigial suture marks the boundary between the presutural and postsutural scutum.

UNIVOLTINE — Having one generation per year.

VEIN R_{4+5} — The position of this vein is shown in fig. 10. Most Trypetini and a few genera of Tephritini have a series of setulae along the dorsal side of R_{4+5}. Some Tephritini have setulae along the ventral side of this vein, a useful character for recognising some *Tephritis* species.

VERTEX — The uppermost part of the head, between the eyes and around the ocellar triangle (fig. 7).

VERTICAL SETAE — There are 2 pairs of verticals on the vertex, placed between the eyes and the ocelli (fig. 7). The pair nearest the ocelli are the inner verticals which are usually long and black. The pair nearest the eyes are the outer verticals; in many species these are well developed black setae; in the Tephritini the outer verticals are white and often scale-like, and sometimes they are difficult to distinguish from the postocular setae.

Check list

Only synonyms and misidentifications of relevance to the British check list (Cogan, 1976), and the standard works of Hendel (1927) and Séguy (1934) are listed. Further synonyms and bibliographic details can be obtained from Foote (1984) and White (1986). Accidentally introduced species, which have not become established, are listed at the end of the main check list. No satisfactory world classification of Tephritidae has been constructed and the following groupings concord with most modern regional classifications.

TEPHRITIDAE

MYOPITINAE
  UROPHORINAE

MYOPITES Blot, 1827
eximia Séguy, 1932

?*frauenfeldi* Schiner, 1864
inulaedyssentericae Blot, 1827
    blotii Brébisson *in* Blot, 1827

UROPHORA Robineau-Desvoidy, 1830
S. UROPHORA s.s.
cardui (Linnaeus, 1758)
cuspidata (Meigen, 1826)
jaceana (Hering, 1935)
quadrifasciata (Meigen, 1826)
solstitialis (Linnaeus, 1758)
spoliata (Haliday, 1839)
stylata (Fabricius, 1775)

TRYPETINAE

EUPHRANTINI

EUPHRANTA Loew, 1862
S. RHACOCHLAENA Loew, 1862
toxoneura (Loew, 1846)

TRYPETINI

ACIDIA Robineau-Desvoidy, 1830
cognata (Wiedemann, 1817)

ANOMOIA Walker, 1835
    PHAGOCARPUS Rondani, 1870
purmunda (Harris, 1780)
    permunda: emend.

CHETOSTOMA Rondani, 1856
curvinerve Rondani, 1856

CRYPTACIURA Hendel, 1927
rotundiventris (Fallén, 1814)

EULEIA Walker, 1835
heracleii (Linnaeus, 1758)
    heraclei: emend.

GONIGLOSSUM Rondani, 1856
wiedemanni (Meigen, 1826)

MYOLEJA Rondani, 1856
    PHILOPHYLLA Rondani, 1870
S. MYOLEJA s.s.
caesio (Harris, 1780)

PLATYPAREA Loew 1862
    PLATYPARELLA Hendel, 1914
discoidea (Fabricius, 1787)
poeciloptera (Schrank, 1776)

RHAGOLETIS Loew, 1862
alternata (Fallén, 1814)
meigenii (Loew, 1844)

TRYPETA Meigen, 1803
S. TRYPETA s.s.
artemisiae (Fabricius, 1794)
immaculata Macquart, 1835
　hamifera (Loew, 1846)
zoe Meigen, 1826
　?*wiedemanni* (Hendel, 1923), preocc. Meigen, 1826

VIDALIA Robineau-Desvoidy, 1830
cornuta (Scolpoli, 1772)
spinifrons (Schroeder, 1913)
　virgata (Collin, 1946)

TEPHRITINAE

TERELLIINI

CERAJOCERA Rondani, 1856
ceratocera Hendel, 1913
plagiata (Dahlbom, 1850)
　microceras Hering, 1935
tussilaginis (Fabricius, 1775).

CHAETORELLIA Hendel, 1927
jaceae (Robineau-Desvoidy, 1830)
loricata (Rondani, 1870)
　falcata: auctt. Brit. partim nec (Scopoli, 1763) (misidentification)

CHAETOSTOMELLA Hendel, 1927
cylindrica (Robineau-Desvoidy, 1830)
　?*onotrophes* (Loew, 1846)

ORELLIA Robineau-Desvoidy, 1830
falcata (Scopoli, 1763)

TERELLIA Robineau-Desvoidy, 1830
colon (Meigen, 1826)
longicauda (Meigen, 1838)
ruficauda (Fabricius, 1794)
serratulae (Linnaeus, 1758)
vectensis (Collin, 1937)
winthemi (Meigen, 1826)

DITHRYCINI
DITHRYCHINI

DITHRYCA Rondani, 1856
guttularis (Meigen, 1826)

NOEETA Robineau-Desvoidy, 1830
S. NOEETA s.s.
　OPLOCHETA Rondani, 1856
pupillata (Fallén, 1814)

TEPHRITINI

ACANTHIOPHILUS Becker, 1908
helianthi (Rossi, 1794)

ACINIA Robineau-Desvoidy, 1830
corniculata (Zetterstedt, 1819)

CAMPIGLOSSA Rondani, 1870
argyrocephala (Loew, 1844)
grandinata (Rondani, 1870)

DIOXYNA Frey, 1945
bidentis (Robineau-Desvoidy, 1830)
   absinthii: Hendel, 1927; Séguy, 1934 nec (Fabricius, 1805) (misidentification)

ENSINA Robineau-Desvoidy, 1830
sonchi (Linnaeus, 1767)

ICTERICA Loew, 1873
westermanni (Meigen, 1826)

OXYNA Robineau-Desvoidy, 1830
flavipennis (Loew, 1844)
nebulosa (Wiedemann, 1817)
   proboscidea (Loew, 1844)
parietina (Linnaeus, 1758)
   nebulosa: auctt. Brit., nec (Wiedemann, 1817) (misidentification)

PAROXYNA Hendel, 1927
absinthii (Fabricius, 1805)
   punctella (Fallén, 1814)
   parvula (Loew, 1862)
lhommei Hering, 1936
loewiana Hendel, 1927
misella (Loew, 1869)
plantaginis (Haliday, 1833)
producta (Loew, 1844)
   tessellata: auctt. nec (Loew, 1844) (misidentification)
solidaginis White, 1986
   loewiana, unnamed var.: Collin, 1947

SPHENELLA Robineau-Desvoidy, 1830
marginata (Fallén, 1814)

TEPHRITIS Latreille, 1804
bardanae (Schrank, 1803)
cometa (Loew, 1840)
conura (Loew, 1844)
formosa (Loew, 1844)
hyoscyami (Linnaeus, 1758)
leontodontis (De Geer, 1776)
   dioscurea: auctt. Brit. nec. (Loew, 1856) (misidentification)
neesii (Meigen, 1830)
   conjuncta (Loew, 1844)
   guttata: auctt. Brit. nec (Fallén, 1814) (misidentification)
praecox (Loew, 1844)
ruralis (Loew, 1844)
separata Rondai, 1871 (?det. see p. 52)
   conjuncta Hendel, 1927, as '*conjuncta* Loew, 1862' preocc. (Loew, 1844)
vespertina (Loew, 1844)

TRUPANEA Schrank, 1795
amoena (Frauenfeld, 1857)
stellata (Fuessly, 1775)

XYPHOSIA Robineau-Desvoidy, 1830
S. XYPHOSIA s.s.
miliaria (Schrank, 1781)

Foreign introductions

Species that have been found in the British Isles but have not become established British species are listed below. Nomenclatorial details of non-British species are available in the following regional catalogues: Afrotropical (Cogan & Munro, 1980); Nearctic (Foote, 1965); Neotropical (Foote, 1967); Oriental (Hardy, 1977); and Palaearctic (Foote, 1984). Imported species of known origin should be identified using the references in these catalogues and with the following key works: Indian genera (Kapoor *et al.*, 1980); Neotropical genera (Foote, 1980); Philippines (Hardy, 1974); and Thailand (Hardy, 1973); for *Anastrepha, Ceratitis, Dacus* and *Rhagoletis* see notes on these genera on pages 36, 34, 31 and 38.

DACINAE

DACUS Fabricius, 1805
S. DIDACUS Collart, 1935
ciliatus Loew, 1862   (Afrotropical and Oriental)

TRYPETINAE

?ACANTHONEVRINI

TAOMYIA Bezzi, 1920
marshalli Bezzi, 1920   (Afrotropical)

CERATITINI

CERATITIS MacLeay, 1829
capitata (Wiedemann, 1824)   (Afrotropical and Mediterranean, intro. to other
                                                         tropical and warm temperate areas)

PARDALASPIS Bezzi, 1918
cosyra (Walker, 1849)   (Afrotropical)

TRYPETINI

ANASTREPHA Schiner, 1868
?obliqua (Macquart, 1835)   (Neotropical)

RHAGOLETIS Loew, 1862
cerasi (Linnaeus, 1758)   (Palaearctic)

Symbols and abbreviations used in the keys

AL = Aculeus length.

WL = Wing length.

TO = Tergal-oviscapal measure; this is the number of tergites before the oviscape whose combined length is equal to the length of the oviscape. This value is only given for species of Terelliini and it should only be used as an approximate guide to ovipositor size.

A description of the layout of the keys is given on page 13.

Simplified key to genera and some species of Tephritidae

1   Wings hyaline (figs 222–225), at most with a slightly darkened cell sc (fig. 223). (WARNING: Teneral specimens of any species could erroneously be run this way; check diagnostic characters carefully.) 2

—   Wings patterned (figs 226–286), usually banded (figs 229–260), reticulate (figs 259–280) or with a star shaped marking (figs 281, 282) 4

2   Two pairs of orbital setae, the posterior pair convergent and the anterior pair not convergent (similar to fig. 99) . . . . **Terellia** Robineau-Desvoidy (p. 43)

—   One pair of orbital setae, which are reclinate (figs 28, 132) 3

3   Head elongate in profile and mouthparts long (fig. 132). Cell cup closed by a concave vein CuA_2, forming a very small cup extension (fig. 184) . . . . . **Ensina sonchi** (Linnaeus) (p. 47)

—   Head higher in profile and mouthparts short (fig. 28). Cell cup closed by a convex vein CuA_2, without any cup extension (fig. 29). . . . . **Urophora spoliata** (Haliday) (p. 33)

4   Ocellar and dorsocentral setae absent. Wing pattern usually confined to a stripe along cell cup and the costal edge of the wing (fig. 285). (Larvae in imported fruit of Old World origin.) . . . . **Dacus** Fabricius (p. 31)

—   Ocellar and/or dorsocentral setae present. Wing pattern of another form 5

5   Apex of vein M turned anteriorly to merge with vein C without any visible angle (fig. 283). (Larvae in imported fruit of Neotropical origin.) . . . . **Anastrepha** Schiner (p. 36)

—   Apex of vein M meeting vein C with a distinct angle. 6

6   Wing pattern confined to a few faint marks in the apical half of the wing and anterior to vein M (fig. 226). (3 pairs of frontal setae. 1 black and 1 white pair of orbital setae, fig. 137. Scutum and scutellum uniformly grey tomentose on a black ground.) . . . . **Acanthiophilus helianthi** (Rossi) (p. 46)

—   Wing pattern of another form. (A few specimens of other species, e.g. *Terellia colon,* sometimes have a wing pattern confined to the same area, but they will not match the other characters given above.) 7

7   Wing with a star shaped pattern in the apical third of the wing (figs 281, 282); basal two-thirds hyaline, except for a mark in sc which sometimes extends obliquely to join the apical star shaped mark (fig. 281) 8

—   Wing pattern of another form. 9

8   Wing without an apical hyaline stripe (fig. 281). Scutellum with 2 pairs of setae . . . . **Tephritis cometa** (Loew) (p. 51)

—   Wing with an apical hyaline stripe (fig. 282). Scutellum with 1 pair of setae . . . . **Trupanea** Schrank (p. 53)

9   Wing as fig. 255 . . . . **Cryptaciura rotundiventris** (Fallén) (p. 37)

—   Wing pattern of another form. 10

10   Wing as fig. 258 . . . . **Anomoia purmunda** (Harris) (p. 36)

—   Wing pattern of another form. 11

11   Wing with brown markings as fig. 259, and remainder of wing pale brown, usually reticulate. (2 pairs of vertical setae well developed and pale in colour. Posterior pair of orbital setae convergent (fig. 136). Vein R_{4+5} with dorsal and ventral setulae.) . . . . **Xyphosia miliaria** (Schrank) (p. 53)

—   Wing usually with coloured markings or a reticulate pattern; if with both, the reticulate area is confined to an area between the subbasal and discal crossbands (*Ceratitis capitata,* reared from imported fruit) (fig. 284) 12

12   Wing with crossbands and reticulate marks between subbasal and discal crossbands (fig. 284). (Larvae in imported fruit.) . . . . **Ceratitis capitata** (Wiedemann) (p. 34)

—   Wing pattern of another form. 13

13   Wing pattern not reticulate, but formed of crossbands, or blocks of colour (figs 227–257). (Head with 2 pairs of black vertical setae.) 14

—   Wing pattern reticulate (figs 260–280). 34

14   Presutural dorsocentral setae present (fig. 85). (Wing, fig. 249.)   **Chaetorellia** Hendel (p. 42)

—   Presutural dorsocentral setae absent 15

15   Parafacial setae well developed (fig. 37) . . . . **Chetostoma curvinerve** Rondani (p. 37)

—   Parafacial setae absent. 16

16   Male 17

—   Female 19

— Scutellum with 2 pairs of black setae. Presutural dorsocentral setae absent. Wing pattern as fig. 261 . . . . **Noeeta pupillata** (Fallén) (p. 45)

36 Vein R_{4+5} with dorsal setulae (care should be exercised in observing this character as the setulae are often not as conspicuous as those on R_1) 37

— Vein R_{4+5} without dorsal setulae, except sometimes at its base 38

37 Wing as fig. 263. Head with 2 pairs of frontal setae (fig. 133)
. . . . **Icterica westermanni** (Meigen) (p. 47)

— Wing as fig. 262. Head with 3 pairs of frontal setae (fig. 135) . . . .
. . . . **Acinia corniculata** (Zetterstedt) (p. 47)

38 Wing as fig. 260 . . . . **Sphenella marginata** (Fallén) (p. 50)

— Wing pattern of another form. 39

39 Presutural dorsocentral setae present . . . . **Oxyna flavipennis** (Loew) (p. 48)

— Presutural dorsocentral setae absent 40

40 Head usually with 1 pair of black frontal setae (fig. 139); if with more than 1 pair, the posterior pair are no higher on the frons than the top of the lunule (fig. 139 inset). (Wings usually as figs 264, 265.) . . . . most **Oxyna** Robineau-Desvoidy species (p. 47)

— Head with 2 pairs of black or brown frontal setae (e.g. fig. 140) 41

41 Cell sc with 2 hyaline areas (fig. 267) . . . . **Campiglossa grandinata** (Rondani) (p. 50)

— Cell sc without, or with 1 hyaline area 42

42 Apical scutellar setae reduced or absent, at most one-quarter as long as basal pair of scutellar setae. (Wing pattern as fig. 268.) . . . . **Dioxyna bidentis** (Robineau-Desvoidy) (p. 49)

— Apical scutellar setae more than one quarter as long as basal pair of scutellar setae 43

43 Cell r_{2+3} with 2 hyaline areas contacting C, the apical of these extending across vein R_{4+5} into cells r_{4+5} (figs 273–280). Vein R_{4+5} usually with ventral setulae (except *T. praecox*). Wing pattern as figs 270, 273–280 . . . . **Tephritis** Latreille (p. 50)

— Cell r_{2+3} usually with 1 hyaline area contacting C (figs 269, 271); if with 2 hyaline areas contacting C, they are both small and do not extend into cell r_{4+5} (fig. 266). Vein R_{4+5} without ventral setulae. Wing pattern as figs 266, 269, 271 44

44 Hind femur with a dorsal preapical seta (fig. 160) . . . . **Paroxyna** Hendel (p. 48)

— Hind femur without a dorsal preapical seta . . . . . **Campiglossa argyrocephala** (Loew) (p. 50)

Key to subfamilies and tribes of Tephritidae

1 Ocellar and dorsocentral setae absent. Wing cell bm about 2 times as broad as cell cu*p* and usually about 2 times as long as broad (fig. 285). (Larvae in imported fruit of Old World origin.) . . . . **Dacinae** (p. 31)

— Ocellar setae usually present; if ocellar setae absent, dorsocentral setae present. Wing cell bm about as broad as cell cu*p* and usually over 4 times as long as broad. (ALL INDIGENOUS SPECIES HERE.) 2

2 Cell cu*p* closed by a convex vein CuA_2, so that there is no cu*p* extension. 1 pair of orbital setae. (Wing patterned with bands or entirely hyaline. Vein R_{4+5} without setulae. Postocular setae all black and slender. 2 pairs of fully developed dark vertical setae.) . . . . **Myopitinae** (p. 31)

— Cell cu*p* usually closed by a concave vein CuA_2, forming a cu*p* extension. Usually with 2 pairs of orbital setae (except *Ensina sonchi, Euphranta toxoneura* and *Vidalia* spp.). (NB, a few species, e.g. *Ensina sonchi, Goniglossum wiedemanni* and *Platyparea discoidea*, only have a very small cu*p* extension that is likely to be missed unless the specimens are examined with great care; however, these species do not fit other characters listed above and should therefore not be mistaken for Myopitinae.) 3

3 Postocular setae all slender and usually all black; posterior pair of orbital setae usually not convergent; if orbital setae convergent there is usually only one pair of orbital setae and vein R_{4+5} has dorsal setulae (*Vidalia cornuta*). Female usually with 3 spermathecae. (Wing patterned with bands. Vein R_{4+5} usually with dorsal setulae; except *Cryptaciura rotundiventris* and most *Rhagoletis* spp. which only have a few setulae at the base of R_{4+5}. 2 pairs of fully developed black vertical setae. Dorsocentral setae usually behind, or in line with the anterior supra-alar setae; if in front of anterior supra-alar setae, they are usually closer to the anterior supra-alar setae than to the vestigial transverse suture, except *Cryptaciura rotundiventris*. Anepisternum with a well developed vertical suture. Female tergite 6 usually shorter than tergite 5.) . . . . 4 **(Trypetinae)**

—   Postocular setae usually not all slender and black, usually some or all are white and scale-like; if all postocular setae black, then with 2 pairs of orbital setae, the posterior pair of which are convergent and vein R_{4+5} is without dorsal setulae except sometimes at the base (Terelliini). Female with 2 spermathecae. (Female tergite 6 usually longer than tergite 5.)
    . . . . .6 **(Tephritinae)**

4   Anatergite with long pale hairs which are distinct from the general pubescence (fig. 31). (NB, this is a very difficult character to observe and our only species, *Euphranta toxoneura*, is easily identified by its characteristic wing pattern.). . . . . **Euphrantini** (p. 34)

—   Anatergite without long pale hairs, at most with a fine pubescence 5

5   Cell cu*p* extension broader in the middle than at its base. Wing reticulate in the area of cells c, br, bm and cu*p* (e.g. fig. 284). (Scutellum convex in profile and polished, largely black. Not an indigenous tribe; larvae in imported fruit, especially organges.) . . . . . **Ceratitini** (p. 34)

—   Cell cu*p* extension not broader in middle than at base. Wing without any reticulation
    . . . . **Trypetini** (p. 35)

6   Posterior pair of orbital setae convergent; vein R_{4+5} without dorsal setulae, except sometimes at its base. (2 pairs fully developed black vertical setae. Dorsocentral setae usually approximately in line with anterior supra-alar setae, never closer to vestigial transverse suture than to anterior supra-alar setae. Anepisternum with a well developed vertical suture. Wing pattern banded or entirely hyaline.). **Terelliini** (p. 40)

—   Posterior pair of orbital setae usually not convergent; if posterior pair of orbital setae convergent then R_{4+5} with dorsal setulae (*Xyphosia miliaria*). (Outer vertical setae usually white and scale-like, often hard to distinguish from the postocular setae. Posterior pair of orbital setae usually white. Anepisternum usually without a well developed suture. Wing pattern usually reticulate.) 7

7   Anterior pair of orbital setae not, or hardly, higher on frons than posterior pair of frontal setae (figs 128–131); orbital plates (area of frons on which the orbital setae are based) extending at least half way down frons. Scutellum convex and polished dark brown to black (a character which only applies to the British fauna). (1st flagellomere dorso-apically pointed and concave on upper surface. Postocular setae mixed black and white. Dorsocentral setae approximately in line with the anterior supra-alar setae.)
    . . . .**Dithrycini** (p. 44)

—   Anterior pair of orbital setae much higher on frons than posterior pair of frontal setae; orbital plates extending less than half way down frons. Scutellum fairly flat and tomentose. (Dorsocentral setae usually in front of anterior supra-alar setae, and often closer to vestigial transverse suture than to anterior supra-alar setae. Abdominal tergites tomentose.) . . . . **Tephritini** (p. 45)

Subfamily Dacinae

Larval Dacinae develop in soft fruits and most species belong to a single genus, *Dacus* Hendel, which contains almost 500 species. The subfamily includes nine other genera and some authors prefer to split *Dacus* s.lat. into several smaller generic units; notably Munro (1984) who divided *Dacus* s.lat. into 50 genera and elevated the group to family rank. Dacines are found throughout the tropical and warm temperate Old World and some species have been found in fruit imported into Britain. In the Palaearctic there are two species of *Callantra* Walker, and 20 species of *Dacus* s.lat., one of which is the notorious olive-fly, *D. oleae* (Gmelin), a serious pest of olives (*Olea europaea*) in the Mediterranean area. Most dacines can be determined with the aid of the following works: Africa (Munro, 1984); Australia (Drew, 1982a); Indian subgenera (Kapoor *et al.,* 1980); Japan (Ito, 1983); Palaearctic (Hendel, 1927); Philippines (Hardy, 1974); South Pacific area (Drew, 1972); and Thailand (Hardy, 1973). Most species have a wing pattern similar to fig. 285.

Subfamily Myopitinae

A group of 10 genera which were keyed by Steyskal (1979); six of these genera occur in

the Palaearctic region. The Palaearctic and Afrotropical species of known biology induce galls in composite plants (Asteraceae).

Key to genera

1 Geniculate mouthparts very long; proboscis and palpi projecting beyond lower facial margin (fig. 27). Veins R_{4+5} and M strongly convergent (fig. 233). (Wings with broken brown crossbands, fig. 233. Distiphallus, fig. 19. Induces galls in the capitula of Inuleae, e.g. *Inula* and *Pulicaria* spp.) . . . . **Myopites** Blot (p. 32)
— Geniculate mouthparts not so long; proboscis and palpi not projecting beyond lower facial margin (fig. 28) (these characters only apply to subgenus *Urophora* s.str.). Veins R_{4+5} and M subparallel (figs 225, 243–246). (Body predominantly black; frons dark orange; scutellum yellow in centre; tibia and tarsi yellow; scutum usually tomentose, except *U. quadrifasciata*. Wings either hyaline or with black crossbands, figs 243–246. Distiphallus of British species, fig. 18. Induces galls in the capitula and stems of Cardueae, e.g. *Centaurea, Cirsium, Carduus* and *Serratula* spp.) . . **Urophora** Robineau-Desvoidy (p. 32)

Genus **Myopites** Blot

A genus of 13 Palaearctic and one Afrotropical species. Species of known biology are associated with the capitula of *Inula* and related genera of composites such as *Dittrichia* and *Pulicaria*. The genus has recently been partly revised and keyed by Dirlbek (1973; 1974) and Freidberg (1980).

Key to species

1 Abdominal tergites predominantly yellow, usually with a pair of small black spots on tergites 3–5 and black at sides. Discal crossband only faintly extending below vein M (fig. 233). Tergite $1+2$ yellow. (Body mainly yellow; scutum with a grey-green tomentum. WL $= 2\cdot5$–$3\cdot3$ mm. AL $= 0\cdot9$–$1\cdot3$ mm. Aculeus, fig. 16.) . . . . **inulaedyssentericae** Blot
Induces a gall in the capitulum of Pulicaria dysenterica. *South coast from Hants to Kent, usually coastal; old record from Surrey. Western, central and eastern Europe.*
— Abdominal tergites usually predominantly black, often yellow at the sides of tergites 3–5, but rarely yellow in the centre of these tergites. Discal crossband distinctly extending across cell dm, usually into cell cua$_1$. Tergite $1+2$ usually black. (Frons, legs and centre of scutellum mainly yellow-orange; rest of body dark; scutum with a grey-green tomentum. WL $= 2\cdot8$–$3\cdot5$ mm. AL $= 0\cdot8$–$0\cdot9$ mm. Aculeus, fig. 15.) . . . . **eximia** Séguy
Induces a gall in the capitulum of Inula crithmoides. *South-east and south England, generally a coastal species. Western and south-western Europe.*

Genus **Urophora** Robineau-Desvoidy

A genus of 64 Palaearctic species to which 46 species from the Afrotropical, Oriental and New World regions are assigned. Most species of known biology induce galls in the capitula of composites belonging to the tribe Cardueae, but *U. cardui* forms a stem gall on *Cirsium arvense*, which is also of the tribe Cardueae. The Palaearctic and New World species were keyed by Steyskal (1979), but some species groups are still in need of revision. No easily interpreted characters for identifying males of *U. cuspidata, U. jaceana* and *U. solstitialis* have yet been found and the account of these species by Collin (1937) is not reliable. Aculeus shape and length are important diagnostic features and it has been shown that ovipositor length, for the flower head species, is correlated with the size of the host's immature flower head (Zwölfer, 1983).

Subgenus **Urophora** Robineau-Desvoidy

A group of 63 Palaearctic species which are separated from s.g. *Asimoneura* Czerny by the short mouthparts and by the predominantly yellow scutellum.

Key to species

1   Wing without crossbands (fig. 225). (Femora black, except at apex. Aculeus with 2 pairs of subapical steps, fig. 22. $WL = 2 \cdot 7 – 3 \cdot 2$ mm. $AL = 1 \cdot 7 – 2 \cdot 0$ mm.) . . . . **spoliata** (Haliday)
    Associated with Serratula tinctoria. *Known only from South Hampshire, including the Isle of Wight.*

—   Wing with 3 or 4 distinct crossbands (figs 243–246) 2

2   Wing with 3 distinct crossbands, the subbasal crossband being absent, or at most reduced to a small black mark which is never fused to the discal crossband, nor connected to the discal crossband by a yellow mark (fig. 243). (Femora yellow or orange, sometimes striped black. Aculeus with 1 pair of subapical steps, fig. 24. Gall, fig. 4. $WL = 4 \cdot 0 – 4 \cdot 8$ mm. $AL = 2 \cdot 9 – 3 \cdot 5$ mm). . . . . **stylata** (Fabricius)
    Induces a multilocular gall in the capitulum of Cirsium vulgare *and sometimes other* Cirsium *species. England, as far north as Yorkshire; Ireland. Europe, Middle East; introduced to Canada as a biocontrol agent; accidentally introduced to Australia.*

—   Wing with 4 distinct crossbands, the subbasal crossband present and either fused to the discal crossband or connected to it by a yellow mark (figs 244–246) 3

3   Subbasal and discal crossbands connected by a yellow mark from vein C to at least R_{2+3} (fig. 244). Femora yellow or orange, sometimes striped black. 4

—   Subbasal and discal crossbands fused from vein C to at least R_{2+3} (figs 245, 246). Femora black, except at apex 7

4   Aculeus apex without any distinct subapical steps (fig. 17). Ovipositor very short; $AL = 1 \cdot 7$ mm. $(WL = 4 \cdot 0$ mm). . . . . sp. indet.
    Known only from a single female collected on 'knapweed' from Hampshire; this may be an undescribed species, or a remarkably aberrant U. jaceana.

—   Aculeus apex with 1 or 2 pairs of distinct supapical steps (figs 20, 21, 23). Ovipositor longer; $AL = 2 \cdot 0 – 3 \cdot 5$ mm 5

5   Aculeus apex with only 1 pair of distinct subapical steps (fig. 23). Ovipositor short; $AL = 2 \cdot 0 – 2 \cdot 6$ mm. $(WL = 3 \cdot 5 – 4 \cdot 3$ mm. Wing, fig. 244.). . . . . **jaceana** (Hering)
    Induces a multilocular gall in the capitula of Centaurea nigra *and probably* C. debeauxii. *Very common throughout the British Isles. Western, north-western and central Europe; accidentally introduced to Canada.*

—   Aculeus apex with 2 pairs of distinct subapical steps (figs 20, 21). Ovipositor long; $AL = 2 \cdot 8 – 3 \cdot 5$ mm 6

6   Aculeus with very prominent steps and a deep apical notch (fig. 20). (Discal crossband often broken into spots. $WL = 4 \cdot 2 – 5 \cdot 2$ mm. $AL = 2 \cdot 8 – 3 \cdot 5$ mm. Wing similar to fig. 244.)
    . . . . **cuspidata** (Meigen)
    Induces a gall in the capitulum of Centaurea scabiosa. *Very local, Dorset and Cambs.; old record from Bedfordshire. Central and eastern Europe.*

—   Aculeus with less prominent steps and with only a shallow apical notch (fig. 21). $(WL = 3 \cdot 1 – 4 \cdot 5$ mm. $AL = 3 \cdot 2 – 3 \cdot 4$ mm. Wing similar to fig. 244) . . . . **solstitialis** (Linnaeus)
    Induces a gall in the capitulum of Carduus nutans *and sometimes other* Carduus *species. Recently, recorded only from Hants and Suffolk; old records from Glamorgan, Somerset, Surrey and Sussex. Europe, North Africa, Middle East to Kazakh S.S.R.*

7   Discal and preapical crossbands separate at hind margin of wing (fig. 245). Size small; $WL = 2 \cdot 3 – 2 \cdot 8$ mm. Aculeus without subapical steps (fig. 26). $(AL = 1 \cdot 5 – 2 \cdot 0$ mm.)
    . . . . **quadrifasciata** (Meigen)
    Induces a gall in the capitulum of Centaurea nigra *and probably* C. debeauxii. *South-east England and East Anglia; unconfirmed record from Yorkshire, Europe, Middle East and North Africa; introduced to Canada as a biocontrol agent; accidentally introduced to Australia.*

—   Discal and preapical crossbands fused at hind margin of wing (figs 1, 246). Size large; $WL = 4 \cdot 9 – 5 \cdot 3$ mm. Aculeus with a pair of subapical steps (fig. 25). (Gall, figs 2, 3. $AL = 1 \cdot 7$ mm)
    . . . . **cardui** (Linnaeus)

Induces a multilocular stem gall on Cirsium arvense. *England, as far north as Peterborough, and South Wales. Western and central Europe; introduced to Canada as a biocontrol agent.*

Subfamily Trypetinae

A group of about 200 genera, about 50 of which occur in the Palaearctic region. Most species of known biology are fruit feeders, but some are stem-borers and leaf-miners, and it is likely that many species of unknown biology are also stem or leaf-miners.

Tribe Ceratitini

The Ceratitini is a predominantly Afrotropical tribe of 16 genera to which a few Oriental genera may also belong, and the genus *Ceratitis* occurs in the Palaearctic region. Most ceratitines are frugivorous, and some species attack a wide variety of plants, including crops such as oranges, mangoes, figs, coffee, guava, peaches and cocoa, although a few species appear to be associated with bamboo shoots. *Ceratitis capitata* (Wiedemann) is the notorious Mediterranean fruit fly, or medfly, which attacks oranges and many other crops in the Mediterranean area and Africa, and it has been accidentally introduced to some parts of the New World tropics. Although it has never become established in Britain, *C. capitata* is often imported in cargoes of soft fruit, especially oranges. Other ceratitines have occasionally been found in Britain, presumably for the same reason, for example *Pardalaspis cosyra* (Walker), a polyphagous species with a preference for mangoes.

Genus **Ceratitis** MacLeay

A genus of six species, two of which have become established in areas outside of Africa and Mediterranean Europe, namely *C. capitata* (Wiedemann) and *C. malgassa* Munro; the latter was recently accidentally introduced to the West Indies (Steyskal, 1982). Males of the four species of subgenus *Ceratitis* s.str. can be separated from all other Ceratitini because the posterior pair of orbital setae are very long and capitate, i.e. expanded apically (fig. 30); *C. capitata* (WL = 4·0–5·0 mm, fig. 284), *C. malgassa* and two other members of this subgenus were keyed by Steyskal (1982).

Tribe Euphrantini

An Old World group of 6 genera which were keyed by Hardy (1983); *Euphranta* is the only genus represented in the Palaearctic region.

Genus **Euphranta** Loew

A genus of about 90 species, mostly in the Oriental and Pacific regions, with 11 Palaearctic species and a few Afrotropical representatives. This genus can be distinguished from other genera of Euphrantini by the following characters: Head with 2–3 pairs of frontal setae; 1 pair of orbital setae; scutellum with 2 pairs of setae.

About half of the species of *Euphranta* belong to this subgenus, which is represented in the Palaearctic region by two species; it is distinguished from the other subgenera by the presence of prescutellar acrostichal setae. Our single British species, *E. (R.) toxoneura* is unique amongst tephritids of known biology; it is a predator and brood parasite in sawfly galls on *Salix* (Kopelke, 1984; 1985). Conversely, *E. (R.) japonica* (Ito) is a cherry (*Prunus avium*) pest in Japan, and some other *Euphranta* species are stem and seed-pod borers (Hardy, 1983).

Head and pleura dull yellow to orange; scutellum and abdomen black; legs orange; scutum tomentose. Wing, fig. 232. Distiphallus, fig. 33. Aculeus, fig. 34. $WL = 3 \cdot 4 – 5 \cdot 4$ mm. $AL = 0 \cdot 6$ mm. . . . . **toxoneura** (Loew)
Attacks Pontania *galls on* Salix. *Recorded from several localities in East Anglia, also from London, Bucks, Gloucester and Yorks. Western and central Europe.*

Tribe Trypetini

A group of 40 genera with representatives in all regions of the World, except perhaps the Afrotropical region; however, this apparent absence is probably caused by regional differences in classification rather than by the zoogeography of the flies. There are about 20 genera of Trypetini represented in the Palaearctic region.

Key to genera

1 Apex of vein M turned anteriorly to merge with C without a distinct angle (fig. 283). (Wing pattern usually similar to fig. 283. Larvae in imported fruit of Neotropical origin.)
. . . . **Anastrepha** Schiner (p. 36)
— Apex of vein M meeting C with a distinct angle. 2
2 Scutellum with 1 pair of setae, apical scutellar setae absent. Dorsocentral setae well forward of anterior supra-alar setae, and closer to vestigial transverse suture than to anterior supra-alar setae. . . . . **Cryptaciura** Hendel (p. 37)
— Scutellum with 2 pairs of setae. Dorsocentral setae at most slightly forward of anterior supra-alar setae, usually level with or behind anterior supra-alar setae; if in front, the dorsocentral setae are closer to the anterior supra-alar setae than to the vestigial transverse suture. 3
3 Mouthparts geniculate and head shape as fig. 35. . . . . **Goniglossum** Rondani (p. 37)
— Mouthparts not geniculate and head not shaped as in fig. 35 4
4 Crossvein dm-cu oblique, so that cell dm is apically pointed; Vein R_1 meeting C at a right angle (fig. 258). . . . .**Anomoia** Walker (p. 36)
— Crossvein dm-cu not oblique; Vein R_1 meeting C acutely (figs 234–242, 252–257) 5
5 Parafacial setae well developed, in large specimens they are almost as long as the head is high (fig. 37) . . . .**Chetostoma** Rondani (p. 37)
— Parafacial areas bare or setulose, without setae. 6
6 Hyaline area contacting C just beyond end of R_1 extending well below M, usually to the hind margin of the wing (e.g. fig. 241). (Katepisternum with a seta near its upper posterior corner.). 7
— Hyaline area contacting C just beyond end of R_1 only extending to R_{4+5} or M (e.g. fig. 252). (N.B., this is difficult to see in faintly marked specimens of *Acidia cognata,* a species which lacks a seta near the upper posterior corner of the katepisternum.). 9
7 Hind femur with strong anteroventral subapical setae (fig. 63). Aculeus long and narrow, without apical serrations (figs 52, 53). Vein R_{4+5} usually without dorsal setulae. 1st flagellomere dorso-apically pointed, fig. 36; often difficult to see. **Rhagoletis** Loew (p. 38)
— Hind femur without strong anteroventral subapical setae. Aculeus short and broad with serrations near apex (figs 58–62). Vein R_{4+5} with dorsal setulae. 1st flagellomere apically rounded, fig. 45. (Body orange, sometimes partly darkened.). . . . .
(see *Trypeta* and *Vidalia* key, p. 40) 8

Genus **Acidia** Robineau-Desvoidy

A genus of three Palaearctic species represented in Britain by *A. cognata,* which is a leaf-miner of some composites of the tribe Senecioneae.

Body and legs orange, abdomen sometimes darkened. Head, fig. 44. Wing, fig. 256. Distiphallus, fig. 74. Aculeus, fig. 54. WL = 5·3–6·9 mm. AL = 1·0 mm . . . . **cognata** (Wiedemann) *Mines the leaves of* Petasites fragrans, P. hybridus *and* Tussilago farfara. *Throughout the British Isles. Europe, except the Mediterranean area.*

Genus **Anastrepha** Schiner

A genus of 155 species which attack a wide range of fruits in South America and in the south of the United States. No *Anastrepha* species have so far become established in the Old World, although a few individuals have been intercepted in imported fruit arriving at British ports. Steyskal (1977) keyed the species by a combination of aculeus shape and wing pattern (e.g. fig. 283).

Genus **Anomoia** Walker

A predominantly Oriental genus of 27 species, with a single Australasian and six Palaearctic species. Larvae of the British *A. purmunda* usually feed in the fruits of hawthorn, but this fly has also been reared from a number of garden shrubs belonging to the families Rosaceae and Berberidaceae.

Head, scutellum, pleura and legs dull yellow to orange; scutum and abdomen black; scutum grey tomentose. Head, fig. 38. Wing, fig. 258. Distiphallus, fig. 70. Aculeus, figs 49, 50. WL = 3·7–5·0 mm. AL = 0·7–0·9 mm . . . . **purmunda** (Harris)

    Attacks the fruits of Crataegus *spp., and sometimes other Rosaceae, and* Berberis *(Berberidaceae). South-east England, East Anglia, the Midlands and throughout Ireland; old records from south Wales, Devon, Hereford and Inverness. Throughout the Palaearctic region, except in the south.*

Genus **Chetostoma** Rondani

A genus of 11 species, including six Palaearctic representatives and other species from the Nearctic and Oriental regions. The biology of our single species is unknown, but the related *C. continuans* Zia develops in the fruit of *Lonicera* species in the U.S.S.R. (Kandybina, 1966), and it is likely that our *C. curvinerve* has a similar biology.

Body and femora dark orange; tibia pale orange. Head, fig. 37. Wing, fig. 239. Distiphallus, fig. 71. Aculeus, fig. 48. WL = 4·7–7·4 mm. AL = 1·2 mm. . . . . **curvinerve** Rondani
Very rare, recently recorded only from Cornwall, Dorset, Surrey and Sussex; old record from Devon. Central and southern Europe, and Israel.

Genus **Cryptaciura** Hendel

A European genus of one species which mines the leaves of a wide range of umbelliferous plants (Apiaceae). British specimens of *C. rotundiventris* have a different wing pattern from continental specimens (White, 1986). Although Munro (1947) placed this genus in the Aciurinae, Freidberg (1984) later restricted that subfamily to species associated with the plant families Acanthaceae, Labiatae and Verbenaceae.

Body dark orange to black; legs orange. Head, fig. 40. Wing, fig. 255. Distiphallus, fig. 66. Aculeus, fig. 55. WL = 3·2–4·4 mm. AL = 0·5–0·6 mm . . . . **rotundiventris** (Fallén)
Leaf-miner of a wide range of umbelliferous plants. Very rare, recently recorded only from Berks, Hants and Co. Wexford; old records from Dumfries, Speyside and Hants. Throughout Europe, except the south.

Genus **Euleia** Walker

A genus of 10 species, including seven Palaearctic species and representatives in the Nearctic and Oriental regions. The British *E. heracleii* mines the leaves of a wide range of umbelliferous plants and is a pest of celery.

Body of first generation specimens red-brown or orange-brown; body of second generation specimens dark orange to black; legs orange. Head, fig. 39. Wing, fig. 252. Distiphallus, fig. 75. Aculeus, fig. 56. WL = 4·3–5·8 mm. AL = 0·5–0·6 mm . . . . **heracleii** (Linnaeus)
Leaf-miner of a wide range of umbelliferous plants. Throughout the British Isles. Most of the Palaearctic region, as far east as Afghanistan.

Genus **Goniglossum** Rondani

A Palaearctic genus of one species whose larvae live in the fruits of *Bryonia* species (Cucurbitaceae).

Head, legs and abdomen orange; scutum and scutellum yellow with large black markings; centre of presutural area tomentose and covered with pale setulae. Cell cu*p* extension very small. Anepisternum with 3 setae. Head, fig. 35. Wing, fig. 247. Distiphallus, fig. 69. Aculeus, fig. 51. WL = 3·0–4·4 mm. AL = 0·7 mm . . . . **wiedemanni** (Meigen)
Attacks the fruit of Bryonia dioica. *England, as far north as Coventry. Europe, North Africa and Israel.*

Genus **Myoleja** Rondani

A genus of 44 species, including 15 Palaearctic species, 26 Oriental and 3 Nearctic members. The biology of most *Myoleja* species, including the British *M. caesio,* is unknown. However, the larvae of the North American *M. limata* (Coquillett) and the European *M. lucida* (Fallén) feed in the fruits of *Ilex* and *Lonicera* species respectively

(Steyskal, 1972; Kandybina, 1977). The aculeus of *M. lucida* is similar to that of our fruit feeding *Anomoia purmunda* (figs 49, 50). Conversely, *M. caesio,* and many other *Myoleja* species have an aculeus typical of leaf-mining Trypetini (figs 54–62). Furthermore, the distiphallus of *M. caesio* is also similar to *Trypeta* and *Vidalia* species (figs 77–81), all of which are leaf-miners. It seems likely that *M. caesio* is a leaf-miner and it has been suggested that it mines *Silene dioica* (Caryophyllaceae) (A. H. Hamm *in litt.,* in Séguy, 1934); however, this requires confirmation and other authors believe *M. caesio* to be frugivorous (Allen, 1963; Fonseca, 1964; Smith, 1956; Uffen, 1964). Recently, Ito (1984c) has split *Myoleja* into a number of separate genera and our *M. caesio* would become *Philophylla caesio*; however, Ito (1984c) made no reference to aculeus structure or biology, so his revision seems poorly founded and premature, and is not followed here. See note on p. 70.

Subgenus **Myoleja** Rondani

A group of 14 Palaearctic species which are separated from s.g. *Acidostigma* Hendel by the short cell sc.

Head, scutellum, pleura and legs orange; abdomen black; scutum grey tomentose. Head, fig. 41. Wing, fig. 257. Distiphallus, fig. 76. Aculeus, fig. 57. WL = 3·4–4·9 mm. AL = 0·6 mm ....**caesio** (Harris)
England, as far north as Yorks, and Wales. Throughout Europe, except the north.

Genus **Platyparea** Loew

A Palaearctic genus of three species the larvae of which are stem-borers. *Platyparea poeciloptera,* the asparagus fly, is a serious pest in France.

Key to species

1   Wing with 2 hyaline areas contacting C in cell r_1, neither of which extend below vein R_{4+5} (fig. 254). 1st flagellomere rounded at apex (fig. 42). Four or more pairs of frontal setae (fig. 42). Scutellum black in centre, pale at sides. Katepisternum without a seta near its upper posterior corner. (Rest of body black; legs orange; scutum tomentose and setulose. Distiphallus, fig. 67. Aculeus, fig. 64. WL = 4·3–5·8 mm. AL = 0·8–0·9 mm)
....**discoidea** (Fabricius)
Believed to bore the stems of Campanula latifolia *(Campanulaceae). Known from a few sites in Yorkshire. Europe, except the Mediterranean area.*

—   Wing with 1 hyaline area contacting C in cell r_1, which extends almost to vein M (fig. 253). 1st flagellomere pointed at apex (fig. 43). 3 pairs of frontal setae (fig. 43). Scutellum uniformly dark brown. Katepisternum with a seta near its upper posterior corner. (Body dark orange to brown; scutum black and tomentose; legs dark orange. Distiphallus, fig. 68. Aculeus, fig. 65. WL = 4·3–5·3 mm. AL = 1·0–1·1 mm.)................**poeciloptera** (Schrank)
Mines the stems of Asparagus officinalis *(Liliaceae). Infested asparagus plots in Hertfordshire in 1936 and 1937; a single specimen was reported from Middlesex in 1947; no other records and probably not an established species. Central, eastern and southern Europe.*

Genus **Rhagoletis** Loew

A predominantly New World genus of 51 species, including 20 Palaearctic and a few Oriental members. Species of known biology have frugivorous larvae and the cherry fly, *Rhagoletis cerasi,* is often accidentally imported into Britain in fruit, but has never become established. Adults of the Palaearctic species have been keyed by Hering (1958) and Rohdendorf (1961), and Kandybina (1961; 1977) gave a larval key. The North American species were keyed by Bush (1966), and Foote (1981) keyed the South

American species. The following key to British species includes *R. cerasi* and is designed to allow for the possibility that other foreign pest species may also be found at our ports in the future.

Key to species

1   Scutum, scutellum and pleura concolorous yellow brown. Preapical and apical crossbands separate at costal margin. (Very few foreign pest species would key this way, an exception being a walnut husk fly, *R. juglandis* Cresson; see Foote, 1981 for a description.) (Rest of body dull orange; scutum setulose.). 2

—   Scutum shining dark brown or black, scutellum yellow, at least centrally, and pleura dark except for a yellow stripe extending from the humerus across the upper part of the anepisternum to the wing base. Preapical and apical crossbands usually joined at costal margin. (Larvae in imported fruit, no indigenous species.) 3

2   Preapical crossband complete (fig. 241). Postocular setae black. (Vein R_{4+5} usually without dorsal setulae, except at base. Distiphallus, fig. 73. Aculeus, fig. 52. WL = 4·0–5·4 mm. AL = 0·9–1·1 mm.) . . . . **alternata** (Fallén)
Associated with the fruits of Rosa *spp. Throughout Great Britain. Most of Palaearctic, except the south.*

—   Preapical crossband only present below vein R_{4+5} (fig. 240). Postocular setae pale. (Vein R_{4+5} often with dorsal setulae as far as r-m crossvein. Distiphallus, fig. 72. Aculeus, fig. 53. WL = 4·2–5·2 mm. AL = 1·1 mm.) . . . . **meigenii** (Loew)
Associated with the fruits of Berberis vulgaris. *Known in Britain from a single male collected at Lyndhurst, Hants., in 1897. Europe, except the Mediterranean area.*

3   Wing with a short dark mark across cells r_1 and r_{2+3} between the discal and preapical crossbands (fig. 286). Femora black. Abdomen predominantly black. (Head black; tibiae and tarsi yellow. Vein R_{4+5} without dorsal setulae, except at base. WL = 2·5–4·0 mm. AL = 0·7–0·8 mm). . . . . **cerasi** (Linnaeus)
Larvae sometimes imported in cherries, Prunus avium *& P. cerasus, (Rosaceae); also attacks* Lonicera *species (Caprifoliaceae). Europe and central Asia.*

—   Without the above combination of characters. . . . . other species

Genera **Trypeta** Meigen and **Vidalia** Robineau-Desvoidy

Trypeta is a genus of 41 species, including 16 Palaearctic members and representatives from the Oriental region and the New World. The closely related genus *Vidalia* has 13 Palaearctic and 12 Oriental species. *Trypeta* and *Vidalia* species of known biology have leaf-mining larvae associated with a wide range of composites and most of the Palaearctic species were keyed by Hering (1937d). More recently, Rikhter & Kandybina (1985) have described and keyed the *Trypeta* species from the U.S.S.R. Male *Vidalia* are characterised by enlarged frontal setae and sometimes by antler-like extensions of the frons; these structures were discussed by Munro (1938). However, it is sometimes difficult to place females correctly into the genera *Trypeta* and *Vidalia* and to facilitate correct identification the following key does not not differentiate between these two genera. Specimens showing aberrant wing patterns should be dissected. The aculeus shapes show only subtle differences between species but they provide good characters for anyone with a drawing tube by which figs 58–62 can be directly matched to a slide mounted aculeus. The distiphallus of each species has two distinct areas of surface sculpture which provide good diagnostic features (figs 77–81). There are differences in the head shape of each species (Rikhter & Kandybina, 1985), but each species varies so much that the interspecific differences are difficult to interpret.

Some authors refer to specimens of *T. zoe* from *Artemisia* as *T. zoe* var. *artemisicola* (Hendel). Recently, Ito (1984c) has elevated this form to species rank. Although it is possible that Ito (1984c) is describing a distinct species from Japan, European specimens reared from *Artemisia* do not differ from other specimens of *T. zoe*; consequently, Ito's conclusion is not accepted here.

Subgenus **Trypeta** Meigen

A group of 15 Palaearctic species which are separated from s.g. *Heliotrypeta* Rikhter & Kandybina by the lack of presutural dorsocentral setae.

Key to species of *Trypeta* and *Vidalia*

1   Scutum with 1, or a pair, of black marks placed anteriorly (just behind the head) between the dorsocentral lines. Wing with preapical crossband usually complete, broadening behind vein M (fig. 242). Male with very long, stout frontal setae, placed as in fig. 47. (1, rarely 2, pairs of orbital setae. Postgenal setae black. Distiphallus, fig. 81. Aculeus, fig. 62. WL = 4·9–5·8 mm. AL = 0·8 mm.) . . . .**Vidalia spinifrons** (Schroeder)
Mines the leaves of Solidago virgaurea *and garden* Aster *species. Recently recorded only from Kent; old records from Herefordshire and Lancashire. Poland and north-west U.S.S.R.*

—   Scutum without anterior black marks. Wing without a complete preapical crossband (figs 234–238). Male usually without very long stout frontal setae (fig. 45); if male with very long stout frontal setae they are placed as in fig. 46. (*V. cornuta*) 2

2   One pair of orbital setae (fig. 46), which are usually convergent. Hind tibia with stout, black, apicoventral setae. Male with long stout frontal setae which are placed on extensions of the frons (fig. 46). (Postgenal setae white. Distiphallus, fig. 80. Aculeus, fig. 61. WL = 5·0–6·5 mm. AL = 0·8 mm.) . . . .**Vidalia cornuta** (Scopoli)
Mines the leaves of Eupatorium cannabinum. *No recent records; old records from Devon and East Anglia. Central Europe, U.S.S.R. to eastern Siberia.*

—   Two pairs of orbital setae (fig. 45). Hind tibia without stout, black, apicoventral setae. Male without enlarged frontal setae and frons not extended (fig. 45). . . . . .3 **(Trypeta)**

3   Crossvein r-m before apex of R_1 (figs 234, 235). Postgenal setae white. Male usually without preapical crossband, and with a very broad apical crossband which extends from near dm-cu crossvein to wing apex (fig. 234). (Distiphallus, fig. 79. Aculeus, fig. 60. WL = 3·7–5·5 mm. AL = 0·5–0·7 mm.) . . . .**zoe** Meigen
Mines the leaves of Artemisia, Eupatorium, Petasites, Senecio *and* Tussilago *species; also garden species of* Aster, Chrysanthemum *and* Leucanthemum. *Throughout the British Isles, more common in the south than in the north. Central Europe and European U.S.S.R.*

—   Crossvein r-m at or beyond apex of R_1 (figs 236, 237). Postgenal setae black. Preapical crossband present in both sexes; apical crossband narrow in both sexes, its inner margin concave and roughly parallel to wing margin (figs 236, 237) 4

4   Preapical and discal crossbands fused in cell cua_1 (fig. 237). Vein R_{4+5} without, or with only 1 seta beyond r-m crossvein. (Distiphallus, fig. 78. Aculeus, fig. 59. WL = 4·6–5·4 mm. AL = 0·5–0·7 mm.) . . . .**immaculata** (Macquart)
Mines the leaves of Taraxacum *and other genera of* Cichorioideae. *North-east Scotland, throughout Ireland. Europe, except Mediterranean area.*

—   Preapical and discal crossbands separate (fig. 236). Vein R_{4+5} usually with 3 or more dorsal setae beyond r-m crossvein. (Ocellar setae always well developed. Distiphallus, fig. 77. Aculeus, fig. 58. WL = 5·3–6·3 mm. AL = 0·7 mm.). . . . . **artemisiae** (Fabricius)
Mines the leaves of Achillea ptarmica, Artemisia, Tanacetum vulgare, Eupatorium *and* Senecio *species. Throughout Great Britain, more common in the north than in the south. Throughout the Palaearctic region except for the Mediterranean and Middle Eastern areas.*

Subfamily Tephritinae

A group of about 100 genera, 40 of which occur in the Palaearctic region; most species of known biology live in the capitula, stems or roots of composite plants (Asteraceae).

Tribe Terelliini

A group of seven Holarctic, Oriental and Afrotropical genera, five of which occur in the Palaearctic region. The generic classification of this group has recently been revised by

Korneev (1985) who provided a key to the genera; the following key covers all the Palaearctic genera.

Key to genera

1　Presutural dorsocentral setae present (fig. 85). (Head, fig. 84). . . **Chaetorellia** Hendel (p. 42)
—　Presutural dorsocentral setae absent 2
2　Extension of cell cu*p* extending well beyond bm-cu crossvein (fig. 251). Anterior supra-alar seta based in a black spot (fig. 101). Scutum with a pair of prominent black spots on the vestigial transverse suture (fig. 101) . . . . **Orellia** Robineau-Desvoidy (p. 43)
—　Extension of cell cu*p* ending approximately in line with bm-cu crossvein (e.g. fig. 250). Anterior supra-alar seta not based in a black spot. Scutum without a pair of prominent black spots on the vestigial transverse suture 3
3　Scutellum with a black apical spot and a pair of black basal spots (fig. 88). (Numerous well developed black genal setae, fig. 89.) . . . . **Chaetostomella** Hendel (p. 42)
—　Scutellum usually without black spots, at most with narrow basal/lateral black spots 4
4　Aculeus apex pointed (e.g. figs 104, 110, 117). Sclerotised parts of distiphallus not reduced to a hook shaped structure (figs 112, 116, 121). Genal margin meeting face with a distinct angle (figs 107, 113–115, 122). Antennal bases separated by less than the diameter of an antenna base; triangular mark on katepisternum black. Pedicel of male not greatly enlarged (figs 107, 113–115, 122) . . . . **Terellia** Robineau-Desvoidy (p. 43)
—　Aculeus apex broadly rounded (fig. 95), or truncate (fig. 94). Sclerotised parts of distiphallus reduced to a hook shaped structure (fig. 93). Genal margin smoothly rounded into face (figs 96, 98). Antennal bases separated by at least the diameter of an antenna base (fig. 92) or triangular mark on katepisternum yellow-brown (a character only applicable to the British species). Pedicel of male often greatly enlarged (fig. 96) (except *C. tussilaginis*, fig. 98) . . . . **Cerajocera** Rondani (p. 41)

Genus **Cerajocera** Rondani

A genus of nine Palaearctic and 2 Nearctic species, the concept of which has recently been greatly expanded by Korneev (1985); however, it is likely that a future revision of the Terelliini will not accept the division of *Cerajocera* and *Terellia* used here. Two of our species, *C. ceratocera* and *C. plagiata,* are clearly separated by both their biology, and larval and pupal morphology (Persson, 1963). However, their adults show no clear diagnostic features except that *C. ceratocera,* which lives in the capitulum of *Centaurea scabiosa* tends to be larger and have more heavily marked wings than *Cerajocera plagiata* which mines the stem of the same plant. Contrary to statements made by earlier authors (Hering, 1935b; Collin, 1937) the relative length of the pedicel to the 1st flagellomere cannot be used as a reliable diagnostic feature because it relates allometrically to body size, regardless of species. The pupae (and third instar larvae) are separated by the key to pupae found in *Centaurea scabiosa* (p. 56). Specimens which appear to be *C. tussilaginis* have on a very few occasions been reared from unusual hosts, e.g. the capitulum of *Cirsium arvense* and the stem of *C. vulgare.* Any further specimens reared from such unusual situations should be examined carefully in case additional species are involved.

Key to species

1　Antennae closer together than the diameter of an antenna base (similar to fig. 99); pedicel of normal proportions in both sexes (fig. 98). Katepisternum with a yellow-brown triangular mark. (Most of body and legs yellow; scutum largely covered by a dull grey-brown mark; prescutellar acrostichal setae based in small black spots that are separate from the large black area on the scutum; abdominal tergites 2–5 often with traces of marks, and some-

times with four large dark marks on each tergite; oviscape yellow or orange. Head, fig. 98. Aculeus, fig. 94. WL = 3·8–5·3 mm. AL = 2·0–2·2 mm. TO = 6.)... **tussilaginis** (Fabricius)
Attacks the capitula of Arctium lappa *and* A. minus. *Throughout England and Wales, common in the south. Throughout most of the Palaearctic, except the far east.*

— Antennae more widely separated than the diameter of an antenna base (fig. 92); pedicel of male greatly enlarged (fig. 96). Katepisternum with a black triangular mark. (Frons, thorax and legs yellow; most of scutum covered by a dull black mark; abdomen dark orange with paired black marks on at least tergites 4 & 5. Aculeus, fig. 95. AL = 2·1–3·0 mm. TO = 6.). 2

2 Larva in the capitulum of *Centaurea scabiosa*. (WL = 4.3–6·4 mm. Wing, fig. 248.)
.... **ceratocera** (Hendel)
South-east England and East Anglia. North and central Europe, western Siberia, Turkey and Kazakh S.S.R.

— Larva in the stem of *Centaurea scabiosa*. (WL = 4·4–5·0 mm.) .... **plagiata** (Dahlbom)
South-east England and East Anglia. Northern, western and central Europe.

Genus **Chaetorellia** Hendel

A genus of 11 Palaearctic species associated with *Centaurea* and *Carthamus*. This is a very difficult genus and the key by Hering (1937d) is of little help. In Britain we only appear to have one species from each of the two very distinct species-groups, and the following key should not be applied to non-British specimens except as a species-group key. The other species belonging to each group were listed by Korneev (1985).

Key to species

1 Anterior supra-alar seta based in a black spot. Cell cu*p* usually extending well beyond end of cell bm. Distiphallus with a sinuate main duct (fig. 82). Aculeus, fig. 86. (Head, thorax and legs dull yellow; scutum with a black spot at the base of all setae except the posterior supra-alar setae; scutellum with a pair of lateral, and an apical black mark; abdomen dull yellow or orange, with paired black marks on tergites 2–5. WL = 3·8–5·1 mm. AL = 1·4–1·8 mm. TO = 4.) .... **loricata** (Rondani)
Attacks the capitulum of Centaurea scabiosa. *Rare, recently recorded only from a single locality in Wiltshire; old records from the Isle of Wight and Surrey. Western, central and eastern Europe.*

— Anterior supra-alar seta based on a yellow ground. Cell cu*p* not extending beyond end of cell bm. Distiphallus main duct not sinuate (fig. 83). Aculeus, fig. 87. (Colour as *C. loricata*, except for base of anterior supra-alar seta. WL = 3·4–4·4 mm. AL = 1·9–2·4 mm. TO = 5. Wing, fig. 249. Head, fig. 84.) .... **jaceae** (Robineau-Desvoidy)
Attacks the capitula of Centaurea nigra *and probably* C. debeauxii. *Very local in south-east England, common in East Anglia; unconfirmed record from Yorks. Western and central Europe.*

Genus **Chaetostomella** Hendel

A genus of 10 Palaearctic, a Nearctic and an Oriental species. The British *C. cylindrica* lives in the capitula of a wide range of composites.
Body and legs mainly yellow; scutum with a large dull black mark, or marks (fig. 88); scutellum with lateral and an apical black mark; abdominal tergites 2–4 each with 4 black spots; tergite 5 with a pair of broad black marks. Postocular setae black. Crossbands of wing perpendicular (fig. 250). Abdominal pubescence mainly black. WL = 2·7–5·0 mm. AL = 1·2–1·8 mm. TO = 2. Head, fig. 89. Distiphallus, fig. 91. Aculeus, fig. 90.......... **cylindrica** (Robineau-Desvoidy)
Attacks the capitula of many species of Cardueae, especially Centaurea nigra *and probably* C. debeauxii. *Throughout the British Isles, very common in southern England. Throughout Europe, North Africa, and Asia as far east as Mongolia.*

Genus **Orellia** Robineau-Desvoidy

A genus of three Palaearctic species, the concept of which has recently been greatly restricted by Korneev (1985).

Head and thorax yellow; abdomen and legs orange; scutum largely covered with a dull black mark; scutum with a shiny black spot at the base of each seta, plus a pair of spots on the vestigial transverse suture (fig. 101); scutellum with a shiny black spot at the base of each seta; abdominal tergites 2–5 each with four small black marks placed basally. Discal and preapical crossbands not united in cell r_1 (fig. 251). WL = 5·1–7·0 mm. AL = 1·5–1·6 mm. TO = 2–3. Head, figs 99, 103. Distiphallus, fig. 102. Aculeus, fig. 100. . . . . **falcata** (Scopoli)
Larvae bore into the stem base and roots of Tragopogon pratensis. *South-east England; unconfirmed records from North Wales and north-east Scotland; old records from East Anglia and Somerset. Europe, except the northern areas, Middle East to Kazakh S.S.R.*

Genus **Terellia** Robineau-Desvoidy

A genus of 27 Palaearctic species, the concept of which has recently been greatly expanded by Korneev (1985). Species of known biology are associated with the capitula of some species of the composite tribe Cardueae.

Key to species

1 Wings entirely hyaline (fig. 224); pubescence on abdominal tergite 3 white. (Most of body and legs yellow or orange-yellow; scutum largely covered by a dull black mark; pleura with a series of pale yellow and orange stripes; abdominal tergites 2–5 each with two or four basal black marks; oviscape orange, black at apex. Distiphallus similar to fig. 121. Aculeus preapical setulae well removed from aculeus apex, figs 104, 105.) 2
— Wings usually with some patterning (figs 227–231); if wings hyaline, pubescence on abdominal tergite 3 black. (Pleura usually without stripes, except *T. ruficauda* which has a dark stripe.) 3
2 Small; male WL = 4·0–4·7 mm; female WL = 4·1–5·2 mm. Aculeus short; AL = 1·5–1·9 mm; oviscape shorter than abdominal segments 3 to 6 combined (TO = 4); this character should be used with caution because a very shrivelled or greatly distended abdomen may lead to misinterpretation. Apex of outer surstylus with fine setulae as well as long setae (fig. 109). (Head, fig. 107. Aculeus, fig. 105.) . . . . **serratulae** (Linnaeus)
   Attacks the capitula of Carduus acanthoides, C. nutans *and* Cirsium vulgare. *Southern and eastern counties of England, and south-east Ireland, very rare in northern Britain; old record from Wales. Throughout the Palaearctic region.*
— Large; male WL = 5·1–5·9 mm; female WL = 5·8–6·2 mm. Aculeus long; AL = 2·3–3·7 mm; oviscape almost as long as the rest of the abdomen (TO = 6); use with caution if the abdomen is distended. Apex of outer surstylus without fine setulae (fig. 108). (Head, fig. 106. Aculeus, fig. 104.) . . . . **longicauda** (Meigen)
   Attacks the capitulum of Cirsium eriophorum. *Southern England and Wales. Throughout the Palaearctic, except in the north and far east.*
3 Apical crossband extending to M; preapical crossband present but broken or faint in cell r_{4+5}; wing pattern as fig. 231. (Ground colour of head, thorax, legs and abdomen yellow-orange; scutum largely covered by a dull black mark; pleura with a broad dark brown stripe covering the lower two-thirds of the anepisternum; abdominal tergites 2–5 each with four large black marks, which are sometimes fused to produce a predominantly black abdomen; oviscape black in basal third, remainder orange-red. Head, fig. 122. Distiphallus, fig. 121. Aculeus preapical setulae well removed from aculeus apex, fig. 123. WL = 3·1–4·8 mm. AL = 1·3–1·7 mm. TO = 3.) . . . . **ruficauda** (Fabricius)
   Attacks the capitula of Cirsium arvense, C. dissectum *and* C. palustre. *England as far north as Yorks., and Ireland. Throughout the Palaearctic region, except the south; accidentally introduced to North America.*
— Apical crossband very reduced, faint or absent; preapical crossband absent, or broken both in cell r_{4+5} and along dm-cu crossvein; wing pattern as figs 227–230 4

4   Scutum with a black line between the posterior supra-alar seta and the intra-alar seta, or the black area of the scutum is extended laterally as far as the supra-alar seta (fig. 111). Size usually large; WL = 3·9–5·4 mm. (Head and legs orange; scutum largely dull black, rest of thorax yellow; abdominal tergites vary from orange-yellow without black marks, through yellow with four black marks on each tergite, to yellow with a black base to each tergite; oviscape orange, black at base. Wing of ♂, fig. 228; ♀, fig. 227. Head, fig. 113. Distiphallus, fig. 112. Aculeus preapical setulae close to aculeus apex, fig. 110. AL = 2·1–2·9 mm. TO = 5–6.) . . . . **colon** (Meigen)
     Attacks the capitulum of Centaurea scabiosa. *England, as far north as Yorks. Throughout Europe.*

—   Scutum without, or with a faint trace of a dark line between the posterior supra-alar seta and the intra-alar seta, never with the black area of the scutum extended laterally beyond the intra-alar seta. Size usually smaller; WL = 3·0–4·3 mm 5

5   Hind margin of black area on scutum with a pair of deep incisions, so that both the dorsocentral and prescutellar acrostichal setae are on a yellow ground (fig. 119). Wing largely hyaline, with 2 faint marks in cell r_1 and often at the apex of r_{2+3} (fig. 229). Genae narrow (fig. 115). Distiphallus, fig. 116. Aculeus perapical setulae close to aculeus apex (fig. 117). (Most of body and legs yellow or orange-yellow; scutum largely covered by a dull black mark; abdominal tergites 2–5 vary from each having four black spots, through to each being completely black; oviscape and often most of tergite 6 orange. WL = 3·1–4·2 mm. AL = 1·3 mm. TO = 3–4.). . . . . **vectensis** (Collin)
     Attacks the capitulum of Serratula tinctoria. *Hants, including the Isle of Wight, and south Wales. Mediterranean.*

—   Hind margin of black area on scutum without a pair of deep incisions, so that both the dorsocentral and prescutellar acrostichal setae are on a black ground (fig. 120). Discal, preapical and apical crossbands often faint, but extending at least from C to R_{4+5} (fig. 230). Genae broad (fig. 114). Distiphallus similar to fig. 121. Aculeus preapical setulae well removed from aculeus apex (fig. 118). (Most of body and legs dull yellow or orange-yellow; scutum largely covered by a dull black mark; abdominal tergites 2–5 each with four basal black marks; oviscape orange, black at base and apex. WL = 3·0–4·3 mm. AL = 1·3 mm. TO = 3–4.). . . . . **winthemi** (Meigen)
     Attacks the capitulum of Carduus acanthoides. *Recently recorded only from a single site in Surrey; old records from Devon and several areas of south-east England. Western Palaearctic to western Siberia, except the south.*

Tribe Dithrycini

A group of 12 genera, five of which occur in the Palaearctic region.

Key to genera

1   Presutural dorsocentral setae present. Scutellum with 1 pair of black setae and no white setae (except for a few basal white scales). Hyaline areas at wing apex not elongate (fig. 272)
     . . . . **Dithryca** Rondani (p. 44)
—   Presutural dorsocentral setae absent. Scutellum with 2 pairs of black setae plus some (usually 4 pairs) white setae. Hyaline areas at wing apex elongate (fig. 261)
     . . . . **Noeeta** Robineau-Desvoidy (p. 45)

Genus **Dithryca** Rondani

A Palaearctic genus of two species. The British *D. guttularis* forms a gall at the base of the stem of *Achillea millefolium.*
Frons dark orange; tibia and tarsi pale yellow; rest of body dark brown to black; scutum grey

tomentose but darkened around setal bases. Head, figs 128, 129. Wing, fig. 272. Distiphallus, fig. 124. Aculeus, fig. 126. WL = 2·8–4·2 mm. AL = 1·2–1·5 mm . . . . **guttularis** (Meigen)
Throughout Great Britain. Throughout most of the Palaearctic region, as far east as Kazakh S.S.R.

Genus **Noeeta** Robineau-Desvoidy

A genus of three Palaearctic species. Larvae of the British *N. pupillata* swell the capitula of *Hieracium* and sometimes other composites.

Subgenus **Noeeta** Robineau-Desvoidy

A group of two species which are separated from s.g. *Paranoeeta* Shiraki by the flat frons, and the swollen and polished scutellum.

Ground colour of body predominantly orange, with black marks around the bases of the thoracic setae; scutellum shiny black; abdomen with some dark areas; female tergite 6 shiny black; oviscape black. Head, figs 130, 131. Wing, fig. 261. Distiphallus, fig. 125. Aculeus, fig. 127. WL = 3·6–4·4 mm. AL = 0·7 mm . . . . **pupillata** (Fallén)
England, as far north as Yorks. Throughout the Palaearctic region, except the Mediterranean area.

Tribe Tephritini

A worldwide group of about 60 genera, about 30 of which occur in the Palaearctic region.

Key to genera

1   Vein R_{4+5} with dorsal setulae at least as far as the r-m crossvein. 2
—   Vein R_{4+5} without dorsal setulae, except sometimes at base. 4
2   Posterior pair of orbital setae convergent; both pairs of orbital setae pale brown (fig. 136)
    . . . . **Xyphosia** Robineau-Desvoidy (p. 53)
—   Posterior pair of orbital setae reclinate; anterior pair of orbital setae brown, posterior pair white (figs 133, 135) 3
3   Head with 2 pairs of frontal setae (fig. 133) . . . . **Icterica** Loew (p. 47)
—   Head with 3 pairs of frontal setae (fig. 135) . . . . **Acinia** Robineau-Desvoidy (p. 47)
4   Head usually with 1 pair of black frontal setae (fig. 139); if with 2 or 3 pairs of black frontal setae the posterior pair is no higher up the frons than the top of the lunule (fig. 139 inset). (Mouthparts geniculate. Genae very deep, about half as high as eye, fig. 139. Cell sc with 2 pale spots, figs 264, 265. Distiphallus and distal end of basiphallus as fig. 156. Frons bright orange; scutum and abdomen with a dark ground colour and covered with a dense grey-green tomentum; legs and sometimes pleura orange.) **Oxyna** Robineau-Desvoidy (p. 47)
—   Head with 2 or 3 pairs of black or brown frontal setae; the posterior pair of black frontal setae are much higher up the frons than the top of the lunule, usually at least one-third of the way between the lunule and the anterior pair of orbital setae (figs 132, 134, 137, 138, 140, 161–165). 5
5   Head with 2 pairs of dark coloured frontal setae (e.g. fig. 140). (British species in these genera usually have reticulate wings, e.g. figs 263, 270, or a wing pattern of reticulate bands, fig. 260, rarely with the pattern reduced to an apical star shaped mark, fig. 281.) 6
—   Head with 3 pairs of dark coloured frontal setae (figs 132, 137, 138). (British species in these genera have either hyaline wings, fig. 223, a wing pattern which is reduced to an apical star shaped mark, fig. 282, or a faint pattern confined to the apical area of the wing, fig. 226. Distiphallus reduced to a sclerotised hook, figs 141, 143, 213.). 10
6   Wing with two crossbands of reticulate pattern, one through the r-m and dm-cu crossveins, and one apically (fig. 260). (Frons with white scale-like setulae.)
    . . . . **Sphenella** Robineau-Desvoidy (p. 50)

— Wing with a reticulate pattern that is not reduced to a pair of crossbands (e.g. figs 263–270), or wing pattern reduced to an apical star shaped mark (fig. 281) 7

7 Cell r_{2+3} with 2 hyaline areas contacting C, one of which is small and placed adjacent to vein R_{2+3}, the other extends into cell r_{4+5} (figs 270–281). Head higher than long and mouthparts short (fig. 140). Vein R_{4+5} usually with ventral setulae. Distiphallus largely membraneous, without a distinct and complex structure (fig. 212). (Frons, legs and scutellum usually orange; rest of body usually dark; most of body covered in a dense grey, grey-green, or sometimes orange, tomentum.) . . . . **Tephritis** Latreille (p. 50)

— Cell r_{2+3} usually with only 1 hyaline area contacting C (e.g. figs 268, 269); if cell r_{2+3} with 2 hyaline areas contacting C, neither area extends into cell r_{4+5} (fig. 266). Head sometimes longer than high and mouthparts sometimes geniculate (fig. 164). Vein R_{4+5} without ventral setulae. Distiphallus well sclerotised and usually of a complex structure (figs 175–183). (Ground colour of body usually dark; frons orange; tibia and tarsi pale; most of body covered in a heavy grey, brown or golden tomentum.) (see *Paroxyna*, *Campiglossa* and *Dioxyna* key, p. 48) 8

8 Apical scutellar setae often absent; if apical scutellar setae present they are usually less than one-quarter as long as the basal scutellar setae (aberrant specimens with long apical scutellar setae have been found; consequently, our only British species is included in the key to species of *Paroxyna*). Distal end of basiphallus without microtrichia (fig. 175). Posterior margin of male sternite 5 without a broad membraneous margin (fig. 166). (Head longer than high and mouthparts geniculate, fig. 164.) . . . . **Dioxyna** Frey (in *Paroxyna* key, p. 48)

— Apical scutellar setae more than one-quarter as long as basal scutellar setae. Distal end of basiphallus with microtrichia (figs 176–183). Posterior margin of male sternite 5 with a broad membraneous margin (figs 167, 168) and often 'V' shaped 9

9 Hind femur without dorsal preapical setae. (Because of the doubtful status of this genus our two species are included in the key to *Paroxyna* species.) . . . . **Campiglossa** Rondani (in *Paroxyna* key, p. 48)

— Hind femur with 1 to 3 dorsal preapical setae (fig. 160) . . . . **Paroxyna** Hendel (p. 48)

10 Head with 1 pair of dark orbital setae and no white orbital setae (fig. 132). (Head longer than high, genae narrow and mouthparts geniculate, fig. 132. Our only British species has hyaline wings, except for a dark area in cell sc, fig. 223.) . . . . **Ensina** Robineau-Desvoidy (p. 47)

— Head with 2 pairs of orbital setae; the anterior pair of orbital setae are dark coloured and the posterior pair are white (figs 137, 138). (Mouthparts short in the British species, figs 137, 138.) 11

11 Scutellum without an apical pair of setae. (The wing pattern in the British species is reduced to an apical star shaped mark, fig. 282. Frons and legs orange; oviscape shiny black; rest of body covered in a dense pale grey tomentum. Head, fig. 138. Distiphallus, fig. 213.) . . . . **Trupanea** Schrank (p. 53)

— Scutellum with both an apical and a basal pair of setae. (The wing pattern in our only species is faint and confined to the apical area of the wing, fig. 226.) **Acanthiophilus** Becker (p. 46)

Genus **Acanthiophilus** Becker

A genus of 12 species including three Palaearctic members, the remaining species being Afrotropical and Oriental. The single British species, *A. helianthi*, has one of the largest host-plant lists of any composite associated tephritid and it is a pest of safflower (*Carthamus tinctorius*) in many Mediterranean, Middle Eastern and Asian countries.

Frons and legs yellow-orange; rest of body with a black ground colour; most of body covered in a dense grey tomentum. Head, fig. 137. Wing, fig. 226. Distiphallus, fig. 141. Aculeus, fig. 147. WL = 3·9–5·1 mm. AL = 1·8–2·2 mm . . . . **helianthi** (Rossi)
In Britain, reared only from Centaurea nigra (possibly a misidentification of C. debeauxii); outside Britain it has been reared from the capitula of about 50 species of Cardueae. Very rare, recently recorded only from Hants, Kent, London and Pembs.; old records from the Isle of Skokholm and Dorset. Throughout the warmer areas of the Palaearctic region, India, Pakistan, Thailand, Ethiopia, Kenya, Madeira and the Sudan.

Genus **Acinia** Robineau-Desvoidy

A Holarctic genus of 15 species, six of which are Palaearctic. The British *A. corniculata* has been swept from *Centaurea nigra*, but it has not yet been reared from any British plant. However, on the continent it has been reared from the capitulum of the closely related *C. jacea*.

Body and legs orange; oviscape dark orange, black at apex. Head, fig. 135. Wing, fig. 262. Distiphallus, fig. 142. Aculeus, fig. 148. WL = 5·0–5·8 mm. AL = 1·4–1·6 mm. . . . .
corniculata (Zetterstedt)
Probably attacks the capitulum of Centaurea nigra. *Very local, East Anglia; old records from Hants, Hereford, Somerset and Surrey. Europe, except the Mediterranean area.*

Genus **Ensina** Robineau-Desvoidy

A Palaearctic genus of 3 species. The British *E. sonchi* has been introduced to other regions on cosmopolitan composite weeds such as *Sonchus oleraceus*.

Head and thorax predominantly yellow; ground colour of scutum black, covered with a grey tomentum; abdomen black. Head, fig. 132. Wing, fig. 223. Distiphallus, fig. 143. Aculeus, fig. 149. WL = 2·3–3·5 mm. AL = 0·7 mm . . . . **sonchi** (Linnaeus)
Attacks the capitula of a wide range of composites. England, as far north as Cheshire; old record from Ireland. Throughout the Palaearctic and many parts of the Oriental region, and Ethiopia; accidentally introduced to the Hawaiian Islands and Peru.

Genus **Icterica** Loew

A genus of two Nearctic species to which three Palaearctic species are currently assigned. The true generic position of the Palaearctic species requires further study (Foote & Freidberg, 1981). The British *I. westermanni* is associated with the capitula of *Senecio* species.

Body and legs dark orange; abdomen and oviscape often almost black. Head, fig. 133. Wing, fig. 263. Distiphallus, fig. 144. Aculeus, fig. 150. WL = 4·8–7·1 mm. AL = 1·1–1·3 mm . . . .
westermanni (Meigen)
Attacks the capitula of Senecio erucifolius *and* S. jacobaea. *Very local, several areas of Cambridgeshire and Kent; old records from many other southern counties of England. Europe, except northern areas.*

Genus **Oxyna** Robineau-Desvoidy

A genus of 22 species, including 18 Palaearctic species and a few Nearctic and Oriental representatives. The larvae of some species with a known biology form root galls, while others bore through the stems of their composite hosts. Most specimens of our three species can easily be identified by simple characters of the chaetotaxy. However, specimens with aberrant chaetotaxy and reduced wing patterning frequently occur. Consequently, two keys are presented here, the first giving only the chaetotactic characters and the second using a more comprehensive range of features. The identity of female specimens may be confirmed by dissection of the aculeus; unfortunately, the male genitalia do not provide any easily interpreted diagnostic characters.

Key to species using chaetotaxy only

1   Presutural dorsocentral setae present . . . . **flavipennis** Loew
—   Presutural dorsocentral setae absent 2

2   Scutellum with 2 pairs of setae .... **parietina** (Linnaeus)
—   Scutellum with 1 pair of setae .... **nebulosa** (Wiedemann)

Key to species

1   Dark areas of wing with both large clear hyaline areas and numerous small semi-hyaline dots
       (fig. 264). Aculeus with 2 pairs of subapical steps and no other steps (fig. 155). Larvae
       stem-boring. (Usually without presutural dorsocentral setae. Scutellum with both a basal
       and an apical pair of setae. WL = 3·2–4·4 mm. AL = 0·9–1·0 mm) . . . **parietina** (Linnaeus)
       Bores the stems of Artemisia vulgaris. *Common in south-east England, also found in East
       Anglia and Yorks. Throughout most of Europe.*
—   Dark areas of wing with large clear hyaline areas and only a few small semi-hyaline dots (fig.
       265). Aculeus with only 1 pair of subapical steps plus a pair of steps at about three-quarters
       the way from base to apex (figs 153. 154). Larvae inducing root galls 2
2   Presutural dorsocentral setae present. Scutellum with both a basal and an apical pair of
       setae. Aculeus with steps about three-quarters the way from base to apex, but these are not
       very pronounced (fig. 153) (WL = 3·4–4·4 mm. AL = 0·8–0·9 mm). . . . . . **flavipennis** Loew
       Induces root galls on Achillea millefolium. *Rare, north Cornwall and Norfolk; old records
       from Suffolk, Sussex and Surrey. Throughout most of the Palaearctic region as far east as
       Mongolia, except the south.*
—   Presutural dorsocentral setae absent. Scutellum with a basal pair of setae, but usually with-
       out an apical pair of setae. Aculeus with steps about three-quarters the way from base to
       apex, which are very pronounced (fig. 154). (WL = 3·0–4·4 mm. AL = 0·8–0·9 mm.)
       . . . . **nebulosa** (Wiedemann)
       No British rearing record; known elsewhere to induce root galls on Leucanthemum vulgare.
       *No recent records; old records from England and Wales, as far north as Hereford. Europe,
       except in the north, and Israel.*

Genera **Paroxyna** Hendel, **Campiglossa** Rondani and **Dioxyna** Frey

Paroxyna is a genus of about 150 species, including 67 Palaearctic species and repre-
sentatives in all other regions. Most species of known biology are associated with the
capitula of composites. Conversely, one generation of *P. misella* induces a stem gall and
in both its biology and morphology it has a lot in common with *Campiglossa* species.
Because some of the wing pattern characters of *Paroxyna* species are very variable, it is
difficult to identify species reliably by any wing pattern features. The most important
diagnostic characters are distiphallus form, colour of certain setae and head shape.
Aculeus shapes do differ between species, but the differences are usually too small to be
interpreted easily.

  Campiglossa is a predominantly Palaearctic genus of 19 species, with two Oriental
and a single Afrotropical representative. The two British species form galls on their
composite hosts, as does *P. misella*. The generic limits of *Campiglossa* and *Paroxyna*
are in need of revision (White, 1986).

  Dioxyna is a genus of 10 species, including two Palaearctic species, and others in the
Afrotropical, Australasian, Neotropical and Oriental regions. Although some species
are recorded from a wide range of composite hosts, the species of known biology all
seem to have a preference for *Bidens* species.

Key to species

1   Postocular setae all white and scale-like (e.g. fig. 161). Posterior notopleural seta white (figs
       169, 170). Main duct in distiphallus turned back on itself before apex (figs 179–182). (Head
       not elongate, genae deep and mouthparts not long, figs 159, 161. Distal end of basiphallus
       with microtrichia, figs 179–182.) 2

— Postocular setae mostly thin and black; only some postocular setae white and scale-like (e.g. fig. 162). Posterior notopleural seta black (fig. 171). Main duct in distiphallus not turned back on itself before apex (figs 175–177), except perhaps in *P. solidaginis* (fig. 183). (Upper anepisternal seta black, fig. 171. Spermatheca with laterally directed whorls of projections. Aculeus similar to fig. 173.). 5

2 Upper anepisternal seta white (fig. 169). (Distiphallus usually as fig. 179, but rather variable. Scutum uniformly grey tomentose. Cell sc usually without a hyaline spot. Femora, in British specimens usually black. Spermatheca with laterally directed whorls of projections. Aculeus, fig. 172. WL = 2·6–3·0 mm. AL = 0·6–0·8 mm.)
. . . . **Paroxyna absinthii** (Fabricius)
Attacks the capitula of Artemisia maritima *and* A. vulgaris. *Recently recorded only from Kent, Norfolk, Surrey and Sussex; old records from Co. Galway and scattered English localities as far north as Yorks. Throughout the Palaearctic region.*

— Upper anepisternal seta black (fig. 170) 3

3 Large; WL = 4·4–4·9 mm. Scutum uniformly dark golden tomentose. Cell sc very much darker than other marked areas of the wing (fig. 271). Distiphallus as fig. 182. Aculeus as fig. 174. Spermatheca with downward directed projections. (Cell sc with a large hyaline spot, fig. 271. Cell r_{4+5} usually without an apical hyaline spot, fig. 271. Femora yellow or orange-yellow. AL = 0·9–1·0 mm.). **Paroxyna plantaginis** (Haliday)
Attacks the capitulum of Aster tripolium. *Coast of England, except the north-west, Wales, and east coast of Ireland. Western European coast.*

— Small; WL = 2·4–4·2 mm. Scutum uniformly grey tomentose. Cell sc not very much darker than all the other marked areas of the wing (similar to fig. 269). Distiphallus not as fig. 182. Aculeus similar to fig. 173. Spermatheca with laterally directed whorls of projections. . 4

4 Distiphallus as fig. 180. Femora usually black, rarely with all femora completely yellow. Cell sc usually with a very small hyaline spot. Cell r_{4+5} usually with an apical hyaline spot. (WL = 2·4–3·9 mm. AL = 0·8–0·9 mm.). **Paroxyna loewiana** Hendel
Attacks the capitulum of Solidago virgaurea. *Throughout the British Isles. Throughout the Palaearctic region.*

— Distiphallus as fig. 181. Femora yellow or orange-yellow. Cell sc without a hyaline spot. Cell r_{4+5} usually without an apical hyaline spot. (WL = 3·3–4·2 mm. AL = 0·8–0·9 mm.)
. . . . **Paroxyna lhommei** Hering
Host unknown; recently found in large numbers on Senecio *sp., and this may be a true host. Very local, coast of Straits of Dover in England and France, and Holland.*

5 Genae narrow, and mouthparts long and geniculate (figs 164, 165). 6

— Genae broad, and mouthparts short (figs 162, 163). (Apical scutellar setae more than one-quarter the length of the basal scutellar setae. Distal end of basiphallus with microtrichia, figs 176, 177, 183.). 7

6 Femora entirely yellow, at most indistinctly darkened. Apical scutellar setae usually less than one-quarter the length of the basal scutellar setae. Distal end of basiphallus without microtrichia (fig. 175). Distiphallus as fig. 175. Scutum golden tomentose, often with dark stripes. (WL = 3·2–3·7 mm. AL = 0·6–0·7 mm. ♂ sternite 5, fig. 166.)
. . . . **Dioxyna bidentis** (Robineau-Desvoidy)
Attacks the capitulum of Bidens tripartita *and probably some other composites; sometimes collected in areas where* Bidens *does not occur. Throughout Great Britain and southern areas of Ireland. Throughout the Palaearctic region.*

— Femora black, or some femora with distinct black marks. Apical scutellar setae more than one-quarter the length of the basal scutellar setae. Distal end of basiphallus with microtrichia (fig. 178). Distiphallus as fig. 178. Scutum grey tomentose, often with dark stripes. (WL = 2·8–3·8 mm. AL = 0·8–0·9 mm. ♂ sternite 5, fig. 168.) . **Paroxyna producta** (Loew)
No British rearing record; outside of Britain it has been reared from the capitula of a wide range of composites most of which belong to the subfamily Cichorioideae. Recently recorded only from a coastal site in Kent; unconfirmed record from a London park; old records from several coastal areas of south-east England and East Anglia. Throughout the Palaearctic region.

7 Femora entirely orange-yellow. Scutum uniformly grey tomentose, without distinct brown stripes. Distiphallus as fig. 183. (WL = 3·2–4·3 mm. AL = 0·8–0·9 mm.)
. . . .**Paroxyna solidaginis** White
Reared from Solidago virgaurea *and presumed to attack the capitulum. Recently recorded only from Hants and Kent; old records from scattered areas of England. Known only from England and Norway.*

49

— Femora black, except at apices. Scutum grey tomentose with distinct brown stripes which are sometimes so broad that most of the scutum is brown tomentose. Distiphallus as figs 176, 177. 8

8 Cell sc with 2 hyaline spots (fig. 267). Frons very broad and antenna bases well separated from each other (fig. 157). (Hind femur without a dorsal preapical seta. WL = 4·4–4·9 mm. AL = 1·1 mm.). . . . . **Campiglossa grandinata** (Rondani)
   No British rearing record, but known outside Britain to induce a stem gall on Solidago virgaurea. *Very rare, old records from three Sussex localities. Throughout most of the Palaearctic region.*

— Cell sc with 1 hyaline spot (figs 266, 269). Frons not so broad and antenna bases only narrowly separated from each other (fig. 158) 9

9 Hind femur without a dorsal preapical seta. Wing with hyaline area in cell r_1 that is immediately past the end of vein R_1, broadly contacting vein R_{2+3} in both sexes (fig. 266). (WL = 3·5–4·4 mm. AL = 0·8–0·9 mm.). . . . . **Campiglossa argyrocephala** (Loew)
   Induces a rosette shaped gall in the capitulum of Achillea ptarmica. *Black Isle and Grampian areas of Scotland. From Europe to Kazakh S.S.R., but not in the southern areas.*

— Hind femur with 1 to 3 dorsal preapical setae (fig. 160). Wing with hyaline area in cell r_1 that is immediately past the end of vein R_1, not reaching vein R_{2+3} in the male and usually only narrowly contacting vein R_{2+3} in the female. (WL = 3·1–4·0 mm. AL = 0·8–1·0 mm.) . . . . **Paroxyna misella** (Loew)
   Usually attacks the flowering spike of Artemisia vulgaris, *inducing a stem gall in the first generation and developing in the capitula in the second generation; sometimes attacks glasshouse* Chrysanthemum *species and there is a single record of a male having been reared from* Centaurea nigra, *possibly a misidentification of* C. debeauxii. *South-east England and East Anglia. Throughout most of the Palaearctic region, except in the south.*

Genus **Sphenella** Robineau-Desvoidy

A predominantly Afrotropical genus of 14 species, three of which are confined to the Palaearctic and another to the Oriental region. *Sphenella marginata* probably has the widest natural distribution of any tephritid. It is associated with the capitula of *Senecio* species throughout the Old World, with distinct subspecies in southern Africa and Australia.

Frons and legs yellow-orange; most other areas of the body with a dark ground colour; most of body covered in a dense grey-green tomentum. Head, fig. 134. Wing, fig. 260. Distiphallus, fig. 145. Aculeus, fig. 151. WL = 3·2–4·4 mm. AL = 0·7 mm . . . . **marginata** (Fallén)
   Attacks the capitula of Senecio aquaticus, S. erucifolius, S. jacobaea, S. viscosus *and* S. vulgaris. *Throughout most of the Palaearctic, except in the far east, eastern and southern Africa, and Australia.*

Genus **Tephritis** Latreille

A worldwide genus of about 140 species, including 92 from the Palaearctic region. Species of known biology are associated with composites, usually living in the capitulum. Most of the world species were keyed by Hering (1944a), and Janzon (1984a) keyed the larvae of the Swedish species. Identification is largely based on wing pattern characters and aculeus shape is of great value in confirming the identity of female specimens with aberrant wing patterning. Unfortunately, the male genitalia do not provide easily interpreted characters. Special care should be exercised in the use of couplet 2 of the following key, because a few specimens of *T. conura, T. ruralis* and sometimes other species, do not have a fully developed mark between the apices of veins R_{4+5} and M; however, separation of the marks is never as great as in *T. bardanae, T. hyoscyami* and *T. formosa* (figs 278–280). This should not cause identification errors provided that the confirmatory characters are checked and both branches from couplet 2 are tested against critical specimens.

Key to species

1   Apical third of wing with a prominent star shaped marking; basal two-thirds of wing largely hyaline except for a mark in cell sc which extends down into cell br, and some small marks in cells dm and cua_1 (fig. 281). Cell c hyaline. (Most of body covered in a pale grey tomentum. Vein R_{4+5} with ventral setulae. Legs orange. Setulae on abdominal tergites 3 and 4 white and scale-like. Oviscape orange to dark orange, black at apex. Aculeus, fig. 204. WL = 3·2–4·2 mm. AL = 0·9 mm.) . . . . **cometa** Loew
Attacks the capitulum of Cirsium arvense. *South-east England and East Anglia. Throughout the Palaearctic region.*

—   Wing more extensively marked (figs 270, 273–280). Cell c usually at least partly divided by a mark 2

2   Hyaline area at apex of cell r_{4+5} extended into cells r_{2+3} and m, so that the small marks at the ends of veins R_{4+5} and M are separated from each other (figs 185, 278–280). (Vein R_{4+5} with ventral setulae.) 3

—   Hyaline area at apex of cell r_{4+5} separate from the hyaline areas at the apices of cells r_{2+3} and m, so that the ends of veins R_{4+5} and M are linked by one marking (figs 186–190, 270, 273–277). 5

3   Cell dm with markings across its whole breadth in both the basal and distal halves (figs 195, 280). Aculeus apex truncate (fig. 201). (Most of body covered in a grey-green tomentum. Legs orange-brown. Setulae on abdominal tergites 3 and 4 white and scale-like. Oviscape dark orange with black mid line and apex. WL = 3·8–4·6 mm. AL = 0·9 mm.)
. . . . **formosa** (Loew)
Attacks and swells the capitula of Sonchus *species. South-east England, Isle of Wight and East Anglia; old records from the Midlands. Europe, except the north, and Middle East to Iran.*

—   Cell dm with markings across its whole breadth only in its distal half, or at most with small marks in basal half (figs 278, 279) 4

4   Cell cup extension surrounded by a marking (fig. 279). Crossvein r-m in a small mark or a broken mark (fig. 200). (Most of body covered in a grey tomentum. Legs largely orange-brown. Setulae on abdominal tergites 3 and 4 white and scale-like. Oviscape black. Aculeus, fig. 203. WL = 4·0–4·8 mm. AL = 1·4–1·8 mm) . . . . **hyoscyami** (Linnaeus)
Attacks the capitula of Carduus acanthoides *and* C. nutans. *South-east England, Isle of Wight, East Anglia, the Midlands and Huntingdon. Throughout the Palaearctic, except in the south.*

—   Cell cup extension in a large hyaline area (fig. 278). Crossvein r-m in a large mark (fig. 199). (Scutum with an orange-grey tomentum; scutellum and abdomen with an orange tomentum. Legs orange. Setulae on abdominal tergites 3 and 4 yellow and scale-like. Oviscape orange, darkening to black in the basal angles. Aculeus, fig. 202. WL = 4·2–5·8 mm. AL = 1·1–1·3 mm) . . . . **bardanae** (Schrank)
Attacks the capitula of Arctium lappa *and* A. minus. *Throughout the British Isles, common in southern England. Western Palaearctic to Kazakh S.S.R.*

5   Cells a_2 and $a_1 + cua_2$ (anal lobe) usually with markings at least across whole breadth of $a_1 + cua_2$ between cup extension and a_2 (figs 270, 273–275); if cells a_2 and $a_1 + cua_2$ largely hyaline (some specimens of *T. conura*) then wing length at least 4·6 mm. 6

—   Cells a_2 and $a_1 + cua_2$ usually hyaline, at most with a mark adjacent to the cup extension, but not reaching vein A_2 (figs 276, 277); wing length at most 4·5 mm. (Vein R_{4+5} with ventral setulae) 9

6   Vein R_{4+5} without ventral setulae. Cell r_1 with 2 large hyaline spots between C and vein R_{2+3}, without a third small spot (fig. 273). Aculeus as fig. 208. Crossvein r-m usually without adjacent hyaline spots (fig. 273). (Scutum with a grey and brown striped tomentum; abdomen with a dark brown tomentum. Legs orange with black marks on femora. Setulae on abdominal tergites 3 and 4 white and scale like. Oviscape black. WL = 1·8–3·2 mm. AL = 0·7 mm). . . . . **praecox** (Loew)
British host unknown; has been reared from Calendula arvensis *in Israel. Known only from old records of single specimens from the Hants and Suffolk coasts. Canary Islands, Mediterranean area and Middle East to Afghanistan.*

—   Vein R_{4+5} with ventral setulae. Cell r_1 with 2 large and a single small hyaline spot between C and vein R_{2+3} (figs 270, 274, 275). Aculeus not as fig. 208. Crossvein r-m usually with adjacent hyaline spots (figs 196–198). 7

7   Apical hyaline area in cell r_{4+5} sometimes absent; if apical hyaline area present, it is small and well separated from the subapical hyaline areas in cells r_{2+3} and m (figs 188–190, 270). Aculeus with an apical notch (fig. 210). (Most of body covered in a brown tomentum; tomentum of scutum sometimes striped grey. Legs dark orange. Setulae on abdominal tergites 3 and 4 white and scale-like. Oviscape orange with a black apex and a black triangular mark at base. WL = 3·7–4·5 mm. AL = 0·8 mm) . . . . **vespertina** (Loew)
     Attacks the capitulum of Hypochoeris radicata *and sometimes other genera of Cichorioideae. Common throughout the British Isles. Western, central Europe, and the Mediterranean area.*

—   Apical hyaline area present and only narrowly separated from the subapical hyaline areas in cells r_{2+3} and m (figs 186, 187). Aculeus without an apical notch (figs 205, 206) 8

8   Crossvein r-m with adjacent small hyaline spots next to vein R_{4+5}, but not M (figs 196, 274). Large; WL = 4·6–5·7 mm. Aculeus apex pointed (fig. 205). Apical hyaline area in cell r_{4+5} usually broadest at vein C (figs 187, 274). Setulae on abdominal tergites 3 and 4 yellow and scale-like. (Scutum and scutellum with an orange grey tomentum; abdomen with a grey tomentum. Legs orange. Oviscape orange to dark orange, black at apex. AL = 1·5–1·8 mm) . . . . **conura** (Loew)
     Attacks the capitula of Cirsium palustre *and* C. helenioides. *Common in Scotland, also occurs in northern England, Wales, Exmoor and Ireland. Throughout Europe, except the south.*

—   Crossvein r-m with adjacent small hyaline spots next to both veins R_{4+5} and M (fig. 197), or with these spots fused to form hyaline stripes on each side of the r-m crossvein (fig. 198). Smaller; WL = 3·1–4·4 mm. Aculeus apex rounded (fig. 206). Apical hyaline area in cell r_{4+5} usually broadest near middle, not at vein C (figs 186, 275). Setulae on abdominal tergites 3 and 4 thin and dark, except at hind margin of tergites where the setulae are white and scale-like. (Scutum with an orange-brown tomentum; abdomen with a dark brown tomentum. Legs orange with black marks on femora. Oviscape orange with a black apex and a black triangular mark at base. AL = 1·2 mm) . . . . **ruralis** (Loew)
     Attacks the capitulum of Hieracium pilosella. *Throughout the British Isles. Throughout Europe, except the south.*

9   Cell r_1 with 2 large hyaline areas; the basal hyaline area in r_1 extends into r_{2+3}, without being staggered at vein R_{2+3}, and it does not reach vein R_{4+5} (fig. 191); the distal hyaline area in r_1 does not reach, or only narrowly reaches, R_{2+3} (fig. 191). Aculeus with a small apical notch; preapical setulae well removed from the notch (fig. 209). (Scutum with a pale grey and brown striped tomentum; abdomen with a grey tomentum. Femora yellow or orange. All setulae on abdominal tergites 3 and 4 white and scale-like. Oviscape largely black, dark orange at sides. WL = 3·6–4·6 mm. AL = 0·7–0·8 mm) . . . . (*separata* Rondani)
     Not reared in Britain; reared from Picris echioides *in Israel. Not a confirmed British species; Mediterranean area, Middle East to Kazakh S.S.R.*
     Two male and two female specimens from Barton Mills, Suffolk (Collin, 1943) may be an aberrant form of *T. separata*. The females have aculeus shapes exactly matching typical continental specimens of *T. separata* (AL = 0·8 mm). However the wing patterns of these specimens are similar to our *T. leontodontis* and *T. neesii* (WL = 3·7–4·1 mm). The above description of *T. separata* was therefore based on typical continental specimens and the identity of the Barton Mills series is further discussed by White (1986).

—   Cell r_1 with 2 large hyaline areas; the basal hyaline area in r_1 does extend into r_{2+3}, but it is staggered at vein R_{2+3}, and it often reaches vein R_{4+5}; the distal area in r_1 broadly reaches R_{2+3} and often extends into cell r_{2+3} (figs 192–194). Aculeus either with a minute apical notch (fig. 207) or with a very large apical notch (fig. 211). (Scutum with a grey and brown striped tomentum; abdomen with a dark brown tomentum.) 10

10   Cell r_{2+3} either with at least 2 hyaline areas below the 2 large hyaline areas of r_1 (fig. 193), or with a single broad area (fig. 194) (a fusion of the 2 areas); if with 2 hyaline areas in r_{2+3}, these both broadly reach veins R_{2+3} and R_{4+5} (fig. 193); if with 1 area in r_{2+3}, it broadly reaches veins R_{2+3} and R_{4+5} (fig. 194). Legs of both sexes orange-brown. Aculeus with a very deep notch, so that the subapical setulae are level with the notch (fig. 211). Crossvein r-m with adjacent hyaline spots or stripes (similar to figs 197, 198). Lower half of cell cua_1 usually marked. Cell sc usually with a hyaline spot. All setulae on abdominal tergites 3 and 4 white and scale-like. (Wing, fig. 276. Oviscape dark orange with a black mid line and apex. WL = 3·5–4·3 mm. AL = 0·7 mm) . . . . **leontodontis** (De Geer)
     Attacks the capitula of Leontodon autumnalis *and* L. hispidus. *Throughout the British Isles, common in Scotland. Europe and North Africa.*

—   Cell r_{2+3} with 1 or 2 hyaline areas below the 2 large hyaline areas in r_1, at most 1 of these

areas in R_{2+3} broadly reaching vein R_{4+5}, the other usually not reaching R_{4+5} (fig. 192), but sometimes narrowly reaching R_{4+5}. Legs of female orange-brown; male femora black, tibia, and tarsi orange-brown. Aculeus with a hardly discernible notch (fig. 207). Crossvein r-m usually without adjacent hyaline areas, at most with hardly discernible spots next to R_{4+5}. Lower half of cell cua_1 usually hyaline. Cell sc completely dark brown. Some setulae in the basal areas of abdominal tergites 3 and 4 thin and dark coloured, the remaining setulae white and scale like. (Wing, fig. 277. Oviscape black. $WL = 3 \cdot 5 - 4 \cdot 5$ mm. $AL = 0 \cdot 9 - 1 \cdot 0$ mm). . . . . **neesii** (Meigen)

Attacks the capitulum of Leucanthemum *species. Throughout the British Isles, common in southern England. Europe, except the Mediterranean area.*

Genus **Trupanea** Schrank

This is the largest genus after *Dacus*, with about 200 world species, including 14 Palaearctic species, most of which were keyed by Hering (1956). Larvae of the British species live in the capitula of a wide range of composites.

Key to species

1 Vein CuA_1 with a brown stripe along it from dm-cu to hind margin of wing. Star shaped mark on wing usually connected to cell sc by a narrow linear mark. (Aculeus, fig. 215. $WL = 2 \cdot 6 - 4 \cdot 3$ mm. $AL = 1 \cdot 2$ mm). . . . . **amoena** (Frauenfeld)
 No British rearing records; elsewhere it has been recorded from a wide range of composites, many of which belong to unrelated groups. Known only from old records of single specimens from the Devon and Suffolk coasts. Central and southern Palaearctic region, Ethiopia, India, Sri Lanka and the Philippines.

— Vein CuA_1 entirely within a hyaline area. Star shaped mark on wing not connected to cell sc (fig. 282). (Aculeus, fig. 214. $WL = 2 \cdot 6 - 3 \cdot 6$ mm. $AL = 0 \cdot 7 - 0 \cdot 8$ mm) . . . . . **stellata** (Fuessly)
 In Britain, usually attacks the capitula of Senecio *spp.; elsewhere it has been reared from a wide range of composites, many of which belong to unrelated groups. Southern and eastern counties of England; old records from the east coast of Ireland. Palaearctic region as far east as Mongolia.*

Genus **Xyphosia** Robineau-Desvoidy

A genus of four Palaearctic and one Oriental species.

Subgenus *Xyphosia* Robineau-Desvoidy

A group of three Palaearctic species which are separated from s.g. *Trichoxyphosia* Hendel by the lack of setae on the underside of the hind femora.

Body and legs orange; oviscape dark orange, black at apex. Head, fig. 136. Wing, fig. 259. Distiphallus, fig. 146. Aculeus, fig. 152. $WL = 3 \cdot 7 - 6 \cdot 3$ mm. $AL = 2 \cdot 0$ mm

. . . .**miliaria** (Schrank)

Attacks the capitula of Cirsium arvense *and* C. palustre. *Very common throughout the British Isles. Throughout most of the Palaearctic region, except the south.*

Pupal stage keys

Although the larvae of many tephritids have been described, few keys to immature stages have been written. The exceptions are a key to Swedish *Tephritis* species (Janzon, 1984a), some British *Urophora* species (Varley, 1937), Palaearctic *Carpomya* and *Rhagoletis* species (Kandybina, 1961, 1965), and a key to some subfamily group-ings (Kandybina, 1977). The only major species key covers 45 Nearctic species, most of

which are frugivorous trypetines (Phillips, 1946), and there are also keys to the larvae of some fruit pest species from Central America (Berg, 1979) and the eastern Palaearctic region (Kandybina, 1966). A comprehensive study of British tephritid larvae was beyond the scope of this work; however, pupal material was available for 54 of our 73 species. Many larval characters, notably the general body shape and number of openings in each spiracle, and the larval mouthparts, are retained by the pupal stage. A study of the available puparia enabled production of the following keys to the pupae of major groups of Tephritidae, and pupae found in some host-plants, namely *Carduus* species, *Centaurea nigra, C. scabiosa* and *Cirsium* species. Larval mouthparts were not dissected from the puparia, but simple external characters of the 54 species examined are tabulated; a more detailed tabulation was presented by Efflatoun (1927) for the Egyptian tephritids.

The specimens used for this study are all in the collections of the British Museum (Natural History), London, and the National Museum of Wales, Cardiff. Data for a further 2 species were extracted from the literature, and a comprehensive list of published larval and pupal descriptions is given in Appendix I. Descriptions of the larvae of *Ceratitis capitata* and *Rhagoletis cerasi* are not included here; they will be given in a forthcoming *Handbook* (this series) on Diptera larvae (K. G. V. Smith, in prep.). Some descriptions of *Anastrepha* and *Dacus* larvae were given by Berg (1979).

The eggs of tephritids are usually simple ovoid structures, usually with a distinct structure at one pole, which is probably a micropyle. Many species were illustrated by Dirlbek (1970) and their ultrastructure was described by Margaritis (1985). The eggs of *Chaetorellia jaceae* and related species are unusual because the micropyle is at the end of a tube that is two to three times the length of the main body of the egg. Some *Urophora* species are also remarkable, because they do not hatch as a first instar larva, but moult within the egg and emerge as a second instar larva; species known to do this are *U. cardui,* (Peschken & Harris, 1975), *U. jaceana* (Varley, 1937) and *U. stylata* (Redfern, 1968).

Tephritid larvae can be distinguished from those of other families with the key by Brindle & Smith (1978), or with the forthcoming larval *Handbook* (this series) (K. G. V. Smith, in prep.). Cyclorrhapha larvae can be differentiated from most other insect larvae by the lack of all appendages and the absence of a sclerotised head capsule. Larvae found in the capitula, stems and roots of composites (Asteraceae) may be differentiated from larval Pallopteridae by the lack of an obvious spine or lobe on the border of each posterior spiracle. Leaf and stem-mining tephritid larvae have three (or two in *Myopites*) elongate slit openings in each posterior spiracle, as opposed to larval Anthomyzidae and Chloropidae which have short elliptical openings. Larval Tephritidae can be separated from larval Agromyzidae by the shape of the anterior spiracles (see second part of couplet 3 in the following key) and from larval Anthomyiidae by the posterior spiracles not being on processes. The only Cyclorrhapha larvae likely to be found in fresh fruit are tephritids and no further characters are needed.

Tephritid puparia usually resemble the final (third) instar larvae, although the puparia of some species have a shrivelled integument. Many larval details, such as the fan of setulae associated with the posterior spiracles appear to be lost and the body often darkens in colour when pupation occurs. However, the larval characters given above should enable recognition of tephritid puparia found within composite host-plants and in cultures of leaf-mining and fruit-feeding species. Figure 216 is a diagrammatic representation of a tephritid puparium.

Key to major groups

1 Anus apparently open; perianal pads visible as clearly differentiated sclerites which are darker coloured than the main body. (Frugivorous or leaf-mining.) **Trypetini** (except *Goniglossum*) 2

— Anus usually closed; if anus appearing to be open, then perianal pads not differentiated, and perianal pads concolorous with main body 5

2 Caudal (posterior) plate with a fish-tail shaped appendage. Segments of body only marked by fine lines .... **Platyparea poeciloptera** (Schrank)

— Caudal plate without a fish-tail shaped appendage. Segments of body clearly marked by deep grooves 3

3 Anterior spiracle openings arranged in rows on a slightly elevated fan shaped structure (fig. 217). In fruit. .... **Anomoia** and **Rhagoletis**

— Anterior spiracle openings arranged in large arcs, not elevated on a fan shaped structure (fig. 219). In leaf-mines 4

4 Posterior spiracles each with the central opening of similar size to the lateral openings (fig. 218). In leaf-mines in umbellifers (Apiaceae) .... **Cryptaciura** and **Euleia**

— Posterior spiracles each with the central opening larger and more raised than the lateral openings (fig. 220). In leaf-mines in composites (Asteraceae) **Acidia, Trypeta** and **Vidalia**

5 Caudal plate invaginated. In fruit. (Segments of body well marked.)
.... **Goniglossum wiedemanni**

— Caudal plate not invaginated. In the capitula, stem or roots of composites (Asteraceae), sometimes in galls .... **Tephritinae** and **Myopitinae**

There are no obvious ways of separating the Tephritinae and Myopitinae using pupal characters; however, the genus *Myopites* is unique in that the pupae have only two openings in each posterior spiracle rather than three; *Urophora* puparia tend to have fewer anterior spiracle openings than species of Tephritinae; and the Terelliinae and *Xyphosia miliaria* tend to have more heavily wrinkled bodies than other Tephritinae. Other characters of interest are as follows: *Noeeta pupillata* is very much broader near its posterior end than at its anterior end; and *Sphenella marginata* has a remarkably shiny integument and is 'C' shaped, so that its ventral side is concave and shorter than its dorsal side.

Keys to puparia found in selected host plants

The following four keys cover 21 of our 56 Tephritinae and Myopitinae species. Furthermore, the key to puparia found in *Centaurea scabiosa* provides the only reliable method of separating *Cerajocera ceratocera* and *C. plagiata*. The abbreviation 'BL' is used for body length and the table which follows these keys should be consulted for confirmatory characters of each species.

Key to puparia found in *Carduus* species

1 Anterior spiracles each with 3 openings. (Usually in *Carduus nutans*)
.... **Urophora solstitialis** (Linnaeus)

— Anterior spiracles each with more than 3 openings 2

2 Body dark brown, black at each end. (In *Carduus acanthoides* and *C. nutans*)
.... **Tephritis hyoscyami** (Linnaeus)

— Body orange, with a black or dark brown caudal area 3

3 Anterior spiracles each with 6 openings. (BL = 3·9–4·6 mm. In *Carduus acanthoides* and *C. nutans*) .... **Terellia serratulae** (Linnaeus)

— Anterior spiracles each with 7 openings. (BL = 3·8 mm. In *Carduus acanthoides*)
.... **Terellia winthemi** (Meigen)

Key to puparia found in *Centaurea nigra* and *C. debeauxii*

1 Body entirely black. (Anterior spiracles each with 5 openings.)
.... **Acanthiophilus helianthi** (Rossi)

— Body not black 2

2   Anterior spiracles each with 6 openings. Body entirely yellow............................
      Chaetorellia jaceae (Robineau-Desvoidy) and **Chaetostomella cylindrica** (Robineau-Desvoidy)
      (The very small differences between these two species are described by Varley, 1937.)
—   Anterior spiracles each with only 2 or 3 openings. Caudal plate dark brown or black 3
3   Anterior spiracles each with 2 openings. (BL = 3·0 mm). . **Urophora quadrifasciata** (Meigen)
—   Anterior spiracles each with 3 openings. (BL = 3·5–4·6 mm).... **Urophora jaceana** (Hering)

Key to puparia found in *Centaurea scabiosa*

1   In the stem. Caudal plate with 2 small tubercles (fig. 221) .. **Cerajocera plagiata** (Dahlbom)
—   In the capitulum (*Cerajocera ceratocera* often pupates in the soil as an alternative to remaining in the host). Caudal plate of another form........................... 2
2   Caudal plate with a fish-tail shaped appendage (fig. 222)......**Cerajocera ceratocera** Hendel
—   Caudal plate without a fish-tail shaped appendage................................... 3
3   Anterior spiracles each with 8 openings. Body entirely yellow ..... **Terellia colon** (Meigen)
—   Anterior spiracles each with 2 openings 4
4   Small; BL = 3·0 mm ....**Urophora quadrifasciata** (Meigen)
—   Large; BL = 4·6–5·4 mm ....**Urophora cuspidata** (Meigen)

Key to puparia found in *Cirsium* species

1   In a stem gall (figs 2, 3). (In *Cirsium arvense*) .... **Urophora cardui** (Linnaeus)
—   In the capitulum 2
2   In a multilocular gall (fig. 4). (Usually in *Cirsium vulgare*).... **Urophora stylata** (Fabricius)
—   Not in a gall... 3
3   Integument smooth. Whole body dark-brown to black............................ 4
—   Integument wrinkled, at least near anterior and posterior ends. Body largely orange or pale brown in colour, sometimes darkened at each end, especially at the posterior end which may be dark brown or black.. 5
4   In *Cirsium arvense*. Anterior spiracles each with 4 openings (needs checking as only one specimen available) .... **Tephritis cometa** (Loew)
—   In *Cirsium palustre* or *C. helenioides*. Anterior spiracles each with 7 openings (needs checking) ....**Tephritis conura** (Loew)
5   Caudal plate concolorous with main body. (In *Cirsium arvense* and *C. palustre*)......... 6
—   Caudal plate darker in colour than main body 7
6   Body yellow. Anterior spiracles each with 6 openings
      ....**Chaetostomella cylindrica** Robineau-Desvoidy
—   Body orange. Anterior spiracles each with 8 openings .... **Xyphosia miliaria** (Schrank)
7   In *Cirsium vulgare*. Anterior spiracles each with 6 openings. Main body orange...........
      ....**Terellia serratulae** (Linnaeus)
—   Not in *Cirsium vulgare*. Anterior spiracles each with more than 6 openings. Main body pale brown... 8
8   In *Cirsium eriophorum*. Anterior spiracles each with 9 openings. Large; BL = 5·2–6·3 mm
      .... **Terellia longicauda** (Meigen)
—   In *Cirsium arvense*, *C. dissectum* or *C. palustre*. Anterior spiracles each with 7 openings. Small; BL = 3·6–3·9 mm............................... **Terellia ruficauda** (Fabricius)

Table of pupal characters

The following tables summarise a few characters of the puparia examined; if used in combination with the host-plant data in Appendix II, these simple characters should allow the puparia and final instar larvae of most species to be tentatively identified. Characters used in the key to major groups and unusual features described in the host keys are not repeated in the following tables.

Column 1 — Name; * = data from a published description.

Column 2 — Body length in mm.

Column 3 — Colour; b = black or dark brown, p = pale brown, o = orange or red-brown, y = yellow, w = white or grey; the three letters represent the anterior/main body/posterior regions. Where variability was observed, a range is given.

Column 4 — Number of openings in each anterior spiracle; for some species with large numbers of spiracular openings these values are approximate and should not be regarded as definitive (using a low power stereoscopic microscope it is often difficult to count the openings accurately).

Column 5 — Number of rows of openings in each anterior spiracle; m = multiple rows arranged in such a way that they cannot be counted.

Stem and leaf-mining species

Name	BL	colour	a.spl.	spl.rows
A. cognata	4·3–5·2	yyy	?32	2
C. rotundiventris	3·5–4·2	yyy	?20	1
E. heracleii	4·2–5·1	yyy	15	1
P. poeciloptera	6·5–7·7	bob	?36	m
T. artemisiae	3·7–4·2	yyy	?20	1
T. immaculata	3·7–4·5	yyy	?16	1
T. zoe	3·7–4·5	yyy	?15	1
V. cornuta	4·6–5·4	yyy	?23	1
V. spinifrons	3·9	yyy	?19	2

Fruit feeding species

Name	BL	colour	a.spl.	spl.rows
A. purmunda	3·7–4·2	www	13	2
G. wiedemanni	4·6	ooo	22–25	1
R. alternata	3·7–4·6	www	?15	2
R. meigenii*	?	?	16–18	1

Non leaf-miners on Asteraceae

Name	BL	colour	a.spl.	spl.rows
M. eximia	2·5–3·2	pyp	2	1
M. inulaedyssentericae	2·4–3·4	ywy	2	1
U. cardui	3·7–5·4	opb	3	1
U. cuspidata	4·6–5·4	opb	2	1
U. jaceana	3·5–4·6	opb	3	1
U. quadrifasciata	3·0	opb	2	1
U. solstitialis	3·9	opb	3	1
U. stylata	4·6	opb	4	1
C. ceratocera	4·8–6·7	yyo	10	1
C. plagiata	4·6–5·8	ywo	5–7	1
C. tussilaginis	2·9–4·1	yyy	9	1
C. jaceae	3·4–4·2	yyy	6	1
C. cylindrica	3·8–4·5	yyy	6	1
O. falcata	7·4–7·8	ywy	?18	m
T. colon	3·9–4·5	yyy	8	1
T. longicauda	5·2–6·3	ppb	9	1
T. ruficauda	3·6–3·9	ppb	7	1
T. serratulae	3·9–4·6	oob	6	1

Name	BL	colour	a.spl.	spl.rows
T. vectensis	3·1–3·5	oob	6	1
T. winthemi	3·8	oob	7	1
D. guttularis	3·6–4·5	bpp	7	1
N. pupillata	3·3–4·1	bbb	7	1
A. helianthi	3·3–4·6	bbb	5	1
D. bidentis	2·9	yyy	4	1
E. sonchi	2·5–3·1	www	?4	1
O. parietina	4·3–5·4	bbb	?5	1
P. absinthii	2·3–2·7	bbb	?7	1
P. loewiana	2·9–3·3	bbb	?11	1
P. misella	2·4–2·8	bpp	4	1
P. plantaginis	3·0–3·9	bbb	25–30	1
P. producta	2·6–3·5	yyy	5	1
S. marginata	2·2–3·3	ooo	3	1
T. bardanae	3·9–4·5	bbb	6	1
T. cometa	3·7	bbb	?4	1
T. conura	4·2	bbb	?7	1
T. hyoscyami	3·9–4·1	bpb–bbb	?5	1
T. leontodontis	3·1–3·6	bbb	5	1
T. neesii*	3·5	bbb	4	1
T. ruralis	3·3	bpb–bbb	?4	1
T. vespertina	3·3	bbb	?4	1
T. amoena	2·9–3·4	bbb	3	1
T. stellata	2·3	bpb	?3	1
X. miliaria	3·9–4·8	ooo	8	1

Appendix I: Host-plants of British Tephritidae

The following host-plant list is compiled from both published sources and collections. Each entry is divided into a British (Br) and non-British (Fn) section. Each of these sections is further divided as follows:

i. Confirmed records; the tephritids were either examined by the author or by another specialist.

ii. Unconfirmed literature records that are thought likely to be correct are each preceded by a '?'.

iii. Literature records that are almost certainly incorrect are listed, but they are marked '??'. Abnormal hosts are also marked '??', but these are briefly discussed.

There is still room for errors in the identification of the plants and a worthwhile research project would be a thorough survey of British tephritid host-plant relationships of the type carried out for western European Cardueae associated insects by Zwölfer (1965), and for the tephritids of Israel (Kugler & Freidberg, 1975), Crete (Neuenschwander & Freidberg, 1983) and Czechoslovakia (Dirlbek & Dirlbeková, 1985). Most of our knowledge of the biology and hosts of British tephritids was gathered by Niblett (1931; 1934a; 1934b; 1935; 1936; 1939; 1940a; 1940b; 1942; 1946a; 1946b; 1947; 1949; 1950a; 1950b; 1951; 1952a; 1952b; 1953; 1955a; 1955b; 1956a; 1956b; 1956c; 1957), who unfortunately failed to maintain a collection; consequently, many of Niblett's host-plant records cannot be verified.

The following list uses the nomenclature of *Flora Europaea* (Moore, Tutin & Walters, 1976) for the Asteraceae (= Compositae) and other nomenclature follows *Flora of the British Isles* (Clapham, Tutin & Warburg, 1962; 1981); the only differences are as follows: *Carduus acanthoides* (= *C. crispus*: auctt. Brit.), *Centaurea debeauxii*

($= C. nigra$ ssp. *nemoralis*), *Cirsium helenioides* ($= C. heterophyllum$), *Crataegus laevigatus* ($= C. oxycanthoides$), *Dittrichia viscosa* ($= Inula viscosa$), *Leucanthemum maximum* ($= Chrysanthemum maximum$), *Leucanthemum vulgare* ($= Chrysanthemum leucanthemum$), *Matricaria perforata* ($= M. maritima$ ssp. *inodora*), *Tanacetum vulgare* ($= Chrysanthemum vulgare$). Only British plants, including some garden plants and naturalised aliens, are included in the list, i.e. many of our British tephritids have a wider range of host-plants than those listed below. There have been several previously published host-plant lists, e.g. Uffen & Chandler (1978) for Britain, Leclercq (1967) for Europe, Hendel (1927) for the Palaearctic, Wasbauer (1972) for North America and Phillips (1946) for all regions.

Selected references describing the biology of British tephritids are also included in this Appendix; for pest species further references are given earlier in this *Handbook* (p. 9). A comprehensive catalogue of larval and pupal descriptions is also included; the term 'present work' indicates that diagnostic characters of the puparium are given in this *Handbook* (p. 56). Furthermore, many of the references included only give an illustration of the larva or pupa; major sources of detailed larval descriptions are Efflatoun (1927), Kandybina (1961; 1962; 1965; 1966; 1970; 1972; 1977), Persson (1963), Phillips (1946) and Varley (1937). Chu (1949) may also be a major source of larval descriptions, but it was not available to the author, and many of the references were copied from Hennig (1968) and *Zoological Record,* and were not examined. Descriptions and illustrations of leaf-mines are given by Vimmer (1931) and Hering (1957), and European galls are keyed by Buhr (1965).

Acanthiophilus helianthi. **Br;** *Centaurea nigra:* **Fn;** *Carduus* sp., *Carlina vulgaris, Carthamus lanatus, C. tinctorius, Centaurea calcitrapa, C. cyanus, C. jacea, C. moschata, C. scabiosa, C. solstitialis, Cirsium arvense, Cnicus benedictus, Cynara scolymus, Leucanthemum vulgare, Scolymus hispanicus, Serratula tinctoria, Silybum marianum, Sonchus oleraceus, Xanthium spinosum,* ? *Centaurea aspera,* ? *Cirsium vulgare.* **Larva;** present work.

Acidia cognata. **Br;** *Petasites fragrans, P. hybridus, Tussilago farfara:* **Fn;** *Homogyne alpina, Senecio* sp., ?? *Arctium lappa.* **Biology:** Vimmer, 1931; Niblett, 1957. **Larva;** Vimmer, 1925, 1931; Hendel, 1927; present work.

Acinia corniculata. **Br;** ? *Centaurea nigra:* **Fn;** *Centaurea jacea,* ?? *Tanacetum vulgare.* **Biology;** Hering, 1941.

Anomoia purmunda. **Br;** *Berberis* sp., *Cotoneaster* sp., *Crataegus monogyna, Pyracantha* sp.: **Fn;** *Crataegus laevigata, Pyrus baccata,* ? *Hippophae rhamnoides,* ? *Sorbus aucuparia.* **Biology;** Niblett, 1940b, 1956c; Kandybina, 1972; Smith, 1984. **Larva;** Dirlbek & Dirlbek, 1959; Kandybina, 1962, 1972, 1977; present work.

Campiglossa argyrocephala. **Br;** *Achillea ptarmica:* **Fn;** ?? *Solidago* sp. **Biology;** Wahlgren, 1944.

Campiglossa grandinata. **Br;** ? *Solidago* sp.: **Fn;** *Solidago virgaurea.* **Biology;** Andersson, 1955.

Cerajocera ceratocera. **Br;** *Centaurea scabiosa:* **Fn;** ?? *Arctium lappa.* **Biology;** Hering, 1935b; Niblett, 1950b, 1955a, 1956b, 1956c; Persson, 1963; **Larva;** Hendel, 1927; Persson, 1963; Kandybina, 1970; present work.

Cerajocera plagiata. **Br;** *Centaurea scabiosa.* **Biology;** Hering, 1935b; Niblett, 1956b, 1956c; Persson, 1963. **Larva;** Persson, 1963; Dirlbek, 1970 (as *C. ceratocera*); present work.

Cerajocera tussilaginis. **Br;** *Arctium lappa, A. minus,* ?? *Cirsium arvense* (confirmed but probably not normal), ?? *C. vulgare* (confirmed but probably not normal): **Fn;** *Arctium tomentosum,* ?? *Centaurea jacea,* ?? *C. nigra,* ?? *Cirsium eriophorum.* **Biology;** Niblett, 1956c. **Larva;** present work.

Chaetorellia jaceae. **Br;** *Centaurea nigra, ? C. debeauxii, ?? C. scabiosa:* **Fn;** *C. debeauxii, C. jacea, ?? Carthamus tinctorius, ?? Centaurea calcitrapa, ?? C. cyanus, ?? Cirsium erisithales, ?? C. vulgare.* **Biology;** Varley, 1937. **Larva;** Varley, 1937; Efflatoun, 1927 (probably a misidentification); present work.

Chaetorellia loricata. **Br;** *Centaurea scabiosa.* **Biology;** Hering, 1936a; Niblett, 1955a, 1956c.

Chaetostomella cylindrica. **Br;** *Centaurea montana, C. nigra, Cirsium arvense, C. palustre, Serratula tinctoria, ? Centaurea debeauxii, ? Cirsium dissectum:* **Fn;** *Carduus acanthoides, C. nutans, C. pycnocephalus, Centaurea calcitrapa, C. cyanus, C. debeauxii, C. jacea, C. montana, C. scabiosa, C. solstitialis, Cirsium acaulon, C. eriophorum, C. helenioides, C. oleraceum, C. palustre, C. tuberosum, Onopordum acanthium, ? Cirsium eriophorum, ? C. vulgare, ?? Arctium lappa, ?? A. tomentosum, ?? Sonchus asper, ?? Taraxacum officinale.* **Biology;** Varley, 1937; Niblett, 1935, 1955a. **Larva:** de Vos-de Wilde, 1935; Varley, 1937; Dirlbek, 1970; Kandybina, 1970; present work.

Chetostoma curvinerve. Host unknown, but almost certainly frugivorous (see Kandybina, 1966, for a larval description of the related *C. continuans* Zia).

Cryptaciura rotundiventris. **Br;** *Heracleum* sp., *? Angelica sylvestris, ?? Arctium* sp.: **Fn;** *Aegopodium podagraria, Angelica sylvestris, ? Pimpinella* sp. **Larva;** present work.

Dioxyna bidentis. **Br;** *Bidens tripartita, ? Galinsoga parviflora, ? Tagetes* sp.: **Fn;** *? Bidens cernua, ? Leucanthemum vulgare, ? Tanacetum vulgare, ? Filago gallica.* **Biology;** Niblett, 1956c; Chandler & Speight, 1982. **Larva;** present work.

Dithryca guttularis. **Br;** *Achillea millefolium:* **Fn;** *Achillea nobilis, ?? Lotus* sp. **Biology;** Collin, 1947; Niblett, 1956c. **Larva;** present work.

Ensina sonchi. **Br;** *Aster tripolium, Hypochoeris radicata, Leontodon autumnalis, L. hispidus, Picris hieraciodes, Sonchus arvensis, S. asper, S. oleraceus, Tragopogon pratensis:* **Fn;** *Cichorium intybus, Cirsium arvense, C. vulgare, Crepis biennis, Hieracium umbellatum, Lactuca serriola, Picris echioides, Taraxacum officinale, ? Carduus nutans, ? Homogyne alpina, ? Senecio jacobaea, ? S. vulgaris, ? Sonchus palustris, ? Tragopogon porrifolius.* **Biology;** Hering, 1937a; Niblett, 1956c; Chandler & Speight, 1982. **Larva;** Hendel, 1927; Okadome, 1962; present work.

Euleia heracleii. **Br;** *Angelica sylvestris, Apium graveolens, A. nodiflorum, Conium maculatum, Heracleum sphondylium, Pastinaca sativa, Smyrnium olusatrum, ?? Cirsium arvense:* **Fn;** *Ammi* sp., *Anthriscus cerefolium, Berula erecta, Bupleurum* sp., *Cicuta* sp., *Coriandrum* sp., *Daucus carrota, Eryngium campestre, Falcaria* sp., *Heracleum mantegazzianum, Levisticum officinale, Ligusticum scoticum, Oenanthe* sp., *Petroselinum crispum, Peucedanum ostruthium, Pimpinella major, P. saxifraga, Seseli* sp., *Tordylium maximum, Torilis* sp., *? Angelica archangelica, ? Anthriscus cerefolium, ? Cicuta virosa, ? Falcaria vulgaris, ? Heracleum persicum, ? Sium latifolium, ? Smyrnium perfoliatum, ?? Arctium lappa.* **Biology;** Niblett, 1957; Labeyrie, 1958; Christenson & Foote, 1960; **Larva;** de Meijere, 1895; Gardner, 1921; Lundblad & Lindblom, 1925; Vimmer, 1931; de Vos-de Wilde, 1935; Keilin & Tate, 1943; present work.

Euphranta toxoneura. **Fn;** *Salix alba, S. caprea, S. cinerea, S. fragilis,* as a predator/brood parasite in the leaf galls of *Pontania* spp. (Hymenoptera, Tenthredinidae). **Biology;** Kopelke, 1984, 1985. **Larva;** Kopelke, 1984.

Goniglossum wiedemanni. **Br;** *Bryonia dioica.* **Biology;** Niblett, 1956c. **Larva;** Sylvestri, 1920; Hendel, 1927; Séguy, 1934; Kandybina, 1977; present work.

Icterica westermanni. **Br;** *Senecio erucifolius, S. jacobaea.* **Biology;** Séguy, 1934.

Myoleja caesio. **Br;** *? Silene dioica, ?? Lonicera periclymenum, ?? Sambucus* spp.: **Fn;** *?? Centaurea* sp. See note on page 70.

Myopites eximia. **Br;** *Inula crithmoides:* **Fn;** *?? Pulicaria dysenterica.* **Biology;** Hering, 1944b; Niblett, 1942. **Larva;** Rivosecchi, 1960 (possible misidentification); present work.

Myopites inulaedyssentericae. **Br;** *Pulicaria dysenterica,* *??* *Inula crithmoides* (confirmed but probably not normal): **Fn;** ? *Dittrichia viscosa,* ? *Inula britannica,* ? *Inula salicina.* **Biology;** Niblett, 1940a, 1956c; Freidberg, 1980. **Larva;** Rivosecchi, 1960; present work.

Noeeta pupillata. **Br;** *Hieracium umbellatum, H.* (section *murorum*) sp., *H.* (section *sabaudum*) sp., *Picris hieracioides:* **Fn;** *Hieracium lachenalii, H. pilosella, H. vulgatum. Senecio jacobaea.* **Biology;** Hering, 1936b, 1951; Niblett, 1942, 1947, 1956c. **Larva;** Reichert, 1916; Dirlbek, 1970; Kandybina, 1970; present work.

Orellia falcata. **Br;** *Tragopogon pratensis.* **Biology;** Niblett, 1956c; Neuenschwander & Freidberg, 1983. **Larva;** Dirlbek, 1970; present work.

Oxyna flavipennis. **Br;** *Achillea millefolium:* **Fn;** *Achillea nobilis.* **Biology;** Niblett, 1956c.

Oxyna nebulosa. **Fn;** *Leucanthemum vulgare,* *??* *Achillea millefolium,* *??* *Artemisia vulgaris.* **Biology;** Buhr, 1965.

Oxyna parietina. **Br;** *Artemisia vulgaris,* ? *A. absinthium,* *??* *Aster tripolium:* **Fn;** ? *Artemisia campestris,* *??* *Achillea millefolium.* **Biology;** Andrews, 1941; Parmenter, 1952; Niblett, 1956c. **Larva;** Séguy, 1934; Dirlbek, 1970; present work.

Paroxyna absinthii. **Br;** *Artemisia maritima, A. vulgaris:* **Fn;** *??* *Bidens* spp., numerous records which are probably all misidentifications of *Dioxyna bidentis,* *??* *Inula britannica.* **Biology;** Uffen & Chandler, 1978. **Larva;** present work.

Paroxyna lhommei. **Br;** ? *Senecio* sp., *??* *Cirsium arvense:* **Fn;** *??* *Carduus* sp., *??* *Leucanthemum vulgare.*

Paroxyna loewiana. **Br;** *Solidago virgaurea.* **Biology;** Niblett, 1956c; Chandler & Speight, 1982. **Larva;** present work.

Paroxyna misella. **Br;** *Artemisia vulgaris, Chrysanthemum* (glasshouse) sp., *??* *Centaurea nigra* (confirmed but probably not normal): **Fn;** *Artemisia absinthium,* *??* *Lactuca serriola* (confirmed but possibly not normal). **Biology;** Hodson & Jary, 1939; Niblett, 1946a, 1955b, 1956c; Uffen & Chandler, 1978. **Larva;** present work.

Paroxyna plantaginis. **Br;** *Aster tripolium.* **Biology;** Niblett, 1956c. **Larva;** present work.

Paroxyna producta. **Fn;** (the following records are all for *P. tessellata,* but most of them probably refer to *P. producta*); ? *Bellis* sp., ? *Calendula arvensis,* ? *Chrysanthemum* sp., ? *Crepis capillaris,* ? *C. paludosa,* ? *Hieracium* spp., ? *Hypochoeris radicata,* ? *Leontodon autumnalis,* ? *Leontodon hispidus,* ? *Sonchus arvensis,* ? *Taraxicum officinale,* *??* *Artemisia campestris,* *??* *Scorzonera* sp. **Biology;** Hering, 1937a, 1937b. **Larva;** present work.

Paroxyna solidaginis. **Br;** *Solidago virgaurea.*

Platyparea discoidea. **Br;** ? *Campanula latifolia:* **Fn;** *??* *Aegopodium podagraria,* *??* *Tussilago farfara.*

Platyparea poeciloptera. **Br;** *Asparagus officinalis.* **Biology;** Dingler, 1934; Niblett, 1956c; Christenson & Foote, 1960. **Larva;** Lesne, 1913; Vimmer, 1925, 1930, 1931; Dingler, 1934; Balachowsky & Mesnil, 1936; present work.

Rhagoletis alternata. **Br;** *Rosa arvensis, R. canina, R. hugonis* var. *platycantha, R. rubiginosa, R. villosa:* **Fn;** ? *Rosa pimpinellifolia,* *??* *Lonicera xylosteum,* *??* *Prunus avium.* **Biology;** Niblett, 1956c, Persson, 1963. **Larva;** Klein-Krautheim, 1937; Persson, 1963; Kandybina, 1961, 1977; Dirlbek, 1970; present work.

Rhagoletis meigenii. **Fn;** *Berberis vulgaris.* **Larva;** Mik, 1887; Vimmer, 1925; Kandybina, 1961, 1977.

***Sphenella marginata*. Br;** *Senecio aquaticus, S. erucifolius, S. jacobaea, S. viscosus, S. vulgaris:* **Fn;** *Senecio erraticus, S. sylvaticus,* ? *S. paludosus,* ? *S. squalidus,* ?? *Calendula arvensis,* ?? *Carthamus lanatus,* ?? *Centaurea paniculata,* ?? *Tanacetum* sp. **Biology;** Niblett, 1950b, 1956c. **Larva;** Efflatoun, 1927; de Vos-de Wilde, 1935; Dirlbek, 1970; present work.

***Tephritis bardanae*. Br;** *Arctium lappa, A. minus:* **Fn;** *Arctium nemorosum, A. tomentosum.* **Biology;** Niblett, 1956c; Chandler & Speight, 1982. **Larva;** Janzon, 1984a; present work.

***Tephritis cometa*. Br;** *Cirsium arvense:* **Fn;** *Cirsium vulgare,* ?? *Arnica montana,* ?? *Doronicum* sp. **Biology;** Hering, 1934, 1937b, 1937c; Niblett, 1956c. **Larva;** Hering, 1937c; present work.

***Tephritis conura*. Br;** *Cirsium helenioides, C. palustre:* **Fn;** *Cirsium acaulon, C. oleraceum,* ? *C. vulgare.* **Biology;** Janzon, 1984b; Seitz & Komma, 1984. **Larva;** Janzon, 1984a, 1984b; present work.

***Tephritis formosa*. Br;** *Sonchus arvensis,* ? *S. asper,* ?? *Hypochoeris radicata;* **Fn;** *Sonchus asper, S. oleraceus, S. palustris,* ?? *Crepis capillaris.* On the continent *T. formosa* does not occur on *S. arvensis,* which is the normal host of *T. dilacerata* (Loew). **Biology;** Berube, 1978.

***Tephritis hyoscyami*. Br;** *Carduus acanthoides, C. nutans:* **Fn;** ?? *Cirsium tuberosum* confirmed but probably not normal). **Biology;** Niblett, 1956c. **Larva;** Persson, 1963; Janzon, 1984a; present work.

***Tephritis leontodontis*. Br;** *Leontodon autumnalis, L. hispidus,* ?? *Leucanthemum vulgare:* **Fn;** ?? *Arnica montana,* ?? *Crepis biennis,* ?? *Taraxacum officinale.* **Biology;** Niblett, 1956c; Uffen & Chandler, 1978. **Larva;** Vimmer, 1925; present work.

***Tephritis neesii*. Br;** *Leucanthemum maximum, L. vulgare:* **Fn;** ?? *Crepis virens,* ?? *Leontodon autumnalis,* ?? *Picris hieracioides,* ?? *Taraxacum officinale.* Niblett, 1956c; Janzon, 1980. **Larva;** Janzon, 1980, 1984a.

***Tephritis praecox*. Fn;** *Calendula arvensis,* ?? *Chrysanthemum* sp., ?? *Filago gallica,* ?? *Senecio* sp.

***Tephritis ruralis*. Br;** *Hieracium pilosella.* **Biology;** Niblett, 1956c; Uffen & Chandler, 1978. **Larva;** Janzon, 1984a; present work.

***Tephritis separata*. Fn;** *Picris echioides.*

***Tephritis vespertina*. Br;** *Crepis* sp., *Hypochoeris radicata:* **Fn;** *Picris echioides,* ? *Tragopogon pratensis,* ?? *Centaurea calcitrapa.* **Biology;** Niblett, 1942, 1946a, 1956c; Chandler & Speight, 1982. **Larva;** present work.

***Terellia colon*. Br;** *Centaurea scabiosa:* **Fn;** ?? *Centaurea cyanus,* ?? *Carthamus lanatus,* ?? *C. tinctorius,* ?? *Daucus carrota,* ?? *Picris hieracioides,* ?? *Tragopogon porrifolius.* **Biology;** Niblett, 1936, 1940b, 1942, 1950b, 1955a, 1956c. **Larva;** Vimmer, 1925, 1930; Hendel, 1927; present work.

***Terellia longicauda*. Br;** *Cirsium eriophorum:* **Fn;** ?? *Carduus nutans.* **Biology;** Niblett, 1956a. **Larva;** Dirlbek, 1970; present work.

***Terellia ruficauda*. Br;** *Cirsium arvense, C. dissectum, C. palustre:* **Fn;** *Cirsium acaulon, C. eriophorum, C. oleraceum,* ?? *Carduus acanthoides,* ?? *Serratula tinctoria.* **Biology;** Niblett, 1956c; Kandybina, 1970; Chandler & Speight, 1982; Forsyth & Watson, 1985. **Larva;** Hendel, 1927; Kandybina, 1970; present work.

***Terellia serratulae*. Br;** *Carduus acanthoides, C. nutans, Cirsium vulgare,* ?? *Helianthus annuus* (confirmed but probably not normal): **Fn;** *Carduus pycnocephalus, C. tenuiflorus, Cirsium oleraceum, C. tuberosum.* **Biology;** Niblett, 1956a, 1956c; Chandler & Speight, 1982. **Larva;** present work.

***Terellia vectensis.* Br**; *Serratula tinctoria.* **Biology**; Niblett, 1940b, 1942. **Larva**; present work.

***Terellia winthemi.* Br**; *Carduus acanthoides,* ? *Cirsium eriophorum,* ? *C. palustre:* **Fn**; *Cirsium palustre,* ?? *Centaurea jacea.* **Biology**; Niblett, 1956c. **Larva**; present work.

***Trupanea amoena.* Fn**; *Calendula officinalis, Carthamus tinctorius, Centaurea* sp., *Lactuca serriola, Picris* sp., *Sonchus asper, S. oleraceus,* ? *Achillea millefolium,* ? *Centaurea calcitrapa,* ? *Chrysanthemum segetum,* ? *Lactuca saligna,* ? *L. sativa,* ? *L. virosa,* ? *Picris hieracioides,* ? *Sonchus arvensis.* **Biology**; Hering, 1937a. **Larva**; Efflatoun, 1927; Trehan, 1947; present work.

***Trupanea stellata.* Br**; *Hieracium* (section *murorum*) sp., *Inula crithmoides, Senecio erucifolius, S. jacobaea, S. squalidus:* **Fn**; *Anthemis arvensis, A. cotula, Artemisia absinthium, Calendula officinalis, Carthamus tinctorius, Chamomilla recutita, Matricaria perforata, Serratula tinctoria, Tripleurospermum maritimum,* ? *Aster tripolium,* ? *Bellis perennis,* ? *Centaurea cyanus,* ? *C. montana,* ? *C. scabiosa,* ? *Chrysanthemum* sp., ? *Crepis paludosa,* ? *Dittrichia viscosa,* ? *Erigeron* sp., ? *Eupatorium cannabinum,* ? *Hieraceum maculatum,* ? *H.* (section *sabaudum*) sp., ? *Inula britannica,* ? *Picris hieracioides,* ? *Senecio paludosus,* ? *S. vulgaris,* ? *Tanacetum parthenium.* **Biology**; Niblett, 1956c. **Larva**; Efflatoun, 1927; present work.

***Trypeta artemisiae.* Br**; *Achillea ptarmica, Artemisia* sp., *Chrysanthemum* (glasshouse) sp., *Eupatorium cannabinum, Senecio* sp., *Tanacetum vulgare;* **Fn**; ? *Artemisia absinthium,* ? *A. vulgaris,* ? *Leucanthemum vulgare,* ? *Senecio vulgaris,* ? *Tanacetum parthenium,* ? *T. vulgare.* **Biology**; Vimmer, 1931. **Larva**; present work.

***Trypeta immaculata.* Br**; *Taraxacum* sp.: **Fn**; *Crepis* sp., *Hieracium* sp., *Hypochoeris* sp., *Lapsana* sp., *Leontodon, Mycelis* sp., *Sonchus* sp., ? *Senecio vulgaris.* **Biology**; Chandler & Speight, 1982. **Larva**; present work.

***Trypeta zoe.* Br**; *Artemisia* sp., *Aster* (garden) sp., *Chrysanthemum* (glasshouse) sp., *Eupatorium cannabinum, Leucanthemum maximum, Petasites* sp., *Senecio erucifolius, S. jacobaea, S. squalidus, S. vulgaris, Tussilago farfara,* ? *Tanacetum parthenium,* ?? *Phlox* sp. — *Polemoniaceae* (confirmed but probably not normal): **Fn**; *Artemisia absinthium, A. vulgaris, Lactuca* sp., *Solidago virgaurea,* ? *Achillea* sp., ? *Arctium lappa,* ? *Doronicum* sp., ? *Helianthus tuberosus,* ? *Leucanthemum vulgare,* ? *Matricaria* sp., ? *Mycelis muralis,* ? *Petasites albus,* ? *Senecio integrifolius,* ? *Tussilago* sp. **Biology**; Vimmer, 1931; Hering, 1936c; Niblett, 1956c, 1957; Chandler & Speight, 1982. **Larva**; Hendel, 1927; Vimmer, 1930; de Vos-de Wilde, 1935; present work.

***Urophora cardui.* Br**; *Cirsium arvense:* **Fn**; ?? *Artemisia vulgaris.* **Biology**; Hering, 1936c; Niblett, 1956c; Peschken & Harris, 1975; Zwölfer, 1979, 1982; Lalonde & Shorthouse, 1982, 1984; Seitz, 1982; Peschken, 1984; Seitz & Komma, 1984; Rotheray, 1986. **Larva**; Mik, 1897; Vimmer, 1925, 1930; Varley, 1937; present work.

***Urophora cuspidata.* Br**; *Centaurea scabiosa:* **Fn**; ?? *Centaurea calcitrapa,* ?? *C. jacea,* ?? *C. montana,* ?? *C. nigra.* **Biology**; Niblett, 1955a. **Larva**; present work.

***Urophora jaceana.* Br**; *Centaurea nigra,* ? *C. debeauxii:* **Fn**; *Centaurea debeauxii, C. jacea,* ?? *C. solstitialis.* **Biology**; Hering, 1935a, 1936c; Varley, 1937, 1947; Niblett, 1956c. **Larva**; Wadsworth, 1914 (as *U. solstitialis*); Mouchet, 1929 (as *U. solstitialis*); Varley, 1937; present work.

***Urophora quadrifasciata.* Br**; *Centaurea nigra,* ? *C. debeauxii:* **Fn**; *Centaurea aspera, C. cyanus, C. calcitrapa, C. debeauxii, C. jacea, C. scabiosa, C. solstitialis, Serratula tinctoria,* ? *C. paniculata,* ?? *Arctium lappa,* ?? *Echinops rito,* ?? *Medicago sativa.* **Biology**; Varley, 1937; Niblett, 1940b, 1942, 1950b, 1955a, 1956c; Harris & Myers, 1984. **Larva**; Varley, 1937; present work.

***Urophora solstitialis.* Fn**; *Carduus nutans, C. pycnocephalus,* ?? *Achillea millefolium,* ?? *Cirsium vulgare,* ?? *Centaurea nigra:* **Fn**; *Carduus acanthoides,* ?? *Carlina vulgaris,* ?? *Carthamus lanatus,* ?? *Centaurea jacea,* ?? *C. montana,* ?? *C. scabiosa.* **Biology**; Niblett, 1956c; Persson, 1963; Zwölfer, 1979. **Larva**; Goureau, 1845 (as *U. cuspidata*); Mellini, 1952; Persson, 1963; present work.

Urophora spoliata. **Br;** *Serratula tinctoria.* **Biology;** Niblett, 1940b.

Urophora stylata. **Br;** *Cirsium arvense, C. palustre, C. vulgaris,* ? *Carduus nutans:* **Fn;** *Cirsium eriophorum,* ? *Carduus acanthoides,* ? *C. pycnocephalus,* ?? *Carthamus lanatus,* ?? *Centaurea calcitrapa,* ?? *Centaurea scabiosa,* ?? *Cnicus* sp., ?? *Dittrichia viscosa,* ?? *Xanthium spinosum.* **Biology;** Niblett, 1956c; Persson, 1963; Redfern, 1968; Kandybina, 1970; Cameron & Redfern, 1974; Harris & Wilkinson, 1984. **Larva;** Varley, 1937; Persson, 1963; Kandybina, 1970; present work.

Vidalia cornuta. **Br;** *Eupatorium cannabinum:* **Fn;** *Senecio nemorensis* (a non-British plant, but the only other confirmed host); ? *Petasites* sp., ? *Tussilago* sp. **Biology;** Hering, 1936c. **Larva;** present work.

Vidalia spinifrons. **Br;** *Aster* (garden) sp., *Solidago virgaurea:* **Fn;** ?? *Cirsium palustre.* **Biology;** Niblett, 1956c, 1957; Hering, 1927. **Larva;** present work.

Xyphosia miliaria. **Br;** *Cirsium arvense, C. palustre,* ? *C. eriophorum,* ?? *Arctium lappa,* ?? *Centaurea nigra* (specimen confirmed, but unlikely to be a normal host): **Fn;** *Carduus acanthoides, C. nutans, Cirsium eriophorum, C. oleraceum, C. vulgare,* ?? *Arctium lappa,* ?? *Leucanthemum vulgare,* ?? *Sonchus* sp. **Biology;** Hering, 1937a; Niblett, 1942, 1956c; Persson, 1963; Kandybina, 1970. **Larva;** Persson, 1963; Kandybina, 1970; present work.

Appendix II: Plants and their associated tephritids

The host genera of British tephritid species are listed under plant family, arranged alphabetically. Because of the large number of composite (Asteraceae) associated species, genera of Asteraceae are arranged according to the classification used in *Flora Europaea* (Moore, Tutin & Walters, 1976). Oligophagous species are named against the higher group to which they are restricted, rather than being named against each genus, e.g. *Acanthiophilus helianthi* appears to be able to live on any species of Cardueae, so it is listed against the name of that tribe rather than against every genus it happens to have been recorded from. Furthermore, atypical host records are omitted from this list, e.g. *Urophora stylata* normally only lives on *Cirsium vulgare;* records of it on other *Cirsium* and *Carduus* species are not listed here as they would be confusing to anyone using this list to help identify a tephritid reared from a *Carduus* species. Consequently, this list is not simply the reverse of the more comprehensive host-plant catalogue given in Appendix I. In a few cases the British host-plant range appears to be more restricted than elsewhere, e.g. in Britain *Trupanea stellata* is usually found only on *Senecio* species, but elsewhere it inhabits a wide range of composites; this is indicated by '(in Brit.)' and '(non.Brit.)' respectively.

The following abbreviations are used: b — brood parasite in the gall of *Pontania;* c — living in the capitulum; f — in fruit; lm — leaf-miner; rt — root or stem-base borer; st — stem-borer; g — used as a suffix for any gall formation.

DICOTYLEDONEAE

APIACEAE (= Umbelliferae)	lm	*Cryptaciura rotundiventris*
	lm	*Euleia heracleii*
ASTERACEAE (= Compositae)	c	*Ensina sonchi*
	c	*Trupanea amoena*
	c	*Trupanea stellata* (non.Brit.)
ASTEROIDEAE	lm	*Trypeta artemisiae*
	lm	*Trypeta zoe*
	lm	*Vidalia cornuta*
EUPATORIEAE		
Eupatorium	lm	*Trypeta zoe* (usual host)

ASTEREAE	lm	*Vidalia spinifrons*
Solidago	stg	*Campiglossa grandinata*
	c	*Paroxyna loewiana*
	?	*Paroxyna solidaginis*
Aster	c	*Paroxyna plantaginis*
INULEAE		
Inula	cg	*Myopites eximia*
Pulicaria	cg	*Myopites inulaedyssentericae*
HELIANTHEAE		
Bidens	c	*Dioxyna bidentis*
ANTHEMIDEAE		
Achillea		
A. millefolium	stg	*Dithryca guttularis*
	rtg	*Oxyna flavipennis*
A. ptarmica	cg	*Campiglossa argyrocephala*
Leucanthemum	rtg	*Oxyna nebulosa*
	c	*Tephritis neesii*
Artemisia	st	*Oxyna parietina*
	c	*Paroxyna absinthii*
	stg/c	*Paroxyna misella*
SENECIONEAE		
Tussilago	lm	*Acidia cognata*
Petasites	lm	*Acidia cognata*
Senecio	c	*Icterica westermanni*
	c	*Sphenella marginata*
	c	*Trupanea stellata* (in Brit.)
CARDUEAE	c	*Acanthiophilus helianthi*
	c	*Chaetostomella cylindrica* (non.Brit.)
Arctium	c	*Cerajocera tussilaginis*
	c	*Tephritis bardanae*
Carduus	c	*Tephritis hyoscyami*
	c	*Terellia serratulae*
	cg	*Urophora solstitialis*
C. acanthoides	c	*Terellia winthemi*
Cirsium		
C. arvense	c	*Tephritis cometa*
	c	*Terellia ruficauda*
	stg	*Urophora cardui*
	c	*Xyphosia miliaria*
C. eriophorum	c	*Terellia longicauda*
C. helenioides	c	*Tephritis conura*
C. palustre	c	*Tephritis conura*
	c	*Terellia ruficauda*
	c	*Xyphosia miliaria*
C. vulgare	c	*Terellia serratulae*
	cg	*Urophora stylata*
Serratula	c	*Terellia vectensis*
	c?g	*Urophora spoliata*
Centaurea	c	*Urophora quadrifasciata* (non.Brit.)
C. nigra group	c	*?Acinia corniculata*
	c	*Chaetorellia jaceae*
	c	*Chaetostomella cylindrica* (in Brit.)
	cg	*Urophora jaceana*
	cg	*Urophora quadrifasciata* (in Brit.)
C. scabiosa	c	*Cerajocera ceratocera*
	st	*Cerajocera plagiata*
	c	*Chaetorellia loricata*
	c	*Terellia colon*
	cg	*Urophora cuspidata*

CICHORIOIDEAE		c	*Paroxyna producta*
		lm	*Trypeta immaculata*
Hypochoeris		c	*Tephritis vespertina*
Leontodon		c	*Tephritis leontodontis*
Tragopogon		rt	*Orellia falcata*
Sonchus		c	*Tephritis formosa*
Hieracium		c	*Noeeta pupillata*
		c	*Tephritis ruralis*
BERBERIDACEAE			
Berberis		f	*Rhagoletis meigenii*
CAMPANULACEAE			
Campanula		?st	*?Platyparea discoidea*
CUCURBITACEAE			
Bryonia		f	*Goniglossum wiedemanni*
ROSACEAE			
Crataegus		f	*Anomoia purmunda*
Rosa		f	*Rhagoletis alternata*
SALICACEAE			
Salix		b	*Euphranta toxoneura*

MONOCOTYLEDONEAE

| LILIACEAE | | | |
| *Asparagus* | | st | *Platyparea poeciloptera* |

Appendix III: Life history data

The following table summarises knowledge of the life-history of tephritids in Britain. The data were extracted from the 'biology' references given in **Appendix I**, collections, and manuscript notes by M. Niblett belonging to the **British Museum** (Natural History).

Column 1 — Name with genus abbreviated; see check list on page 23 for full names.

Column 2 — Number of generations per year. Species which have been known to have partial carry-over to a second or third year are marked as having 0·5 or 0·33 generations per year.

Column 3 — Larvae develop in; C = capitulum; CG = capitulum gall; CS = capitulum swollen; F = fruit; B = brood parasite in the leaf gall of a sawfly; L = leaf-mine; RT = root borer; RTG = root gall; S = stem-mine; SB = stem-base mine; SBG = stem-base gall; SG = stem gall.

Column 3 — Further details, when known, are given in parenthesis after the above codes; A = achenes; O = ovary (from which the achene later develops); R = receptacle; ST = top of stem, next to receptacle.

Column 4 — Pupa in; H = host; S = soil. A 'P' in parenthesis indicates that a cocoon is formed of pappus hairs.

Column 5 — Overwintering stage; A = adult; L = larva; P = pupa.

Column 6 — Recorded months as larvae for individuals developing from the previous calendar year's eggs.

Column 7 — Recorded months of emergence for individuals developing from the previous calendar year's eggs. Figures in parenthesis are for individuals passing a second winter before emergence. In a few cases the earliest date may be unnaturally early due to emergence having been accelerated in a warm room; records which were obviously unnaturally early were not accepted for the table.

Column 8 — Recorded months as larvae for individuals completing development from egg to adult within the same calendar year.

Column 9 — Recorded months of emergence for individuals completing development from egg to adult within the same calendar year.

* — against an insect name indicates that some non-British life-cycle data were used.

? — data not available; if used in front of a table entry, the entry was estimated from known facts about the species or its relatives and confirmation is needed.

Note that *Paroxyna misella* has two generations per year, one spent gregariously in a unilocular stem gall at the stem top of *Artemisia vulgaris*; the other with solitary larvae in the capitulum of *A. vulgaris* (Uffen & Chandler, 1978).

Adults of most species continue to be active for one or two months after emergence; species which overwinter as adults can be found as adults throughout most of the year.

MYOPITINAE

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ. gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
M. eximia	0.5–1	CG(R + A)	H	?L	?	8–9(6–7)	—	—
M. inulaedyssentericae	0.5–1	CG(R + A)	H	L	8–6	8–9(6–7)	—	—
U. cardui	1	SG	H	L	7–4	5–7	—	—
U. cuspidata	1	CG(R)	H	L	?8–5	5–7	—	—
U. jaceana	1	CG(R)	H	L	7–4	5–7	—	—
U. quadrifasciata	2	CG(O)	H	L	9–3	5–7	7–8	7–8
U. solstitialis	1	CG(R)	H	L	8–4	5–6	—	—
U. spoliata	?1	?CG	?H	?L	?	6–7	—	—
U. stylata	1	CG	H	L	8–4	5–7	—	—

TRYPETINAE (fruit feeding and inquiline larvae)

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ.gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
A. purmunda	1	F	S	P	9–10	4–6	—	—
C. curvinerve	?1	?F	?S	?P	?	?	—	—
E. toxoneura	?1	B	?S	?P	?	?5–6	—	—
G. wiedemanni	1	F	S	P	8–9	5–6	—	—
R. alternata	1	F	S	P	9–10	4–6	—	—
*P. meigenii	?1	F	?S	?P	?	?	—	—

TRYPETINAE (leaf- and stem-mining larvae)

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ.gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
A. cognata	1	L	S	P	10–11	5–6	—	—
C. rotundiventris	?	L	?S	?P	?	?6	—	—
E. heracleii	2	L	S	P	?	?5–6	6–7	7–8
M. caesio	?	?L	?S	?P	?	?7	?	?
P. discoidea	?	S	?	?P	?	?	?	?
*P. poeciloptera	1	S	H	?P	8–?	6–7	—	—
T. artemisiae	?1	L	?S	?P	?	?6	—	—
T. immaculata	?1	L	H	P	10	5	—	—
T. zoe	1–2	L	S	P/A	9	4–5	5–7	6–8
V. cornuta	?1	L	?S	?P	?	?	—	—
V. spinifrons	?1	L	S	P	?	4	—	—

TERELLIINI

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ.gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
C. ceratocera	1	C(R)	H/S	P/A	7–9	6–7	—	—
C. plagiata	1	S	H	L	9–3	6–7	—	—
C. tussilaginis	1	C(A)	H	L	8–3	5–7	—	—
C. jaceae	1–2	C(R)	H	L	?	6–7	?7–8	8
C. loricata	2	C(?R)	H	L	?	6	?7	7–8
C. cylindrica	1–2	C	H	L	?	5–6	?6–7	7
O. falcata	1	RT/SB	H	P	7–11	5–6	—	—
T. colon	1–2	C(?R)	H(P)	L	9–5	5–7	7–8	7–8
T. longicauda	1	C	H	?L	?	6–7	—	—
T. ruficauda	1	C(R+ST)	H(P)	L	7–3	5–7	—	—
T. serratulae	1	C	H(P)	L	8–4	6–7	—	—
T. vectensis	0.33–1	C	H	?L	?	5–7	—	—
T. winthemi	1	C	H	L	7–3	5–7	—	—

DITHRYCINI

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ.gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
D. guttularis	?1	SBG	H	?	7	7–8	—	—
N. pupillata	2	CS	H	?P	8–11	4–6	7–8	7–9

TEPHRITINI

1	2	3	4	5	6	7	8	9
					Winter gen.		Summ. gen.	
Name	Gen.	Larv.in	Ppin	Wnt	Ml	emerg	Ml	emerg
*A. helianthi	?	C	H	?	?	?	?	?
*A. corniculata	?1	C	?H	?	?	?	—	—
C. argyrocephala	?1	CG	?H	?	?	7	—	—
*C. grandinata	?1	SG	?H	?	?	?	—	—
D. bidentis	?1	C	H	A	—	—	8–9	8–9

Name	Gen.	Larv.in	Ppin	Wnt	Winter gen.		Summ.gen.	
					Ml	emerg	Ml	emerg
E. sonchi	?2	C	H	?	?	?	6–9	6–9
*I. westermanni	?1	C	?H	?	?	?7	—	—
O. flavipennis	1	RTG	?H	?	6–7	7	—	—
*O. nebulosa	?1	RTG	?H	?	?	?	—	—
O. parietina	1	S	H	L	9–3	4–6	—	—
P. absinthii	?1	C	S	?	?	?	—	—
P. lhommei	?1	?	?	?	?	?7	—	—
P. loewiana	1	C	H/S	P	9–10	5–6	—	—
P. misella Gen. 1	—	SG	H	?A	6–7	6–7	—	—
P. misella Gen. 2	—	C(A)	H	—	—	—	?7	?8–10
P. plantaginis	1	C	H	P	9–10	5–7	—	—
*P. producta	?	C	H	?	?	?	?	?
P. solidaginis	?1	C	?	?	?	?	—	—
S. marginata	?1	CS	H	?	—	—	7–9	7–9
T. bardanae	1	C(A)	H	A	—	—	7–8	8–10
T. cometa	1	C	H	A	—	—	7–8	8
*T. conura	1	C	H	A	—	—	6–7	8
*T. formosa	?1	CS	?H	?A	—	—	?	?
T. hyoscyami	1	C	H	A	—	—	6–7	7–8
T. leontodontis	?1	C/ST	H	A	—	—	?	?
T. neesii	1	C	H	A	—	—	6–7	6–8
*T. praecox	?1	C	?H	?A	—	—	?	?
T. ruralis	?1	CS	H	A	—	—	?	?
*T. separata	?1	C	?H	?A	—	—	?	?
T. vespertina	2	C	H	A	—	—	5–8	6–8
*T. amoena	?1	C	H(P)	?	—	—	?	?
T. stellata	1	C	?H	?	—	—	8	8–9
X. miliaria	2	C	H(P)	L	?9–3	5–7	?7–9	7–9

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Note added in proof—a reference to the biology of *Myoleja caesio* was overlooked during the compilation of this *Handbook*. Ferrar (1987) notes that Beiger (1968) reared *M. caesio* from mines in the petioles of an *Urtica* sp. (Urticaceae). The larva is described as having 19–20 anterior spiracle lobes, a number typical of stem- and leaf-mining Trypetini.

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74

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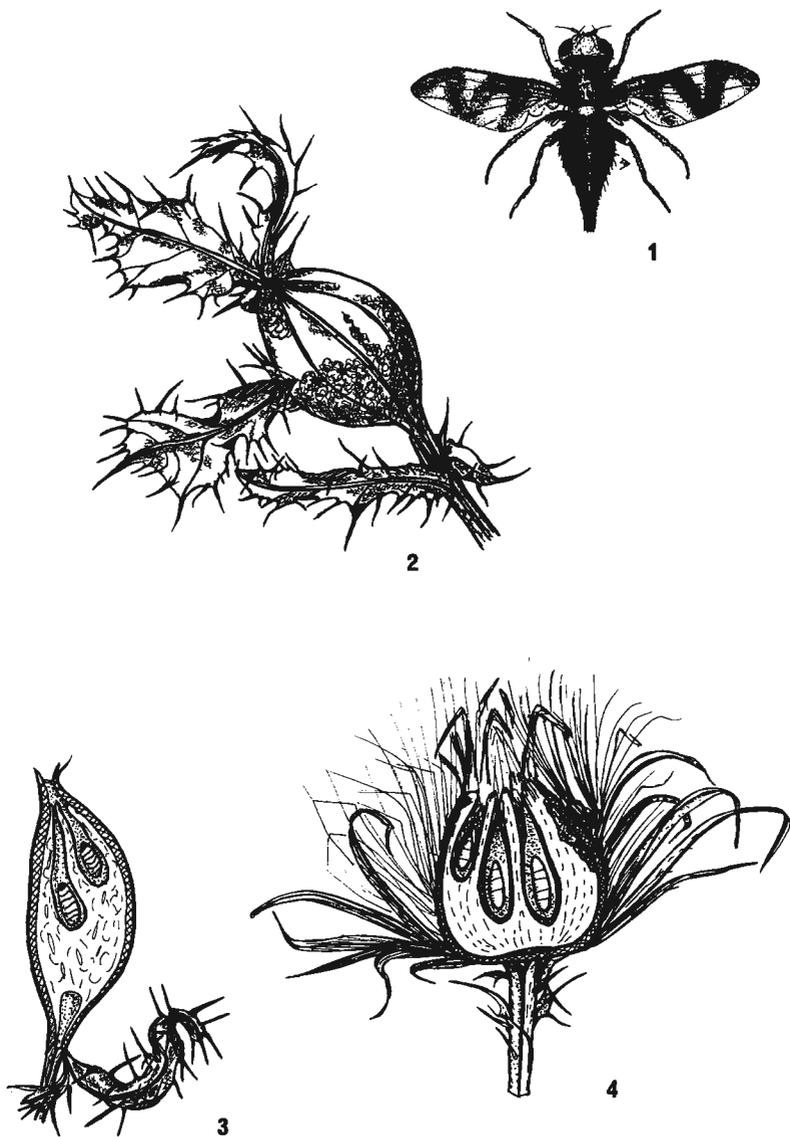
Figs 1–4. Myopitinae. 1, *Urophora cardui,* female. 2–4, galls. 2, *Urophora cardui* stem gall on *Cirsium arvense,* 3, *U. cardui,* section through gall, 4, *U. stylata,* section through gall on *C. vulgare.*
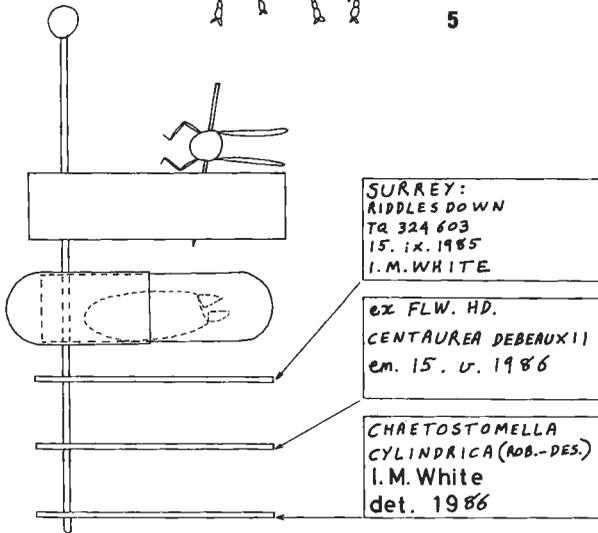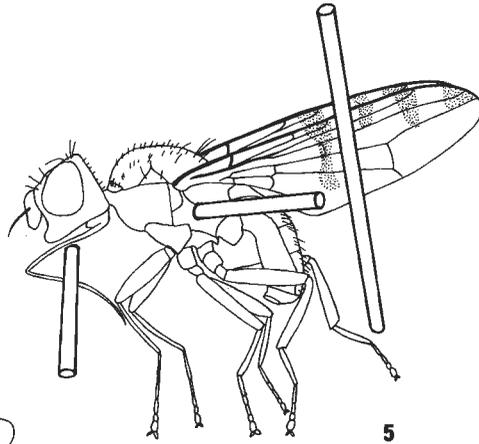
Figs 5–6. Tephritidae; setting and staging. 5, setting a tephritid, with a pin placed through the side of the thorax and pins to temporarily hold the wings and mouthparts, 6, staging and labelling a pinned specimen.
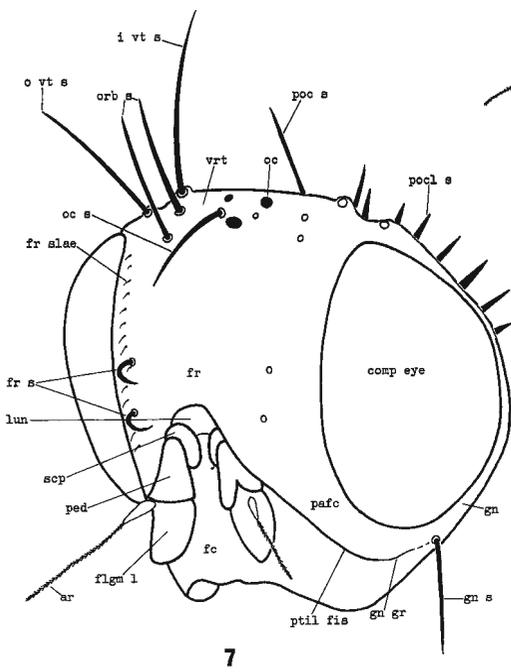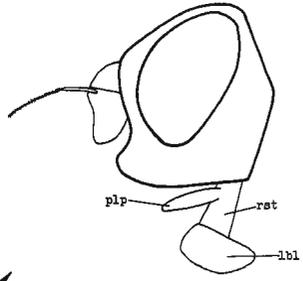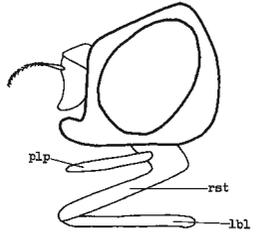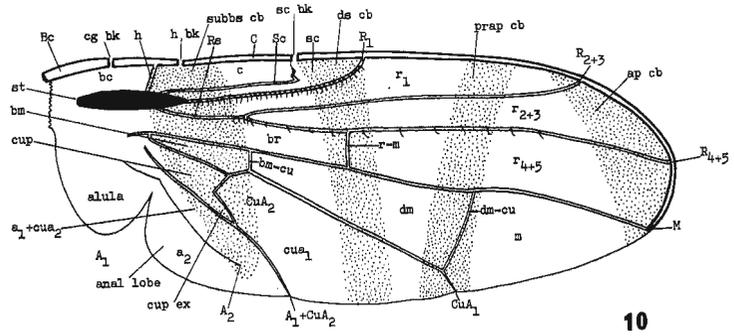
Figs 7–10. Tephritidae; head and wing. 7, head, 8, mouthparts, 9, geniculate mouthparts, 10, wing veins, cells and crossbands. Abbreviations are listed on p. 17 and p. 18.
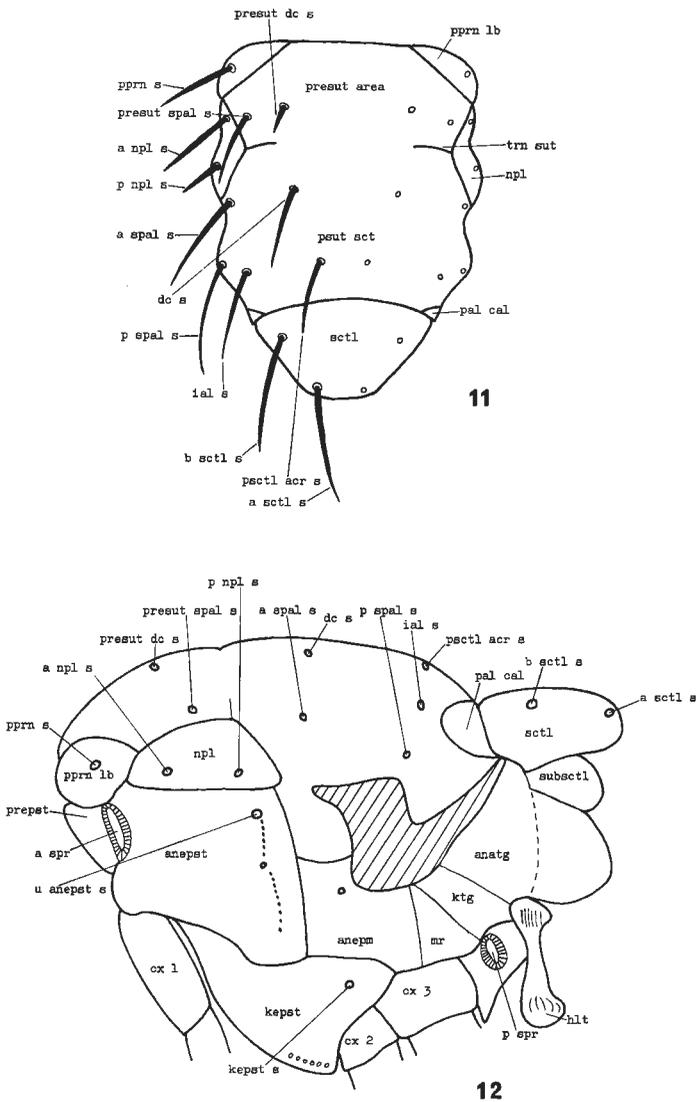
Figs 11–12. Tephritidae; thorax. 11, thorax, dorsal features, 12, thorax, lateral features. Abbreviations are listed on p. 18.
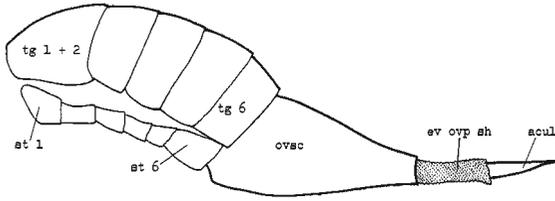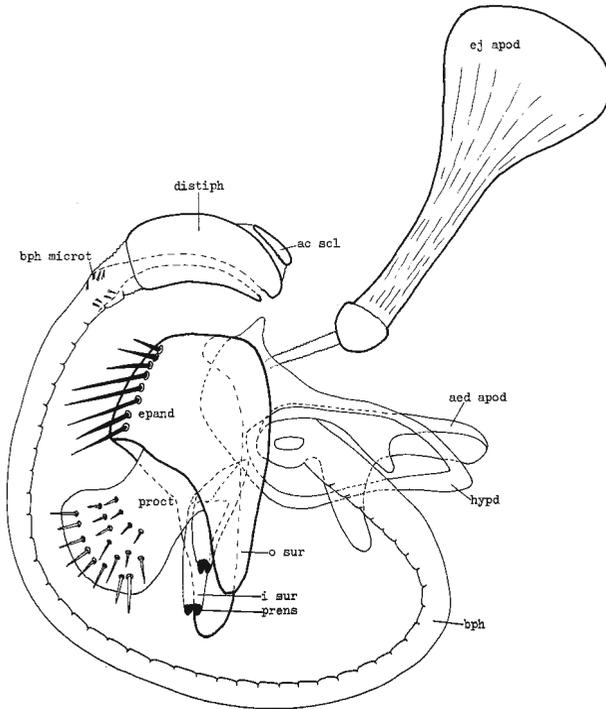
Figs 13–14. Tephritidae; abdomen and terminalia. 13, abdominal segmentation and female terminalia, 14, male terminalia. Abbreviations are listed on p. 18.
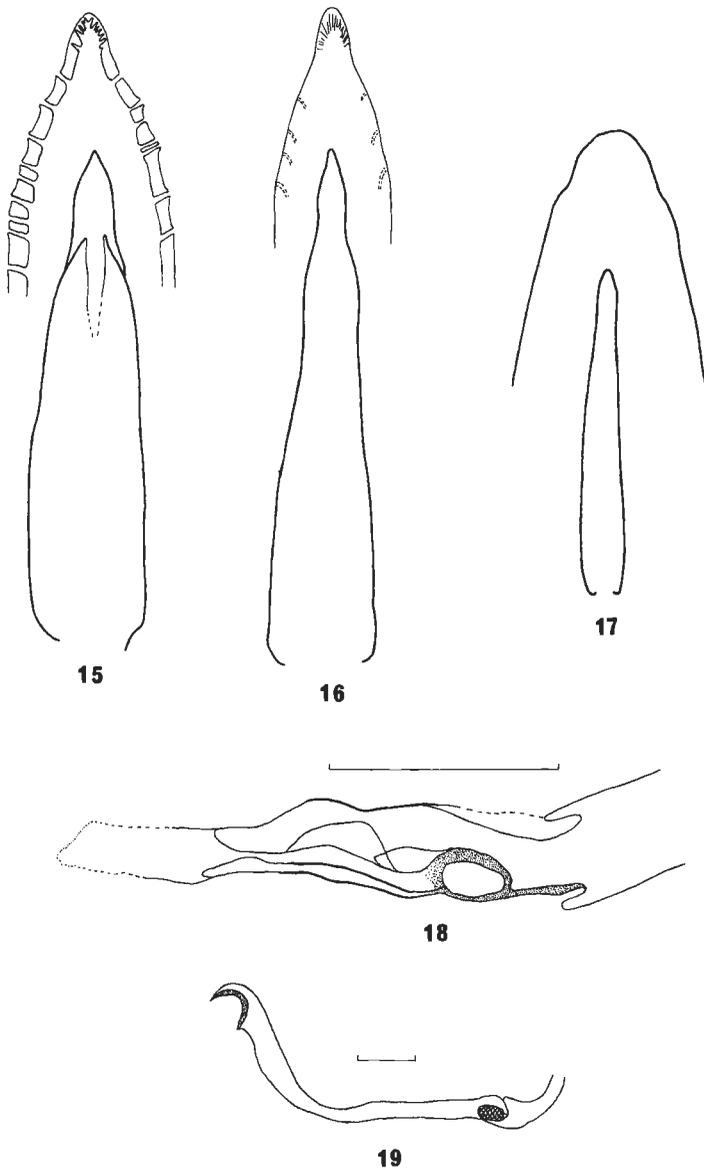
Figs 15–19. Myopitinae. 15–17, aculeus, dorsoventral outline with detail of apex. 15, *Myopites eximia*, 16, *M. inulaedyssentericae*, 17, *Urophora*, indet.sp. 18–19, distiphallus. 18, *Urophora solstitialis* (other *Urophora* species are similar). 19, *M. eximia* (*M. inulaedyssentericae* is very similar). Scale lines = 0·1 mm.
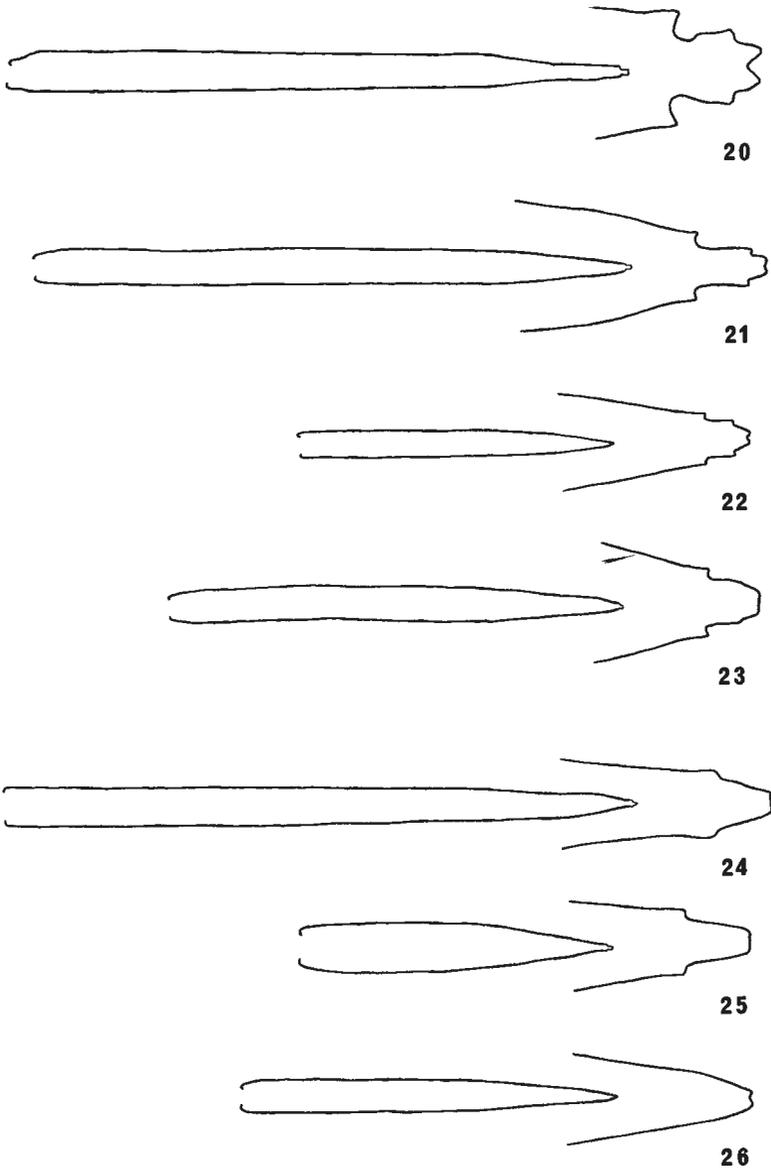
Figs 20–26. Myopitinae; *Urophora* aculeus, dorsoventral outline with detail of apex. 20, *U. cuspidata*, 21, *U. solstitialis*, 22, *U. spoliata*, 23, *U. jaceana*, 24, *U. stylata*, 25, *U. cardui*, 26, *U. quadrifasciata*.
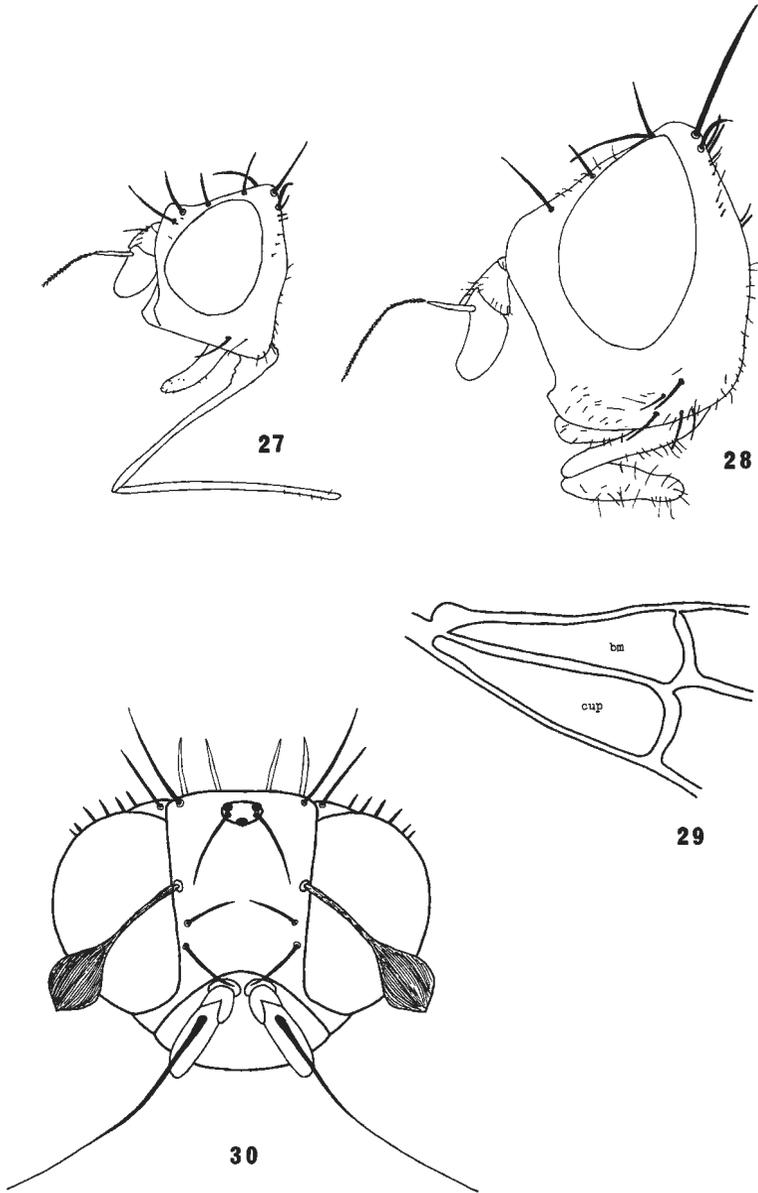
Figs 27–30. Myopitinae and Ceratitini. 27, *Myopites inulaedyssentericae*, head profile (*M. eximia* is similar). 28, *Urophora cardui*, head profile (other *Urophora* species are similar). 29, *U. quadrifasciata*, cell cu*p* shape. 30, *Ceratitis capitata* ♂, head, dorsal view.
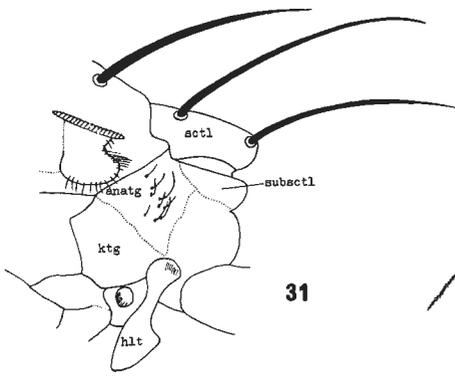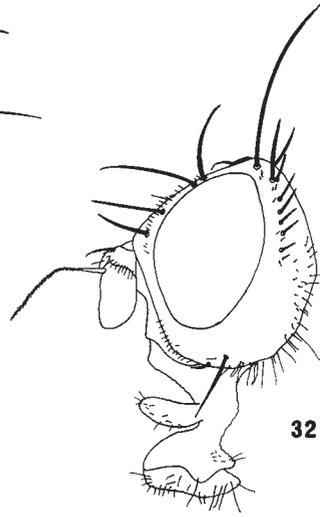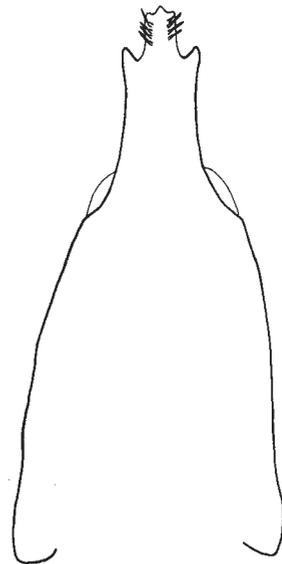
Figs 31–34. Euphrantini; *Euphranta toxoneura*. 31, anatergite. 32, head profile. 33, distiphallus. 34, aculeus, dorsoventral outline. Scale line = 0·1 mm. *anatg*, anatergite. *hlt*, halter, *ktg*, katatergite. *sctl*, scutellum. *subsctl*, subscutellum.
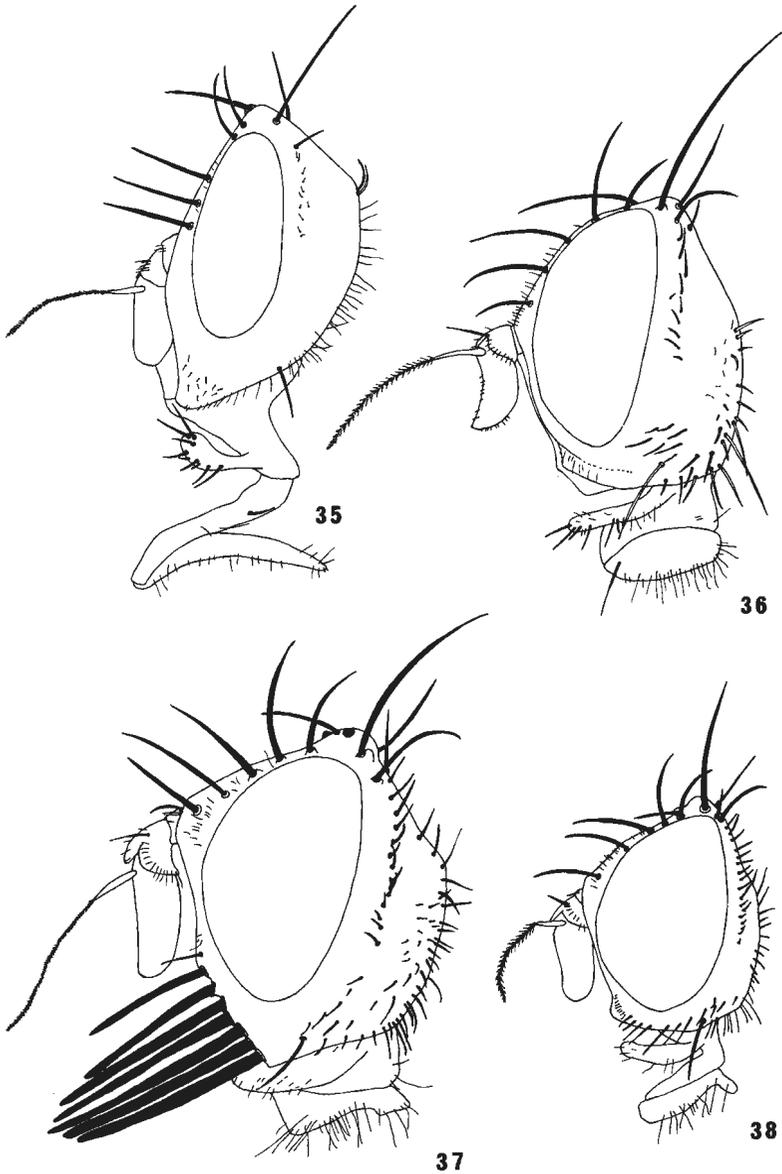
Figs 35–38. Trypetini (frugivorous species); head profile. 35, *Goniglossum wiedemanni,* 36, *Rhagoletis alternata* (*R. meigenii* is similar), 37, *Chetostoma curvinerve,* 38, *Anomoia purmunda.*
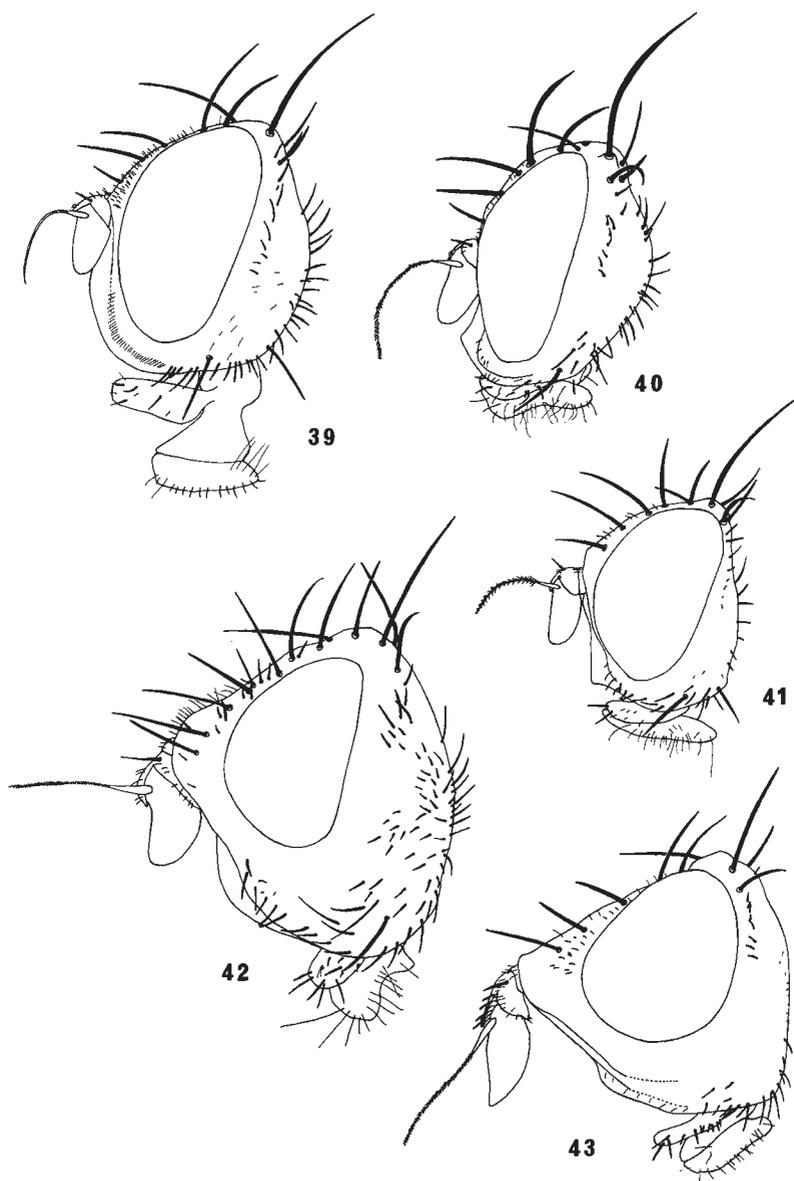
Figs 39–43. Trypetini (leaf-mining and stem-boring species); head profile. 39, *Euleia heracleii,* 40, *Cryptaciura rotundiventris,* 41, *Myoleja caesio,* 42, *Platyparea discoidea,* 43, *P. poeciloptera.*
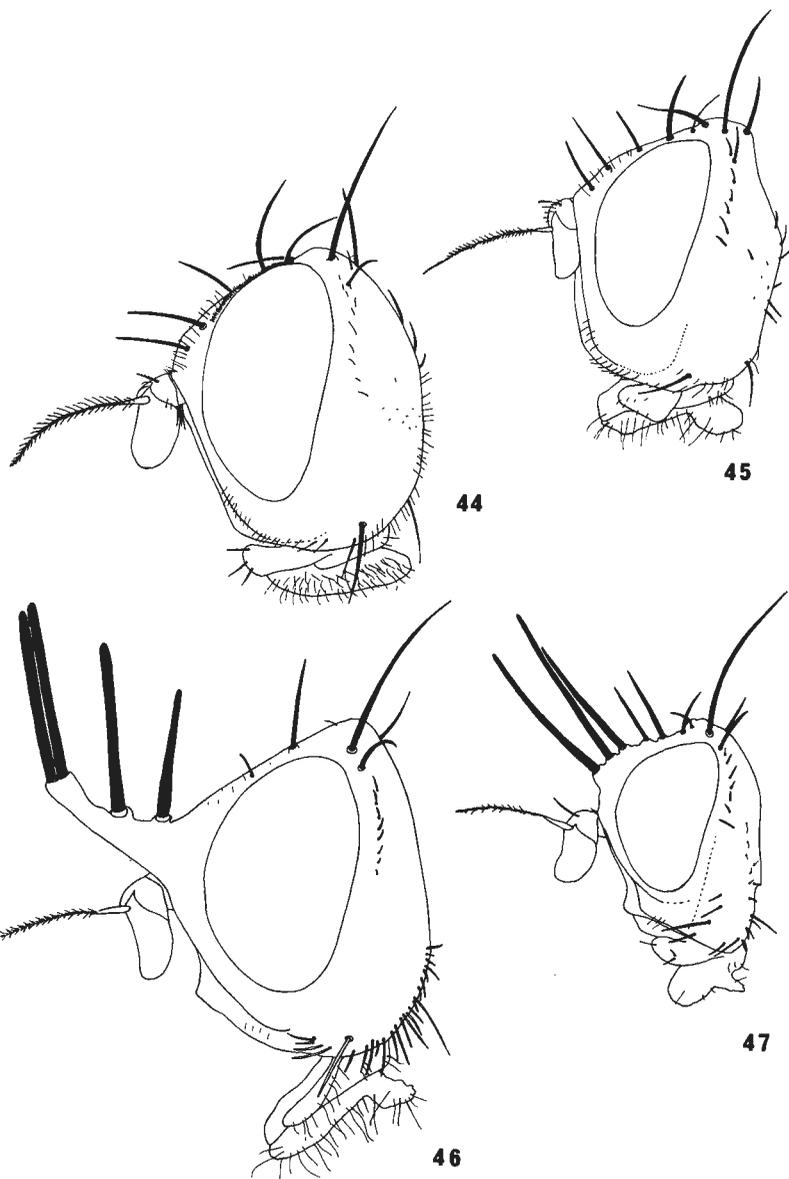
Figs 44–47. Trypetini (leaf-mining species); head profile. 44, *Acidia cognata*, 45, *Trypeta artemisiae* (other *Trypeta* and ♀ *Vidalia* species are similar), 46, *Vidalia cornuta* ♂, 47, *V. spinifrons* ♂.
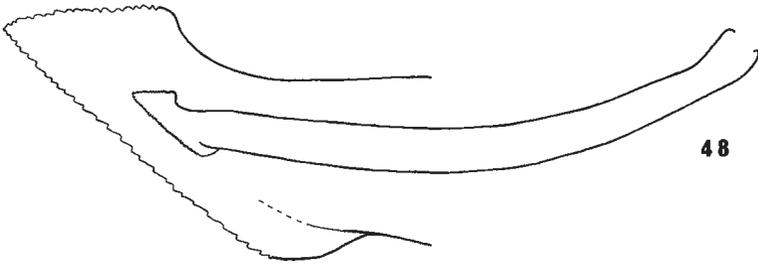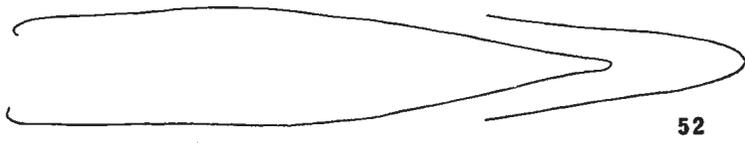
Figs 48–53. Trypetini (frugivorous species); aculeus. 48, *Chetostoma curvinerve*, lateral view with detail of apex. 49, *A. purmunda*, lateral view of apex. 50–53, aculeus, dorsoventral outline with detail of apex. 50, *Anomoia purmunda*, 51, *Goniglossum wiedemanni*, 52, *Rhagoletis alternata*, 53, *R. meigenii*.
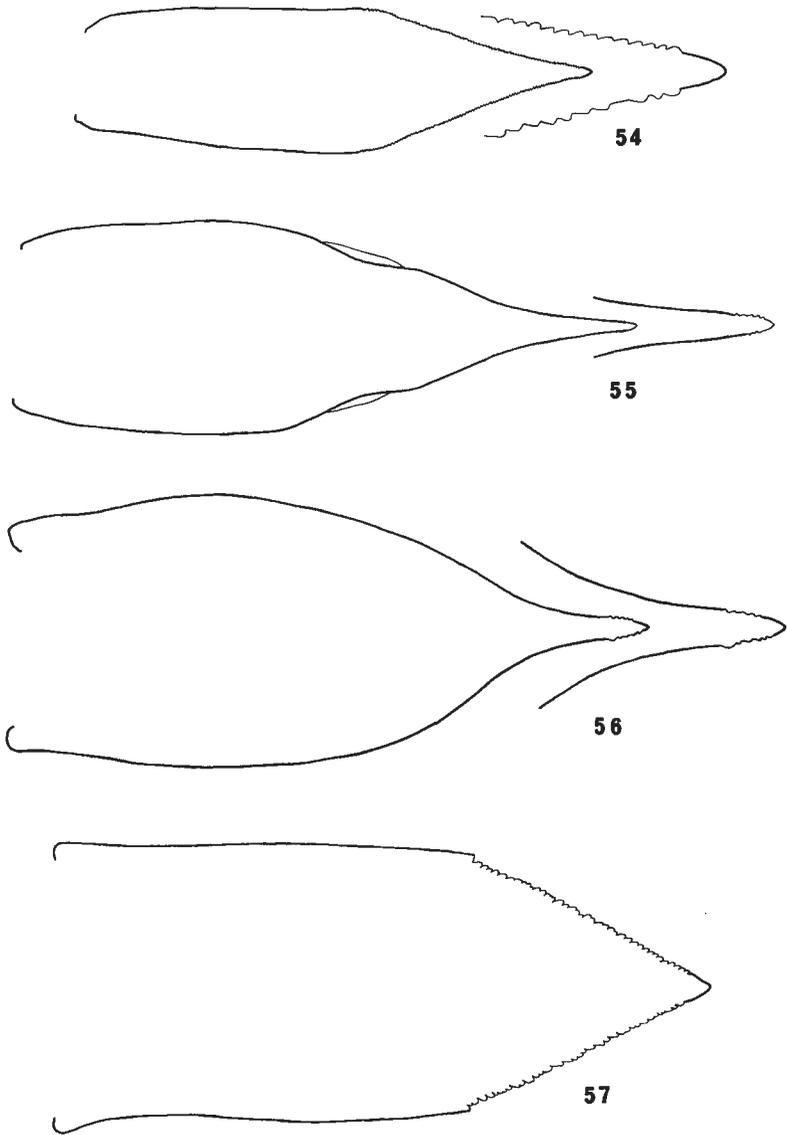
Figs 54–57. Trypetini (leaf-mining species); aculeus, dorsoventral outline. 54–56, with detail of apex. 54, *Acidia cognata*, 55, *Cryptaciura rotundiventris*, 56, *Euleia heracleii*, 57, *Myoleja caesio*.
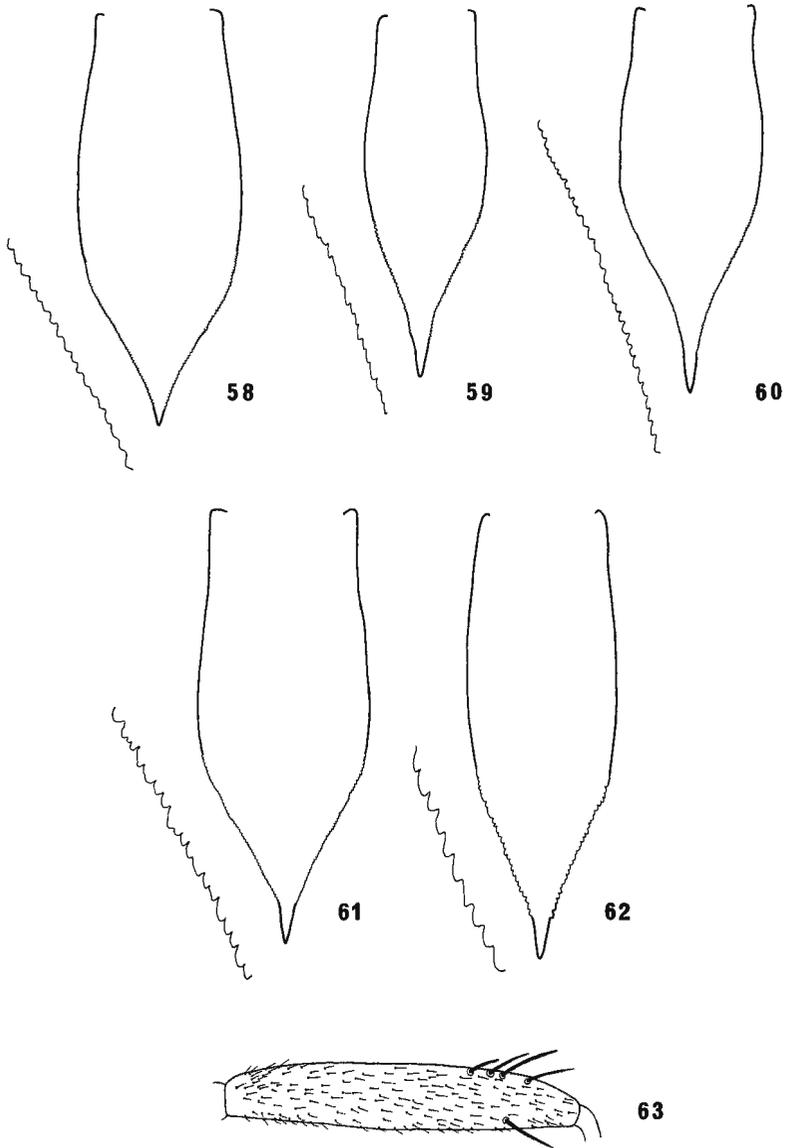
Figs 58–63. Trypetini. 58–62, (leaf-mining species); aculeus, dorsoventral outline with detail of preapical serrations. 58, *Trypeta artemisiae*, 59, *T. immaculata*, 60, *T. zoe*, 61, *Vidalia cornuta*, 62, *V. spinifrons*. 63, *Rhagoletis alternata*, hind femur in posterior view.
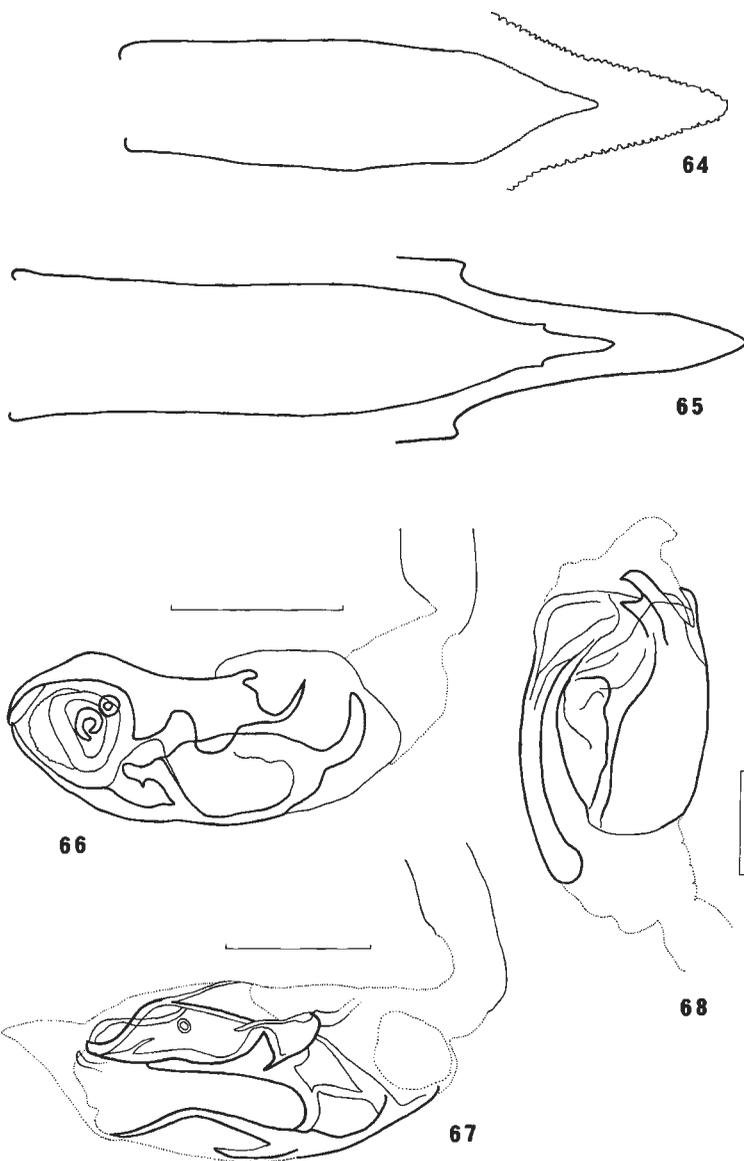
Figs 64–68. Trypetini (leaf-mining and stem-mining species). 64–65, aculeus, dorsoventral outline with detail of apex. 64, *Platyparea discoidea,* 65, *P. poeciloptera.* 66–68, distiphallus. 66, *Cryptaciura rotundiventris,* 67, *P. discoidea,* 68, *P. poeciloptera.* Scale lines = 0·1 mm.
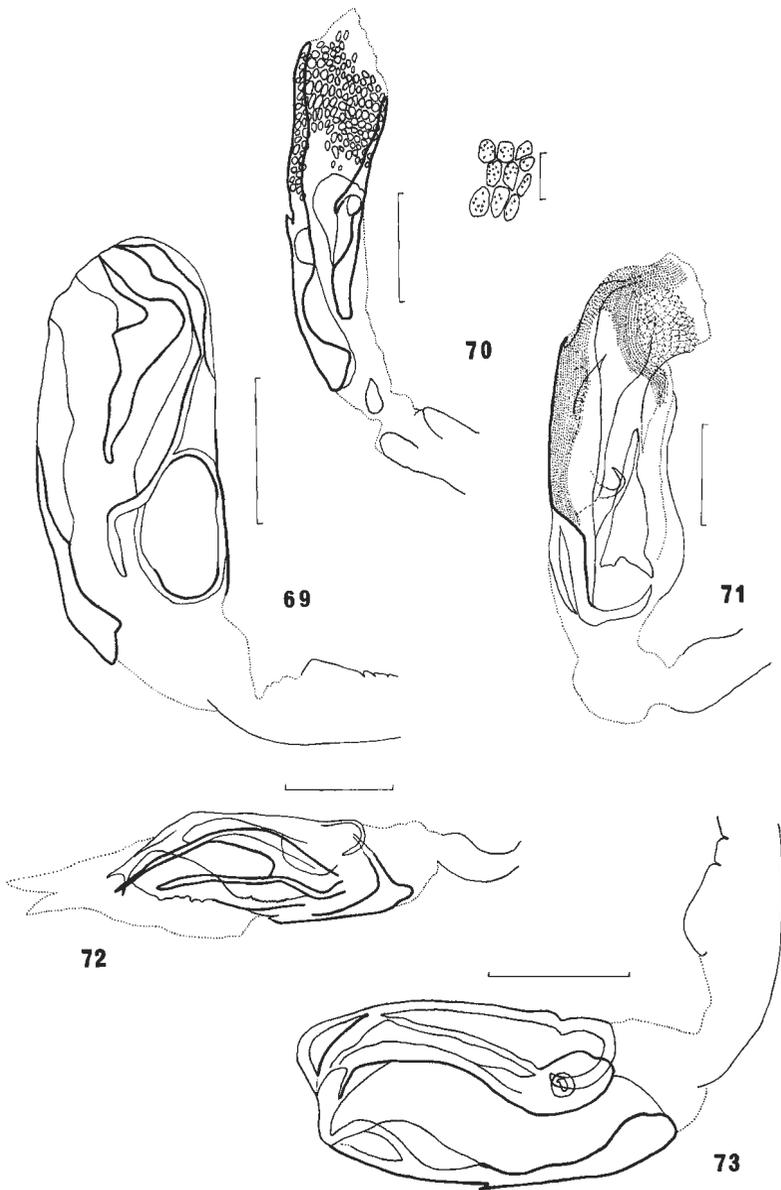
Figs 69–73. Trypetini (frugivorous species); distiphallus. 69, *Goniglossum wiedemanni*, 70, *Anomoia purmunda* (inset shows detail), 71, *Chetostoma curvinerve*, 72, *Rhagoletis meigenii*, 73, *R. alternata*. Scale lines = 0·1 mm; scale line of detail = 0·02 mm.
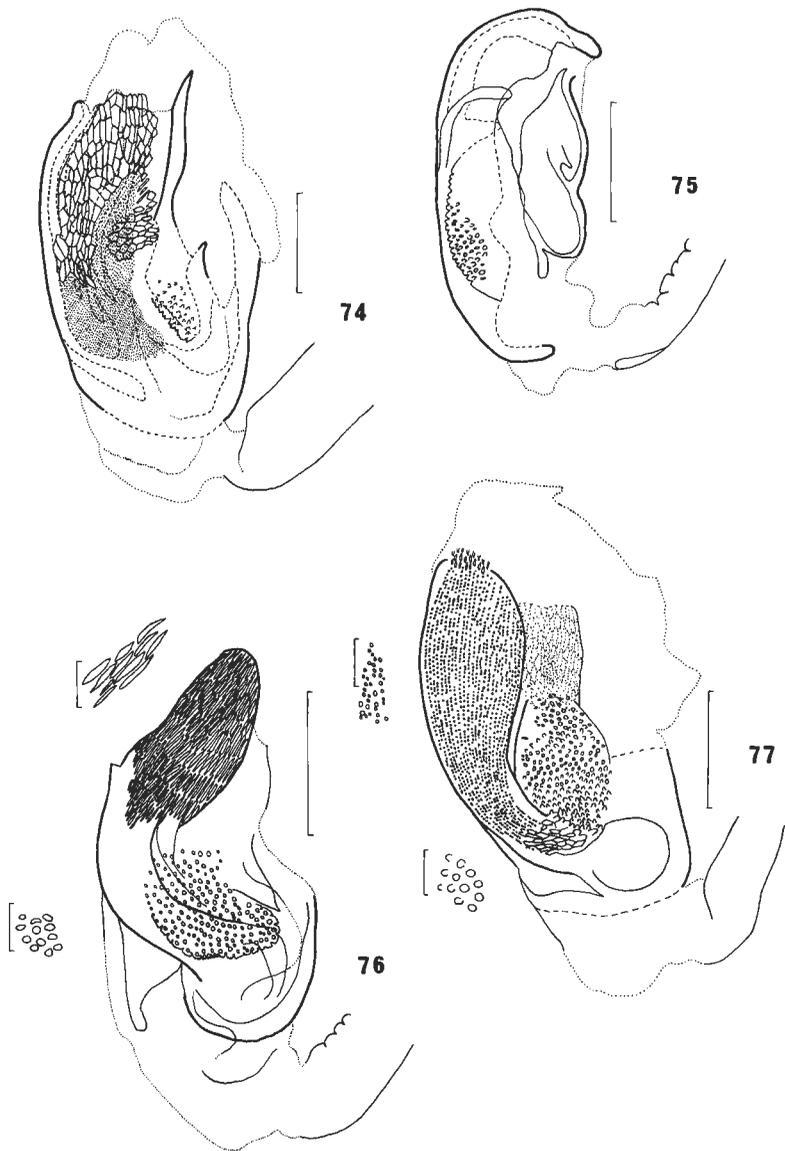
Figs 74–77. Trypetini (leaf-mining species); distiphallus (insets show detail). 74, *Acidia cognata*, 75, *Euleia heracleii*, 76, *Myoleja caesio*, 77, *Trypeta artemisiae*. Scale lines = 0·1 mm; scale lines of detail = 0·02 mm.
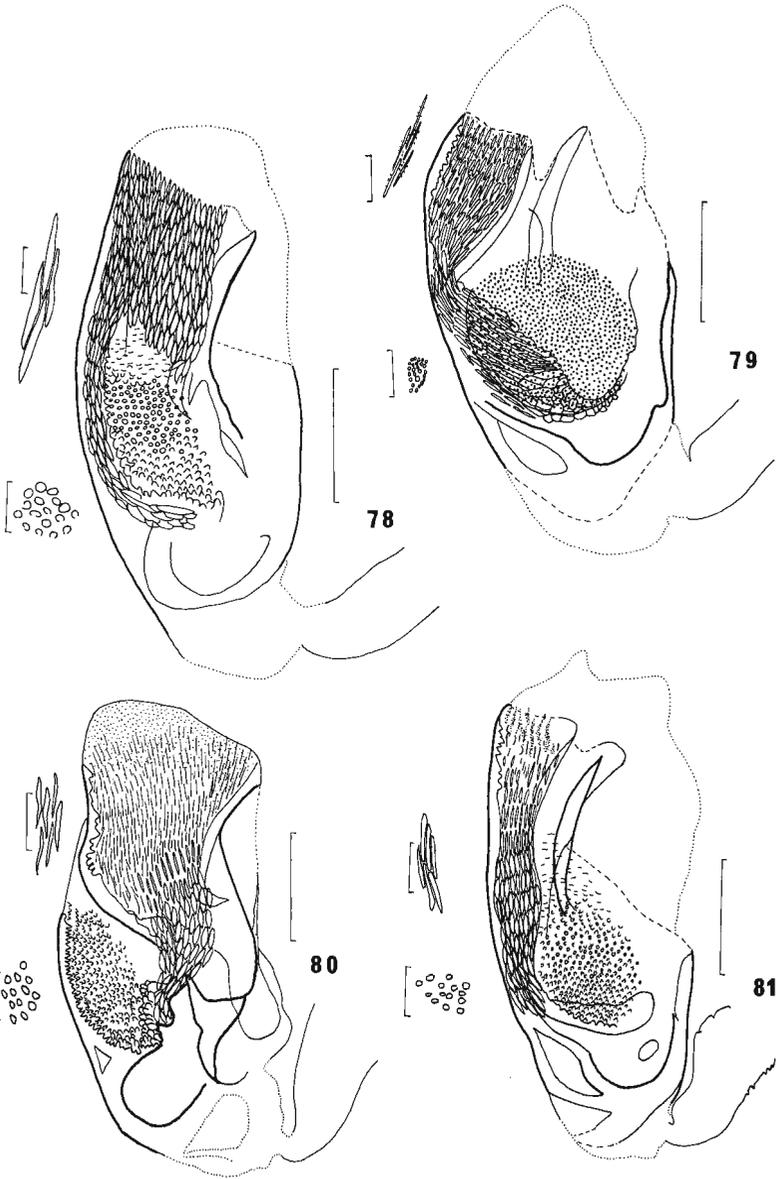
Figs 78–81. Trypetini (leaf-mining species); distiphallus (insets show detail). 78, *Trypeta immaculata*, 79, *T. zoe*, 80, *Vidalia cornuta*, 81, *V. spinifrons*. Scale lines = 0·1 mm; scale lines of detail = 0·02 mm.
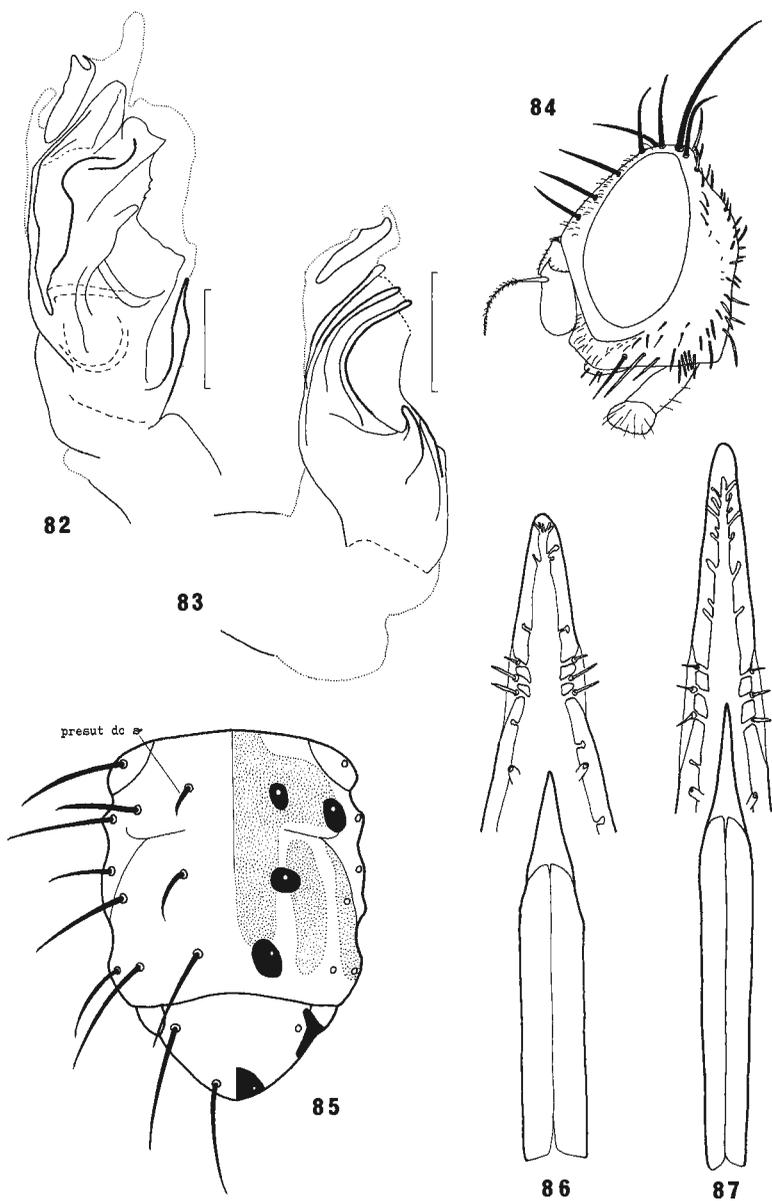
Figs 82–87. Terelliini; *Chaetorellia*. 82–83, distiphallus. 82, *C. loricata*, 83, *C. jaceae*. 84, *C. jaceae*, head profile (*C. loricata* is similar). 85, *C. jaceae*, scutum. 86–87, aculeus, dorsoventral outline with detail of apex. 86, *C. loricata*, 87, *C. jaceae*. Scale lines = 0·1 mm.
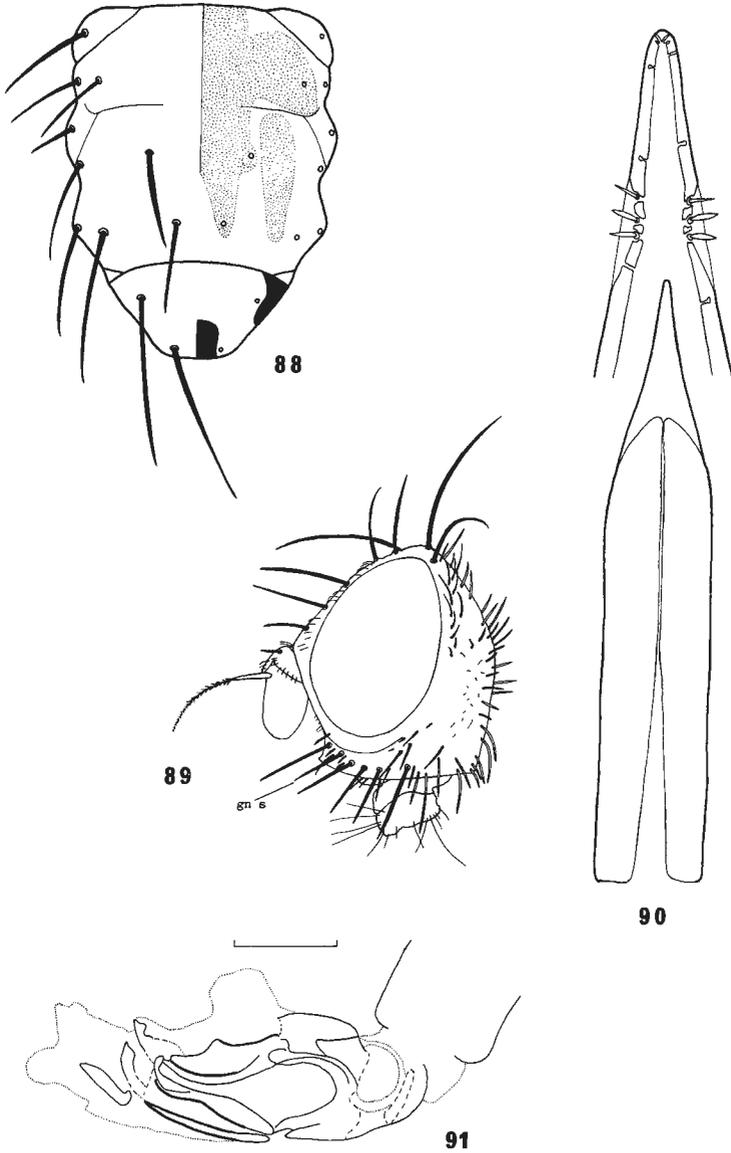
Figs 88–91. Terelliini; *Chaetostomella cylindrica*. 88, scutum. 89, head profile. 90, aculeus, dorso-ventral outline with detail of apex. 91, distiphallus. Scale line = 0·1 mm. *gn s*, genal seta.
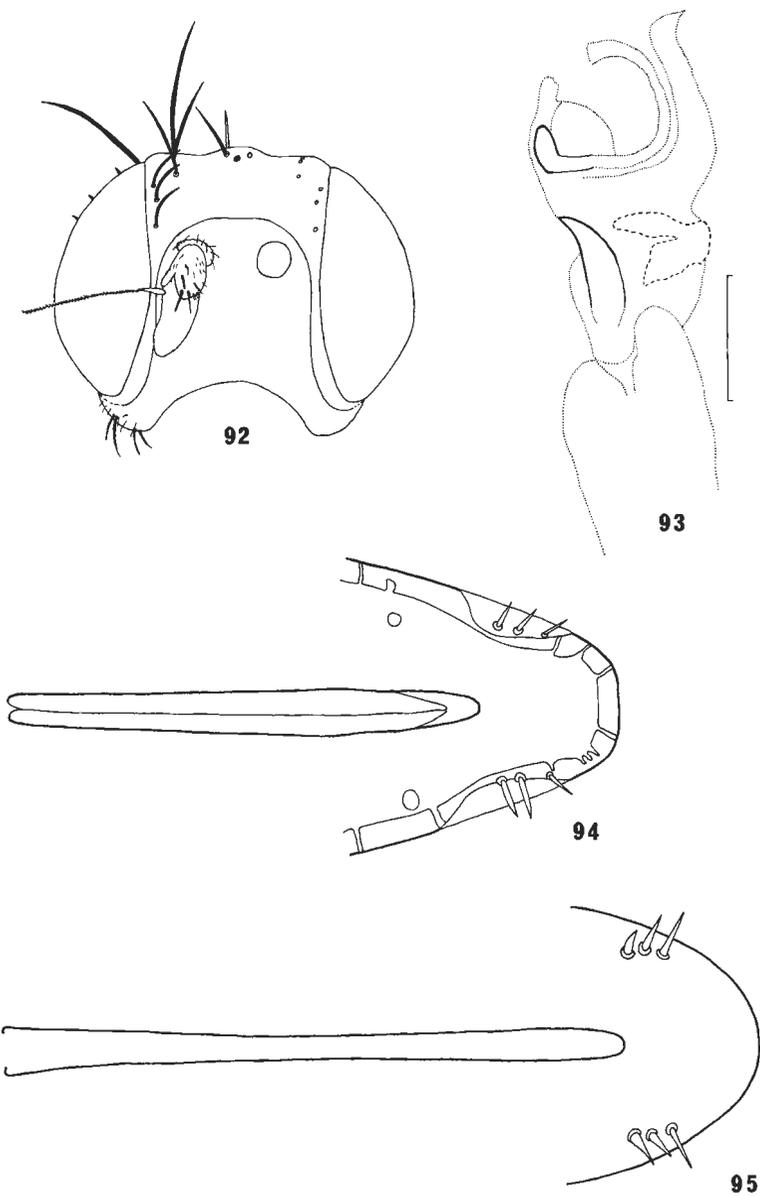
Figs 92–95. Terelliini; *Cerajocera*. 92, *C. plagiata* ♀, head in anterior view (♀ *C. ceratocera* is similar). 93, *C. tussilaginis,* distiphallus (other *Cerajocera* species are similar). 94–95, aculeus, dorsoventral outline with detail of apex. 94, *C. tussilaginis,* 95, *C. ceratocera* (*C. plagiata* is similar). Scale line = 0·1 mm.
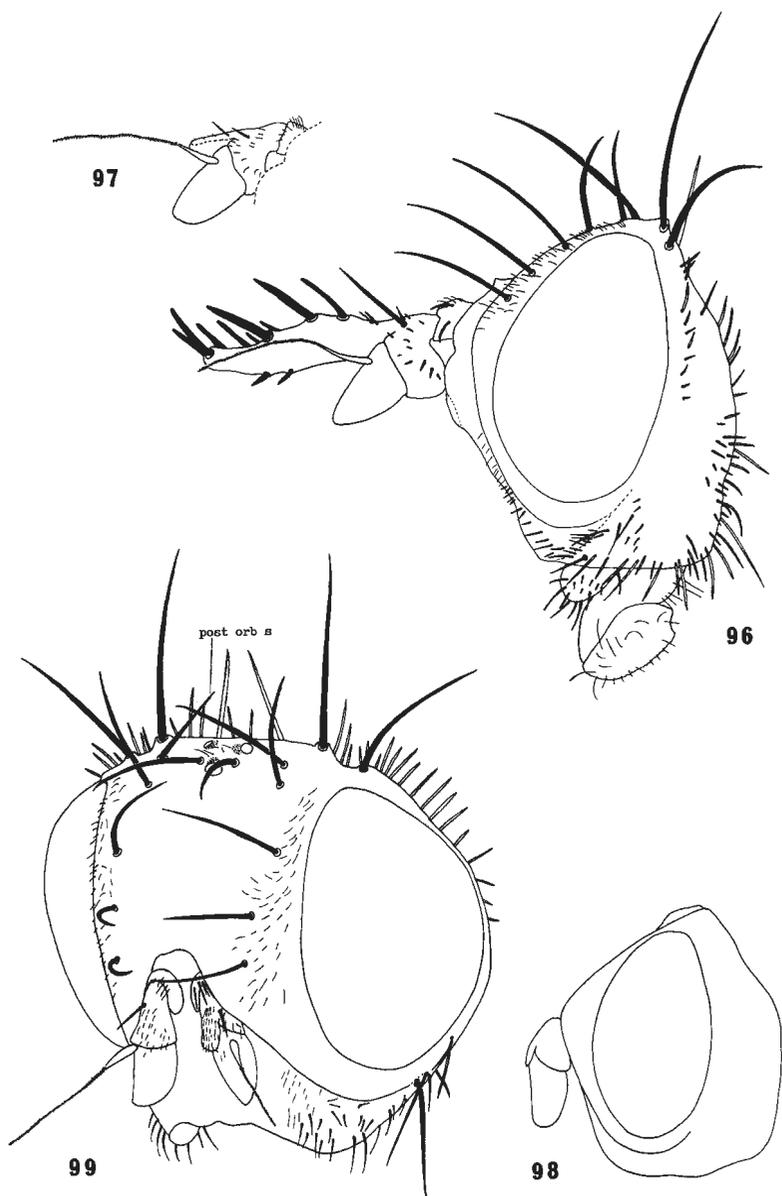
Figs 96–99. Terelliini; *Cerajocera* and *Orellia*. 96–97, *C. ceratocera* (*C. plagiata* is similar). 96, head profile of ♂, 97, antenna of ♀ in lateral view. 98, *C. tussilaginis,* head profile outline. 99, *O. falcata,* head in oblique view. *post orb s,* posterior orbital seta.
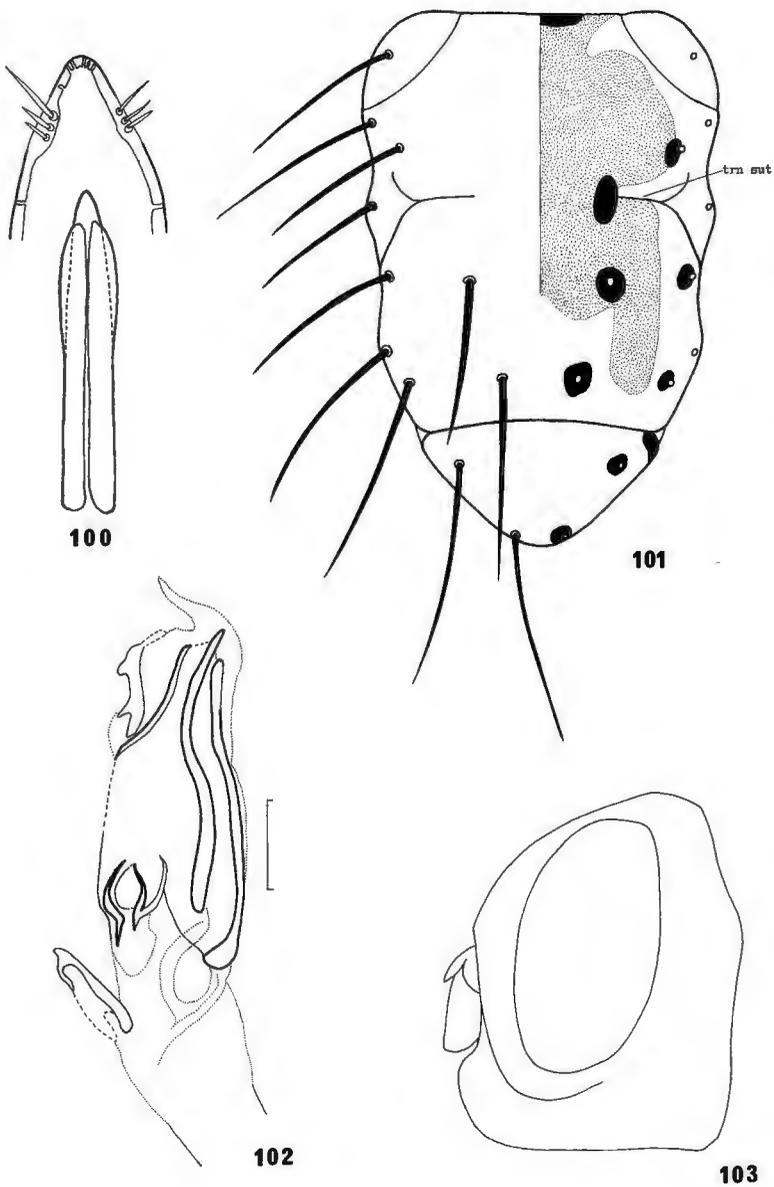
Figs 100–103. Terelliini; *Orellia falcata.* 100, aculeus, dorsoventral outline with detail of apex. 101, scutum. 102, distiphallus. 103, head profile outline. Scale line = 0·1 mm. *trn sut,* transverse suture.
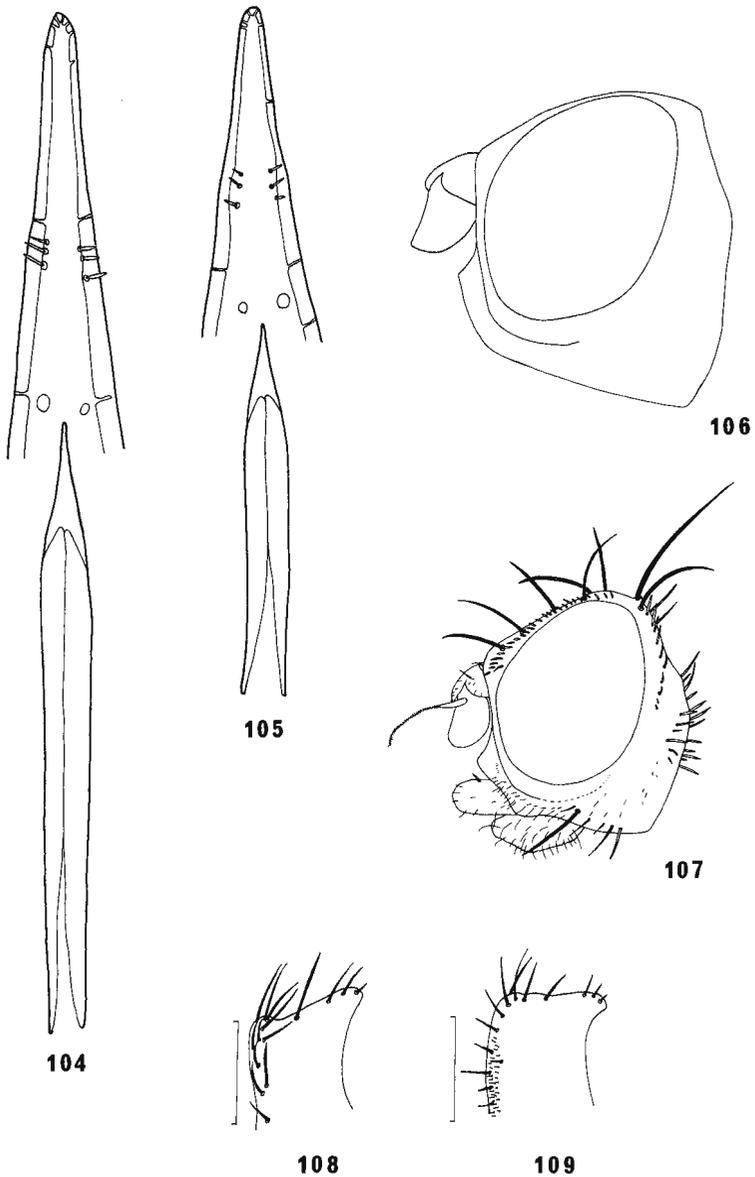
Figs 104–109. Terelliini; *Terellia*. 104–105, aculeus, dorsoventral outline with detail of apex. 104, *T. longicauda*, 105, *T. serratulae*, 106, *T. longicauda*, head profile outline. 107, *T. serratulae*, head profile. 108–109, lateral view of outer surstylus. 108, *T. longicauda*, 109, *T. serratulae*. Scale lines = 0·1 mm.
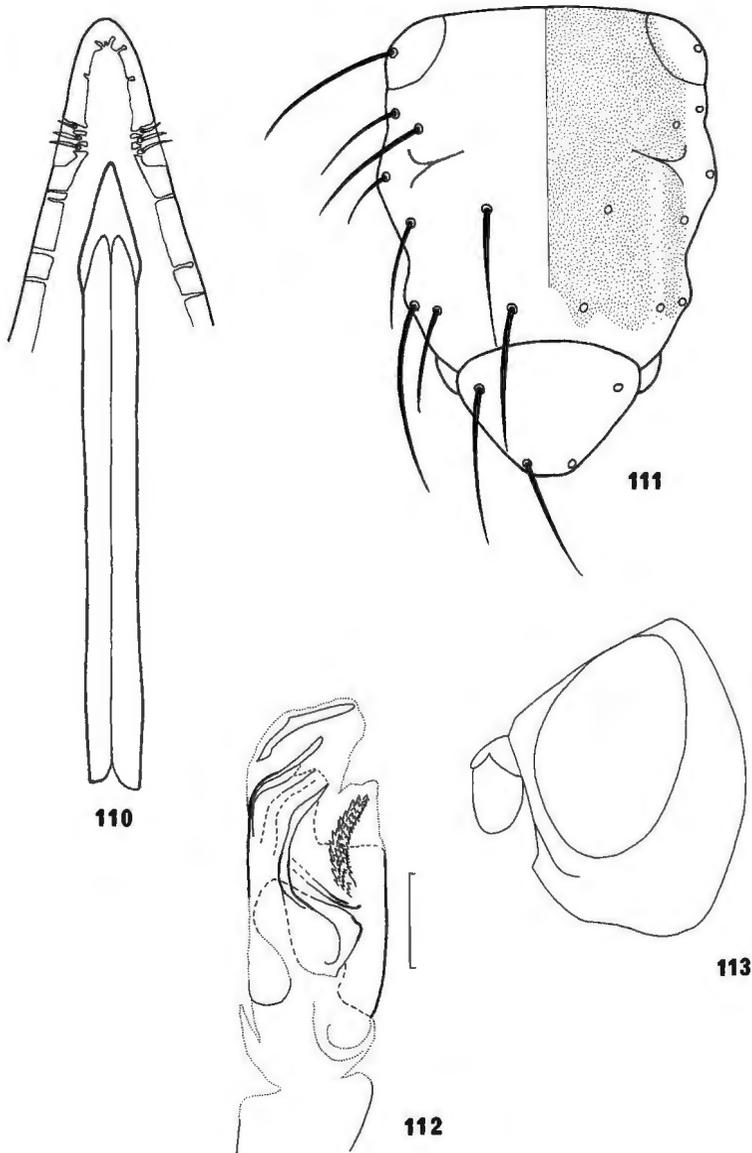
Figs 110–113. Terelliini; *Terellia colon.* 110, aculeus, dorsoventral outline with detail of apex. 111, scutum. 112, distiphallus. 113, head profile outline. Scale line = 0·1 mm.
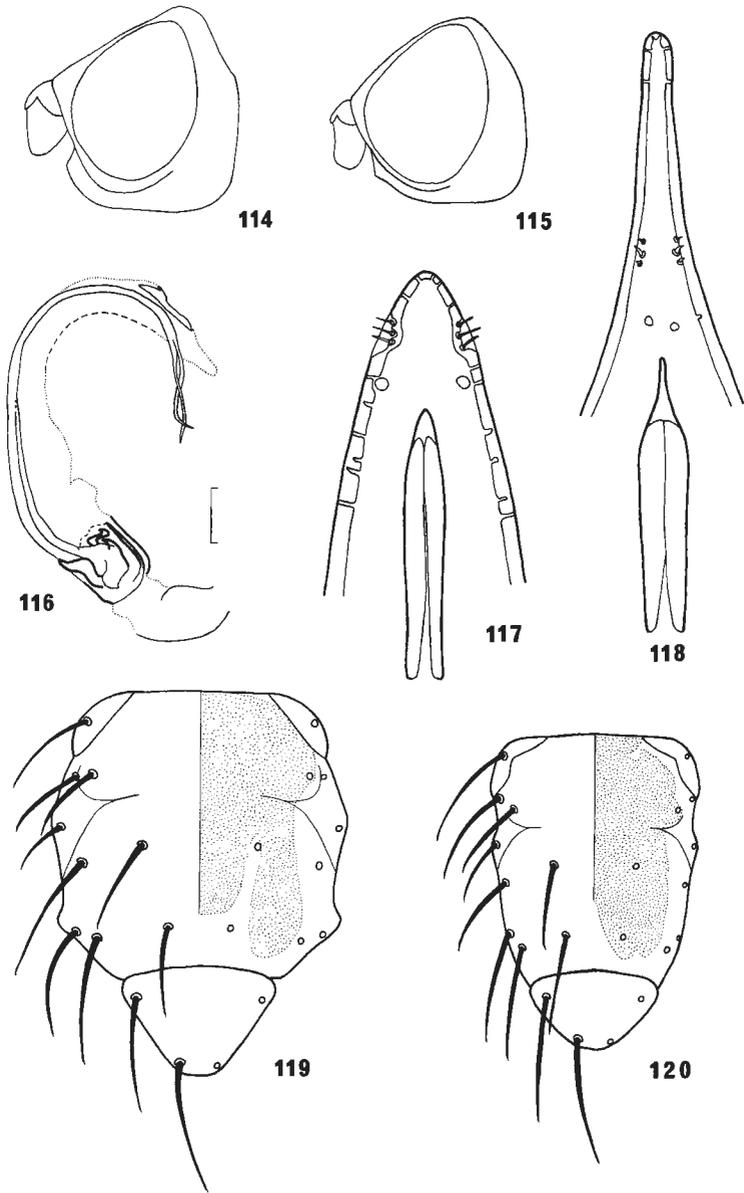
Figs 114–120. Terelliini; *Terellia*. 114–115, head profile outline. 114, *T. winthemi*, 115, *T. vectensis*. 116, *T. vectensis*, distiphallus. 117–118, aculeus, dorsoventral outline with detail of apex. 117, *T. vectensis*, 118, *T. winthemi*. 119–120, scutum. 119, *T. vectensis*, 120, *T. winthemi*. Scale line = 0·1 mm.
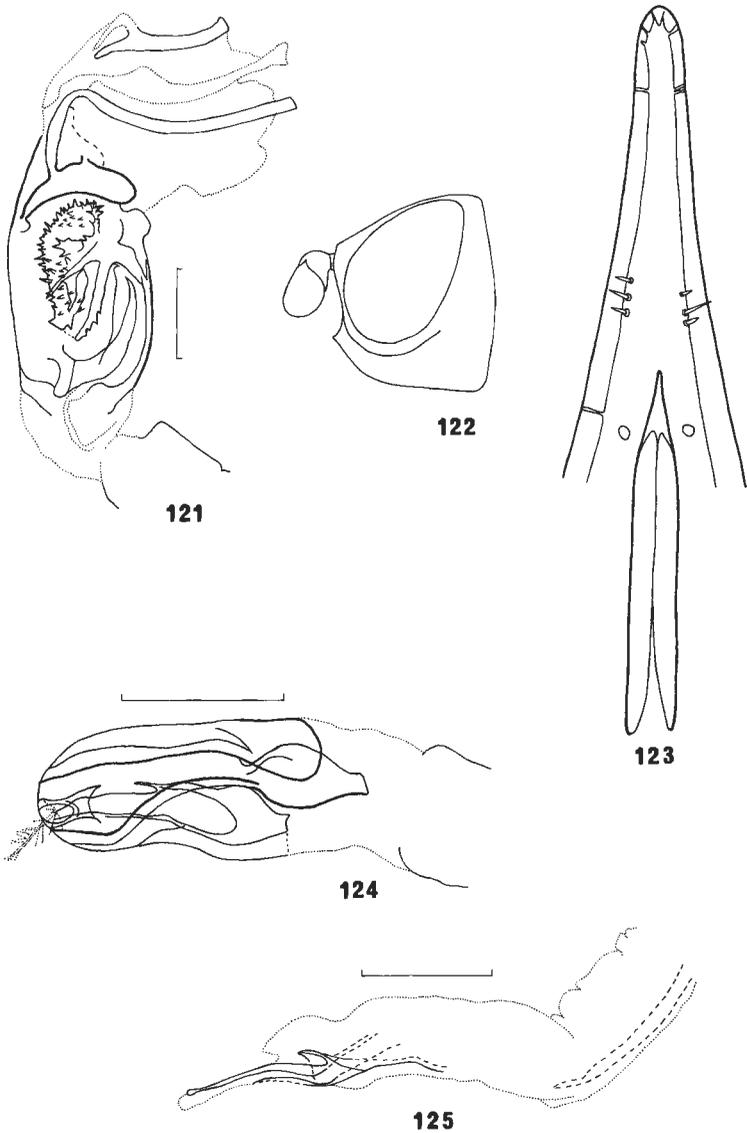
Figs 121–125. Terelliini and Dithrycini; 121–123, *T. ruficauda*. 121, distiphallus (*T. longicauda, T. serratulae* and *T. winthemi* are similar). 122, head profile outline. 123, aculeus, dorsoventral outline with detail of apex. 124–125, Dithrycini; distiphallus. 124, *Dithryca guttularis,* 125, *Noeeta pupillata.* Scale lines = 0·1 mm.
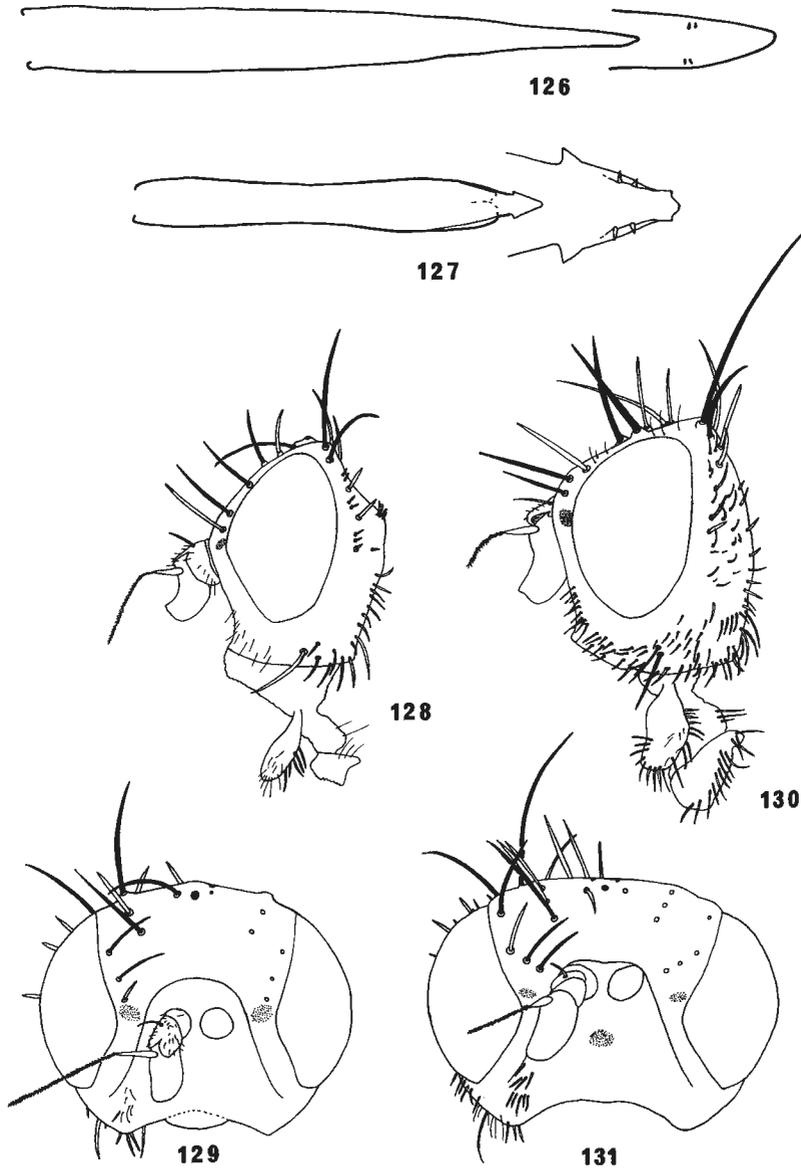
Figs 126–131. Dithrycini; 126–127, aculeus, dorsoventral outline with detail of apex. 126, *D. guttularis,* 127, *N. pupillata.* 128–129, *Dithryca guttularis.* 128, head profile. 129, head in anterior view. 130–131, *Noeeta pupillata.* 130, head profile. 131, head in anterior view.
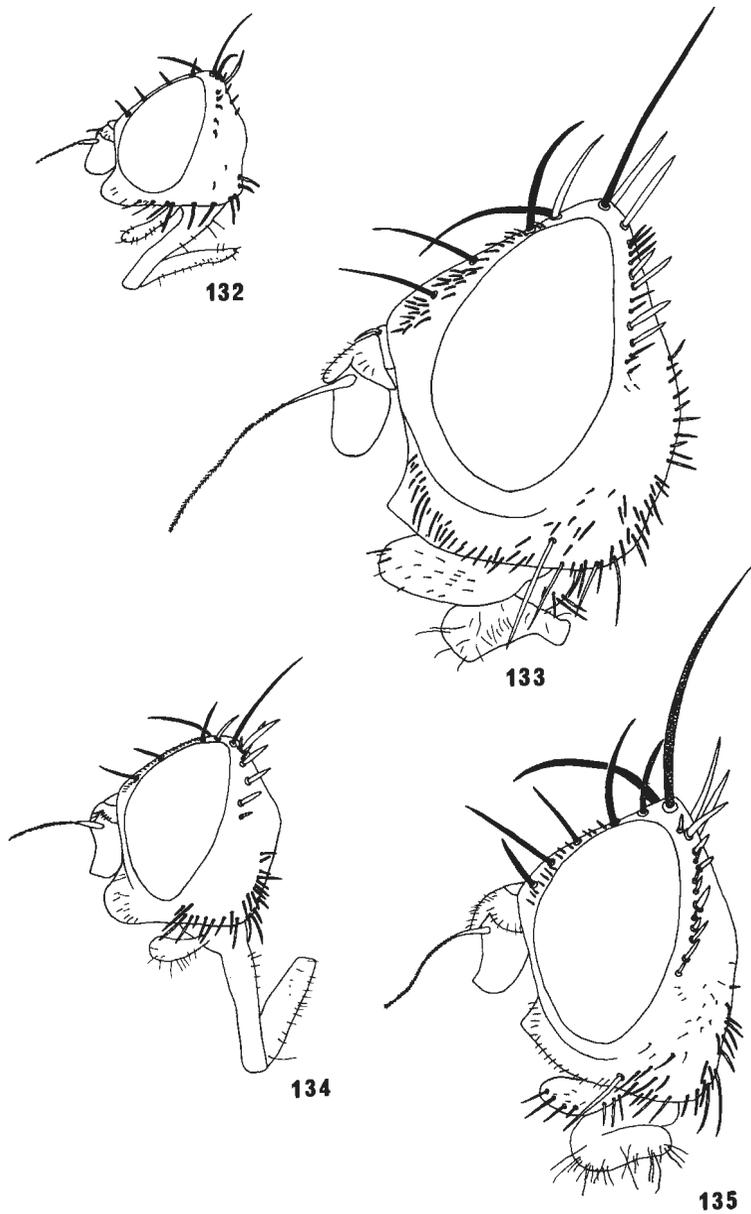
Figs 132–135. Tephritini; head profile. 132, *Ensina sonchi*, 133, *Icterica westermanni*, 134, *Sphenella marginata*, 135, *Acinia corniculata*.
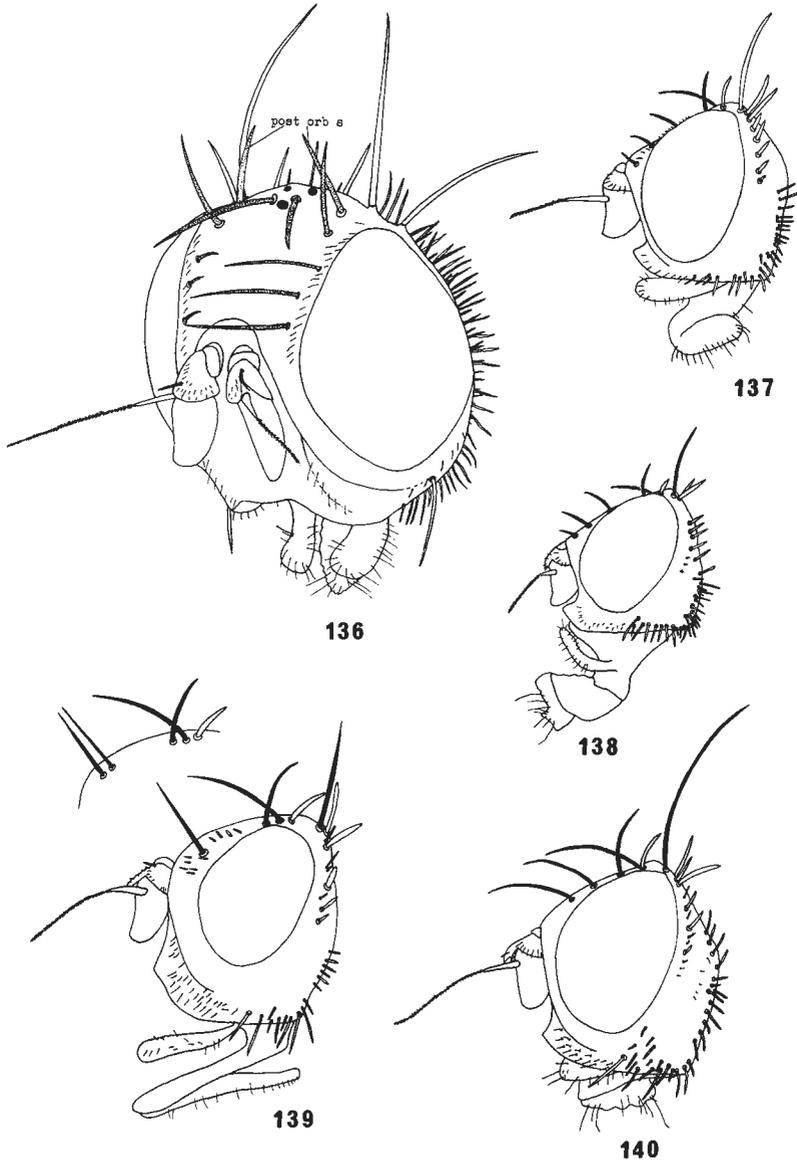
Figs 136–140. Tephritini; head. 136, *Xyphosia miliaria,* head in oblique view. 137–140, head profile. 137, *Acanthiophilus helianthi,* 138, *Trupanea stellata* (*T. amoena* is similar), 139, *Oxyna parietina* (inset showing aberrant form with more than a single pair of frontal setae; other *Oxyna* species are similar), 140, *Tephritis bardanae* (other *Tephritis* species are similar). *post orb s, posterior orbital seta.*
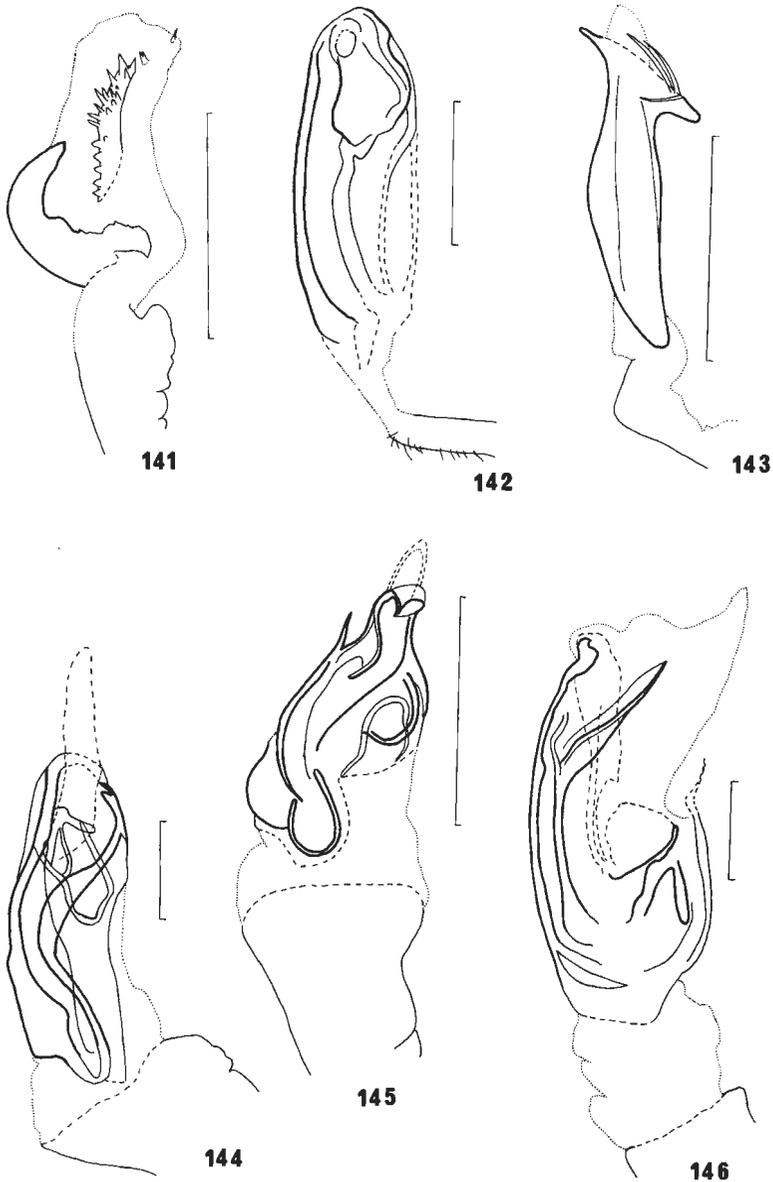
Figs 141–146. Tephritini; distiphallus. 141, *Acanthiophilus helianthi*, 142, *Acinia corniculata*, 143, *Ensina sonchi*, 144, *Icterica westermanni*, 145, *Sphenella marginata*, 146, *Xyphosia miliaria*. Scale lines = 0·1 mm.
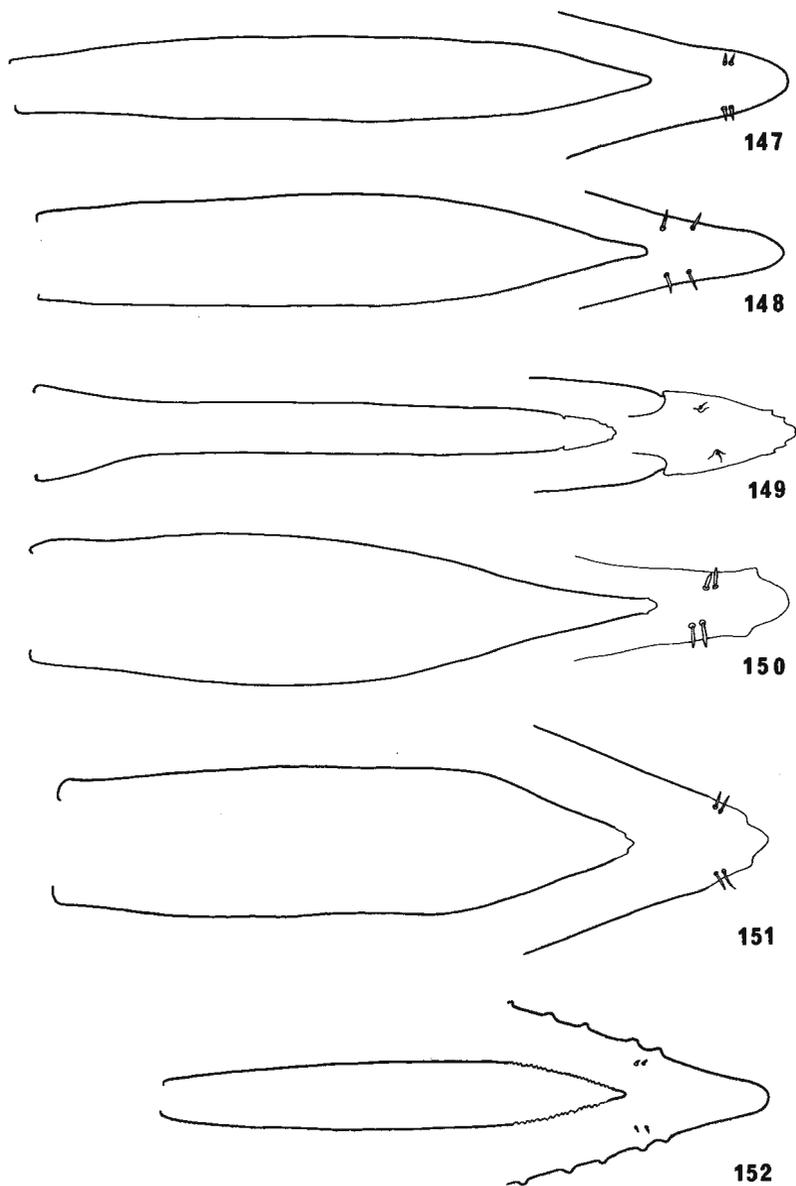
Figs 147–152. Tephritini; aculeus, dorsoventral outline with detail of apex. 147, *Acanthiophilus helianthi*, 148, *Acinia corniculata*, 149, *Ensina sonchi*, 150, *Icterica westermanni*, 151, *Sphenella marginata*, 152, *Xyphosia miliaria*.
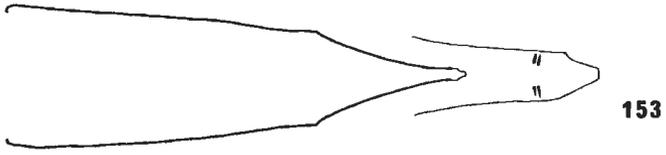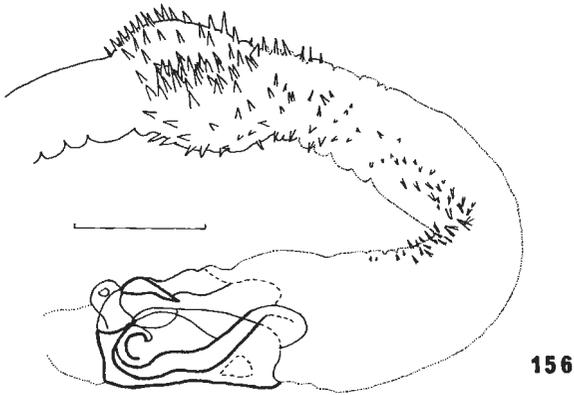
Figs 153–156. Tephritini; *Oxyna*. 153–155, aculeus, dorsoventral outline with detail of apex. 153, *O. flavipennis,* 154, *O. nebulosa,* 155, *O. parietina.* 156, *O. parietina,* distiphallus (other *Oxyna* species are similar). Scale line = 0·1 mm.
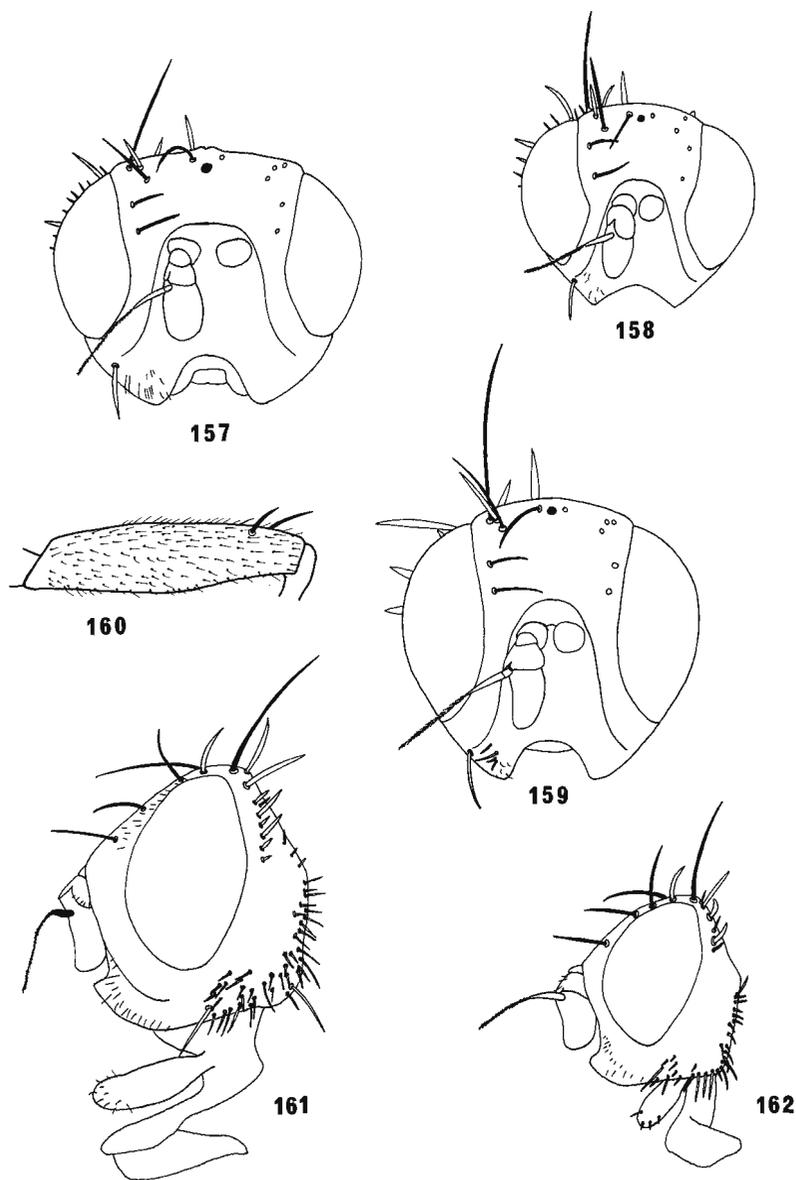
Figs 157–162. Tephritini; *Campiglossa* and *Paroxyna*. 157–159, head in anterior view. 157, *C. grandinata*, 158, *P. misella*, 159, *P. plantaginis*. 160, *P. plantaginis*, hind femur in posterior view. 161–162, head profile (most other *Paroxyna* species are similar). 161, *P. plantaginis*, 162, *P. misella*.
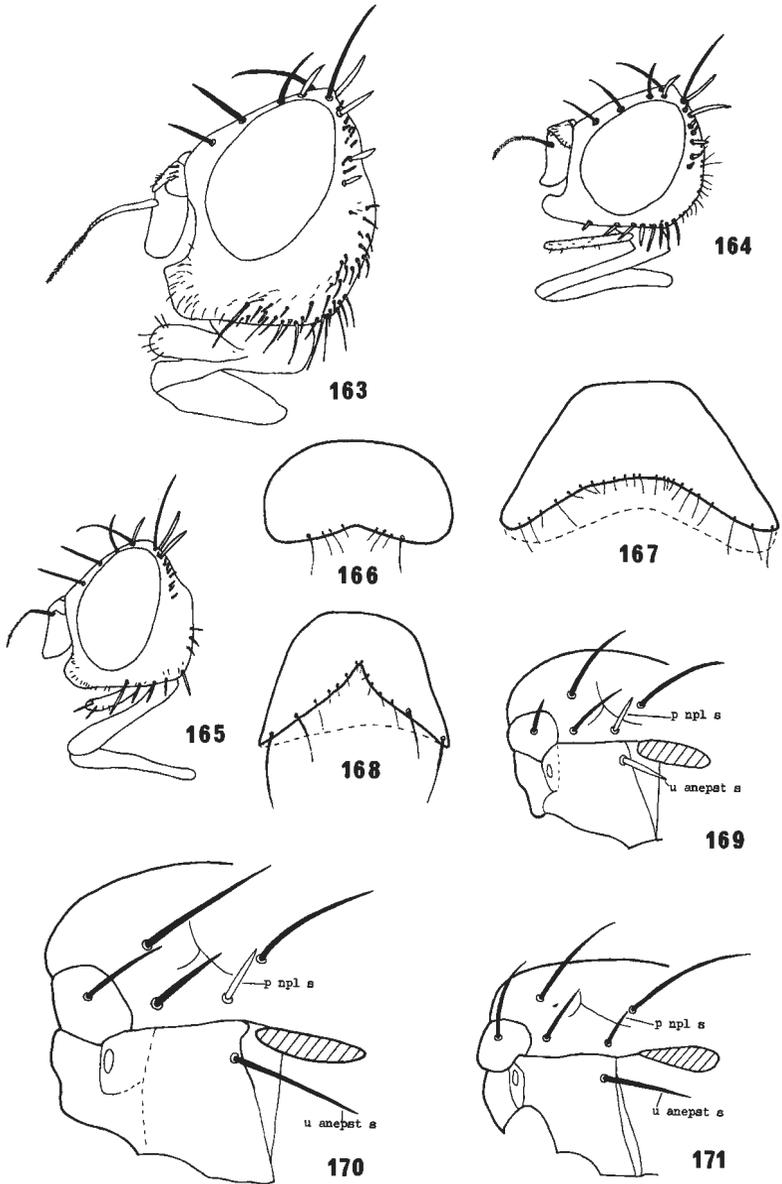
Figs 163–171. Tephritini; *Campiglossa, Dioxyna* and *Paroxyna*. 163–165, head profile. 163, *C. grandinata* (*C. argyrocephala* is similar), 164, *D. bidentis*, 165, *P. producta*. 166–168, sternite 5 of ♂. 166, *D. bidentis*, 167, *P. lhommei*, 168, *P. producta*. 169–171, thorax, lateral view showing colour of setae. 169, *P. absinthii*, 170, *P. plantaginis*, 171, *P. misella*. *p npl s*, posterior notopleural seta. *u anepst s*, upper anepisternal seta.
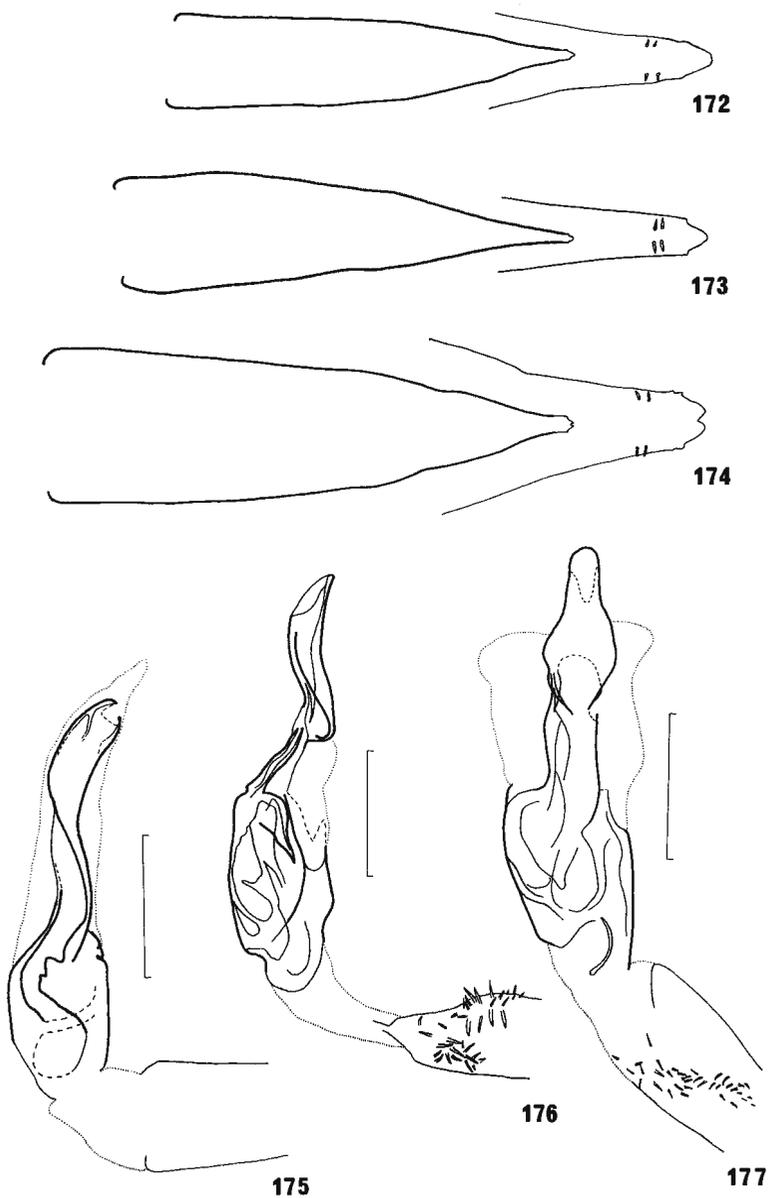
Figs 172–177. Tephritini; *Campiglossa, Dioxyna* and *Paroxyna*. 172–174, aculeus, dorsoventral outline with detail of apex. 172, *P. absinthii*, 173, *P. misella*, (other *Paroxyna, Campiglossa* and *Dioxyna* species are similar), 174, *P. plantaginis*. 175–177, distiphallus. 175, *D. bidentis*, 176–177, *P. misella* in different view (*Campiglossa* species are very similar). Scale lines = 0·1 mm.
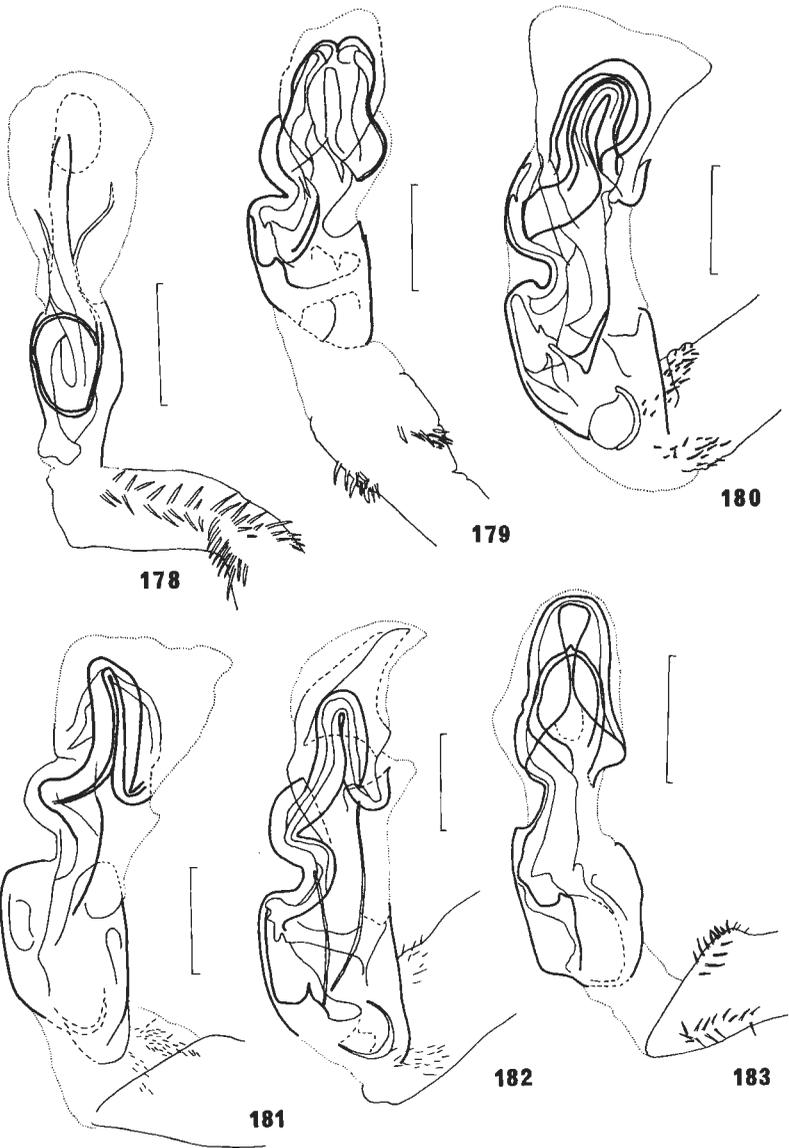
Figs 178–183. Tephritini; *Paroxyna,* distiphallus. 178, *P. producta,* 179, *P. absinthii,* 180, *P. loewiana,* 181, *P. lhommei,* 182, *P. plantaginis,* 183, *P. solidaginis.* Scale lines = 0·1 mm.
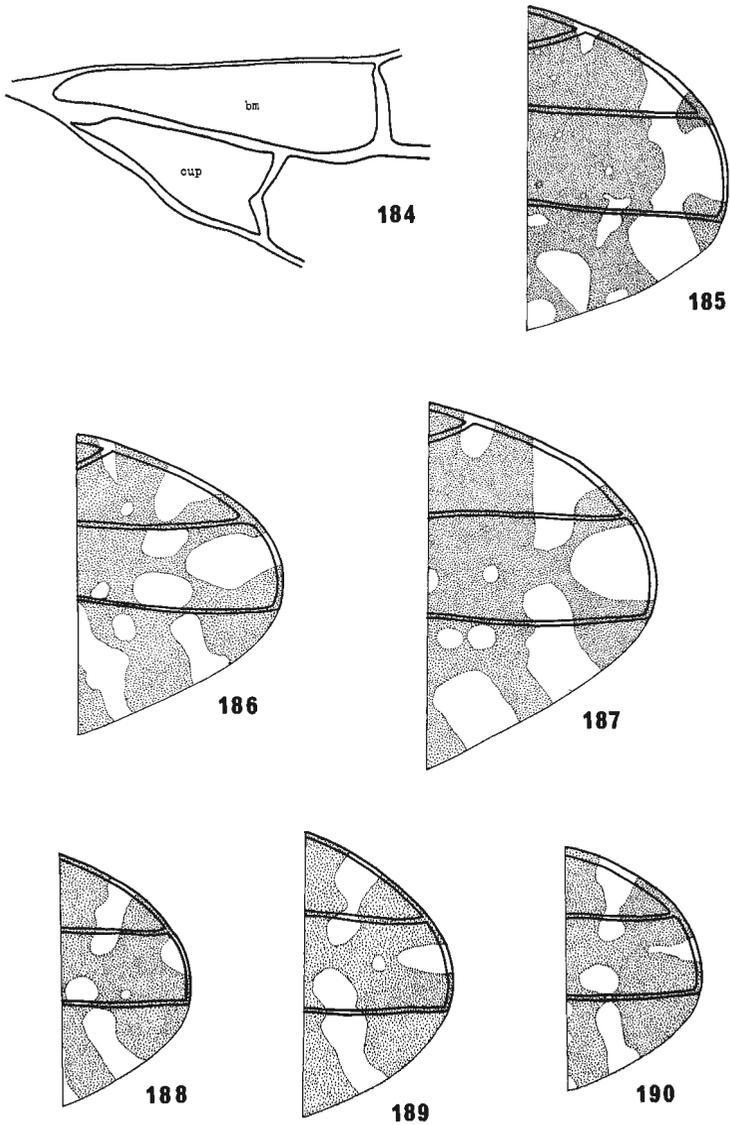
Figs 184–190. Tephritini; wing details. 184. *Ensina sonchi*, cell cup shape. 185–190, *Tephritis*, wing apex pattern. 185, *T. bardanae*, 186, *T. ruralis*, 187, *T. conura*, 188–190, *T. vespertina*.
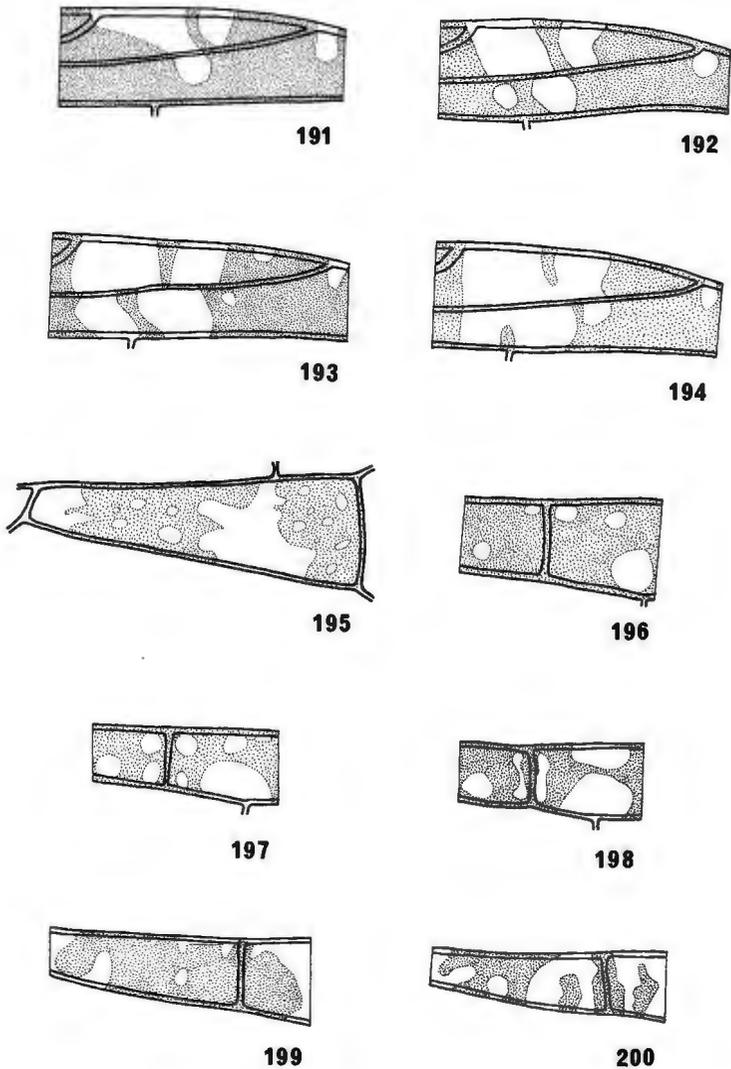
Figs 191–200. Tephritini; *Tephritis,* wing details. 191–194, cell r_1 and part of cell r_{2+3}. 191, *T. separata* (typical continental form), 192, *T. neesii,* 193–194, *T. leontodontis.* 195, *T. formosa,* cell dm. 196–200, area of r-m crossvein. 196, *T. conura,* 197–198. *T. ruralis,* 199, *T. bardanae,* 200, *T. hyoscyami.*
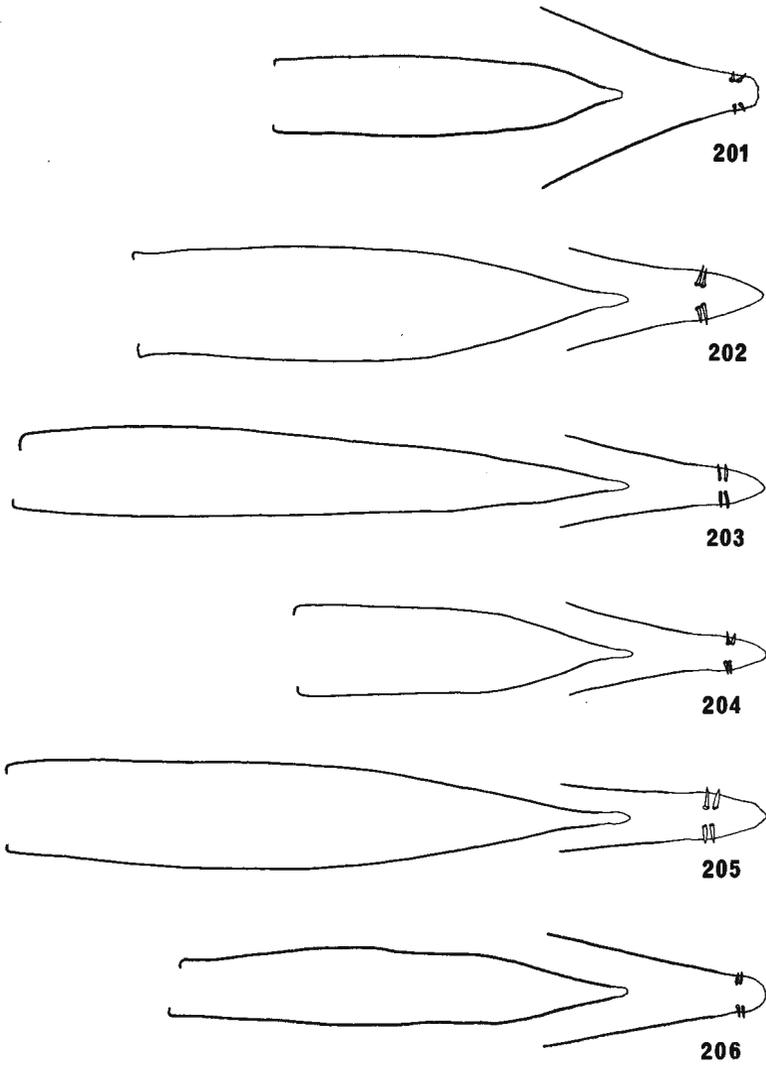
Figs 201–206. Tephritini; *Tephritis*, aculeus, dorsoventral outline with detail of apex. 201, *T. formosa*, 202, *T. bardanae*, 203, *T. hyoscyami*, 204, *T. cometa*, 205, *T. conura*, 206, *T. ruralis*.
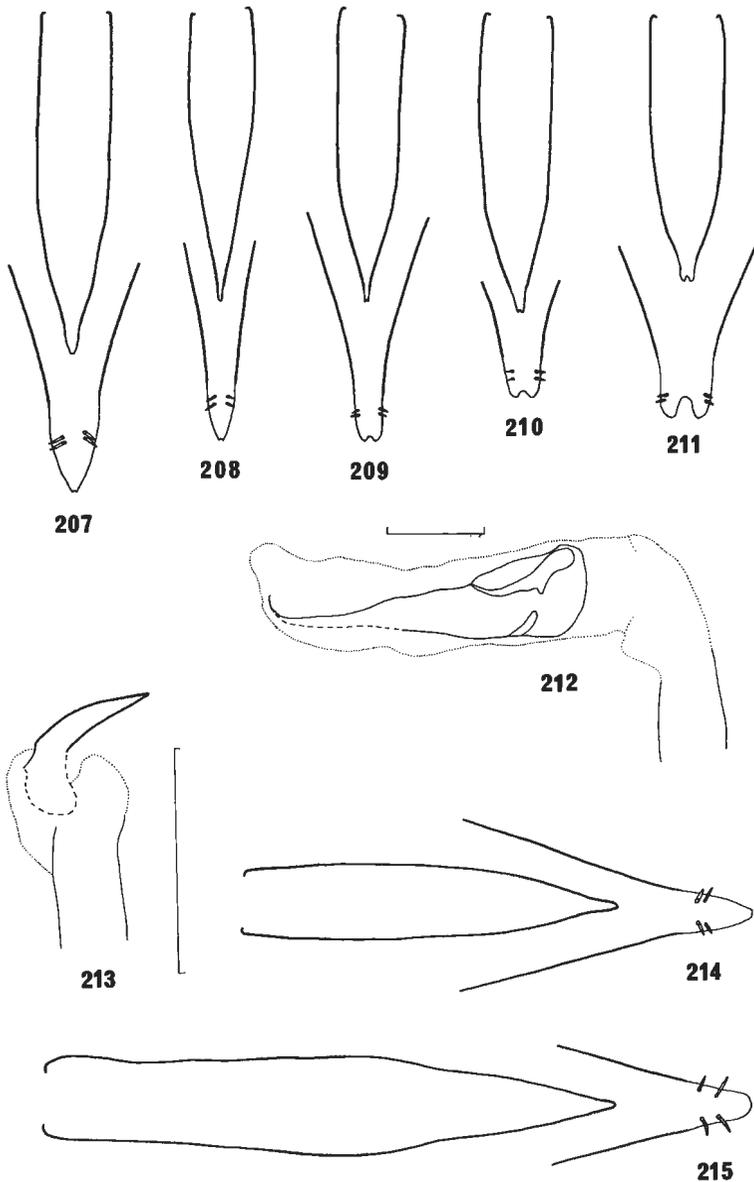
Figs 207–215. Tephritini; *Tephritis* and *Trupanea*. 207–211, *Tephritis*, aculeus, dorsoventral outline with detail of apex. 207, *Tephritis neesii*, 208, *T. praecox*, 209, *T. separata*, 210, *T. vespertina*, 211, *T. leontodontis*. 212, *T. bardanae*, distiphallus (other *Tephritis* species are similar). 213, *Trupanea stellata*, distiphallus (*T. amoena* is similar). 214–215, *Trupanea*, aculeus, dorsoventral outline with detail of apex. 214, *T. stellata*. 215, *T. amoena*. Scale lines = 0·1 mm.
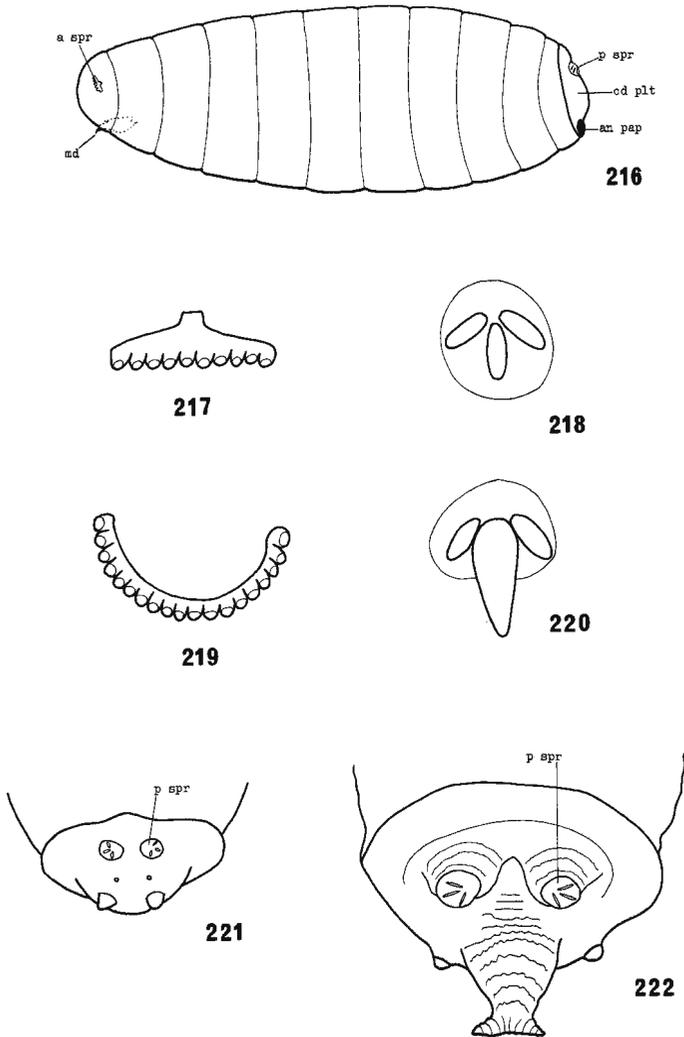
Figs 216–222. Tephritidae; pupae. 216, a typical puparium in lateral view. 217–218, spiracles of a typical tephritid species. 217, anterior spiracle, 218, posterior spiracle. 219–220, spiracles of some leaf-mining species. 219, anterior spiracle, 220, posterior spiracle. 221–222, *Cerajocera,* caudal plate in posterodorsal view. 221, *C. plagiata,* 222, *C. ceratocera. a spr,* anterior spiracle. *an pap,* perianal pad. *cd plt,* caudal plate. *md,* mandible (dotted line shows internal position of larval mouthparts). *p spr,* posterior spiracle.
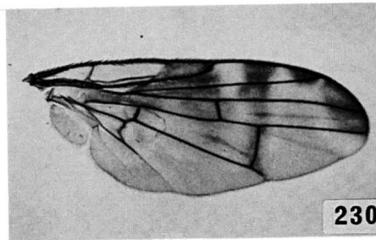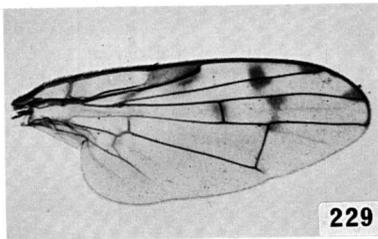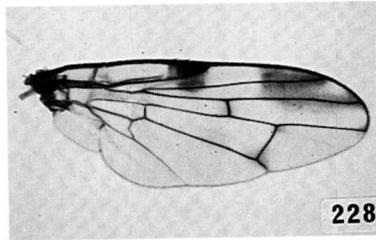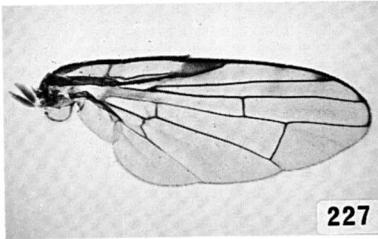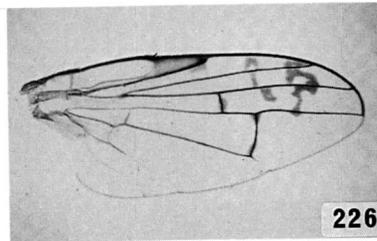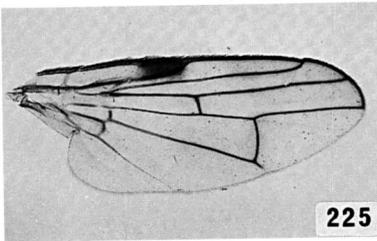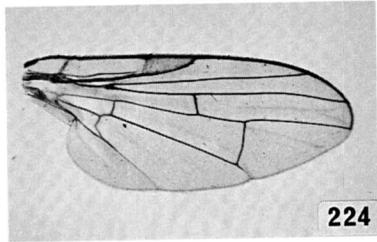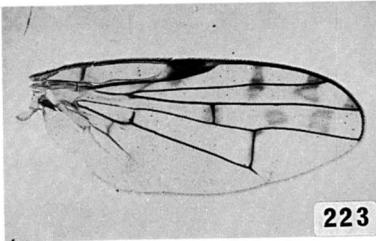
Figs 223–230. Tephritidae; wing hyaline or poorly marked. 223, *Ensina sonchi*, 224, *Terellia serratulae* (*T. longicauda* is similar), 225, *Urophora spoliata*, 226, *Acanthiophilus helianthi*, 227, *Terellia colon* ♀, 228, *T. colon* ♂, 229, *T. vectensis*, 230, *T. winthemi*.
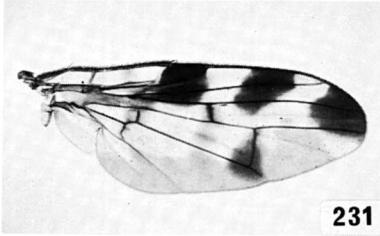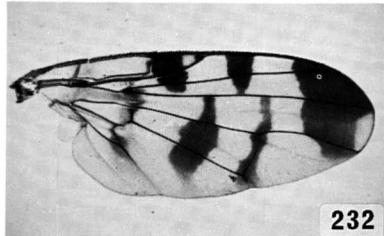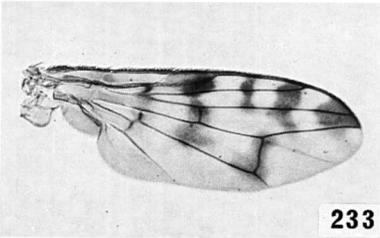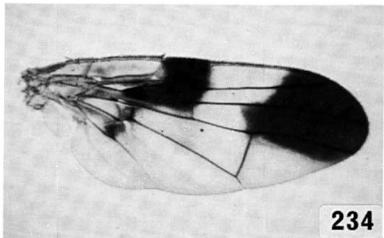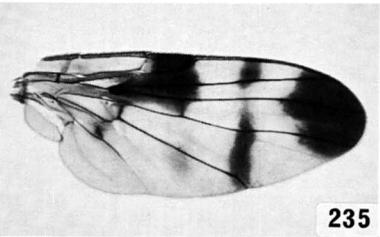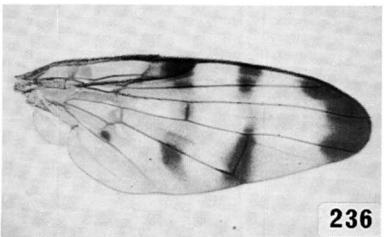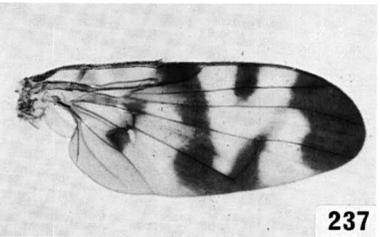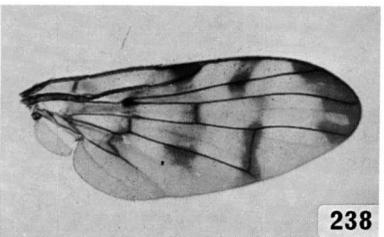
Figs 231–238. Tephritidae; wing with incomplete crossbands and no reticulation. 231, *T. ruficauda,* 232, *Euphranta toxoneura,* 233, *Myopites inulaedyssentericae* (*M. eximia* is similar), 234 *Trypeta zoe* ♂, 235, *T. zoe* ♀, 236, *T. artemisiae,* 237, *T. immaculata,* 238, *Vidalia cornuta.*
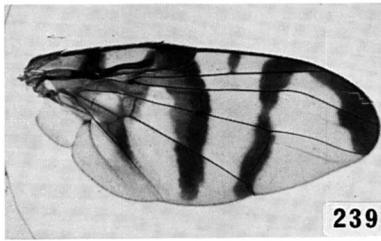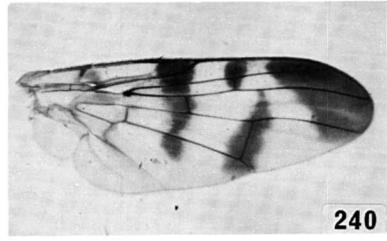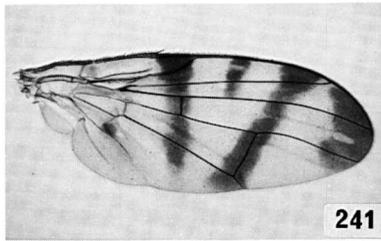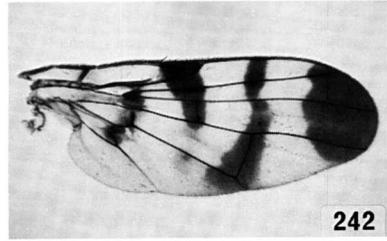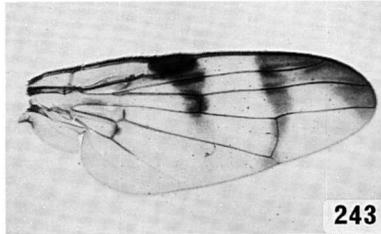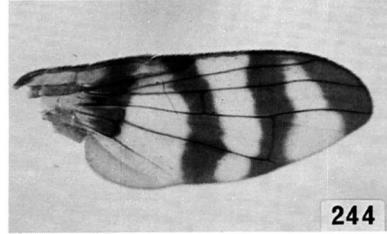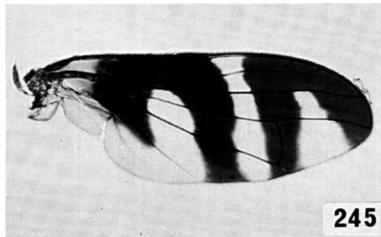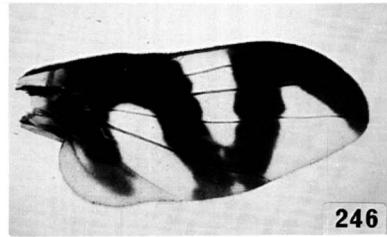
Figs 239–246. Tephritidae; wing with some or all crossbands complete and no reticulation. 239, *Chetostoma curvinerve*, 240, *Rhagoletis meigenii*, 241, *R. alternata*, 242, *Vidalia spinifrons*, 243, *Urophora stylata*, 244, *U. jaceana* (*U. cuspidata* and *U. solstitialis* are similar), 245, *U. quadrifasciata*, 246, *U. cardui*.
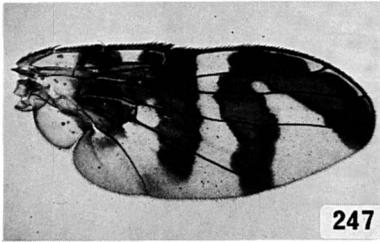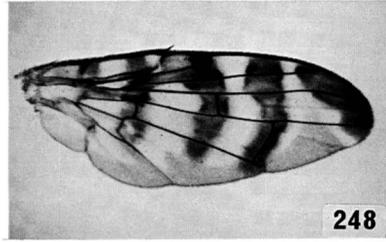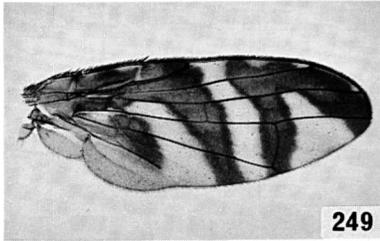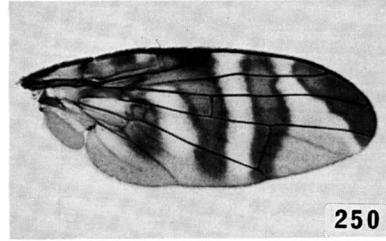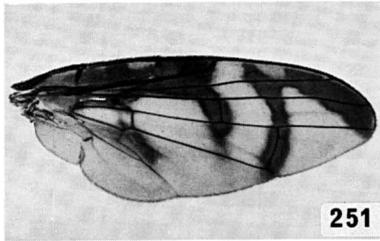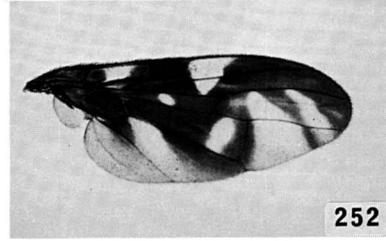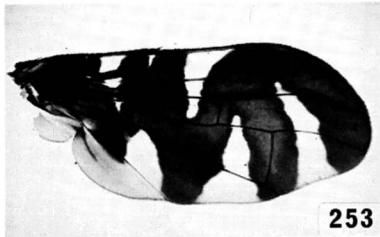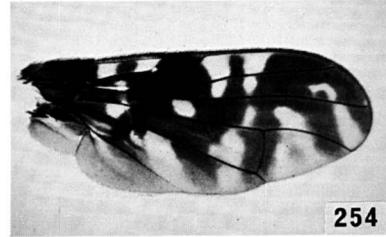
Figs 247–254. Tephritidae. 247–251, wing with some or all crossbands complete and no reticulation. 247, *Goniglossum wiedemanni*, 248, *Cerajocera ceratocera* (other *Cerajocera* species are similar), 249, *Chaetorellia jaceae* (*C. loricata* is similar), 250, *Chaetostomella cylindrca*, 251, *Orellia falcata*. 252–254, wing pattern formed by hyaline wedges cutting-in from margin and no reticulation. 252, *Euleia heracleii*, 253, *Platyparea poeciloptera*, 254, *P. discoidea*.
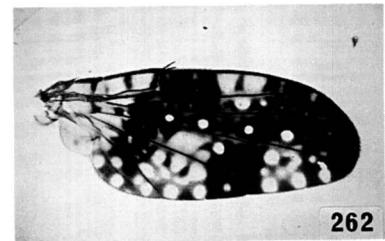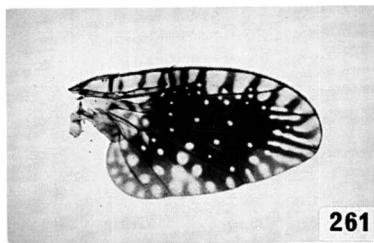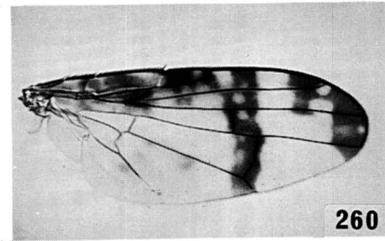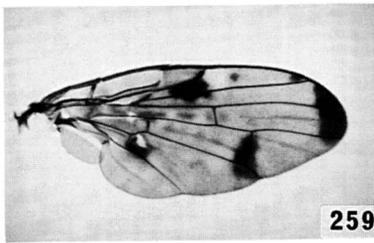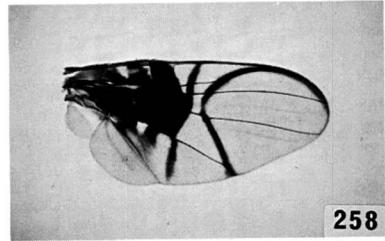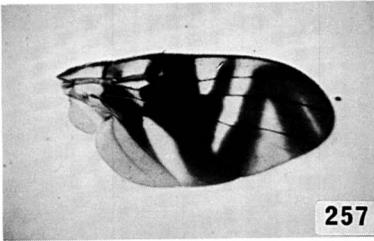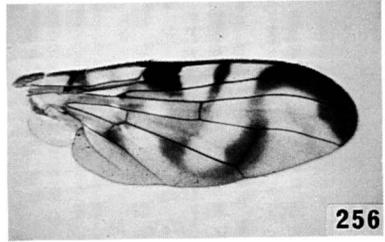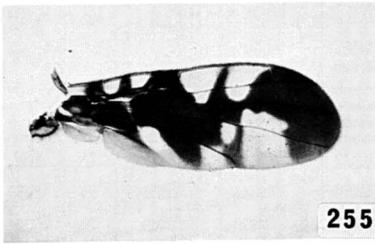
Figs 255–262. Tephritidae. 255–258, wing pattern formed by hyaline wedges cutting-in from margin and no reticulation. 255, *Cryptaciura rotundiventris*, 256, *Acidia cognata*, 257, *Myoleja caesio*, 258, *Anomoia purmunda*. 259, wing with blocks of pattern and a faint reticulate background, *Xyphosia miliaria*. 260, wing with reticulate crossbands, *Sphenella marginata*. 261, wing pattern reticulate and with elongate marginal hyaline areas, *Noeeta pupillata*. 262, wing pattern reticulate and with a very small hyaline spot at apex of cell r_{4+5}, *Acinia corniculata*.
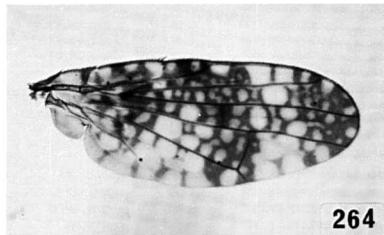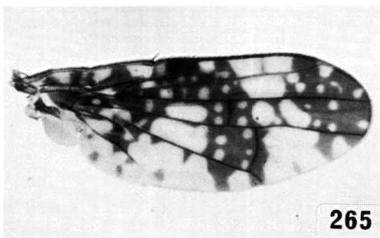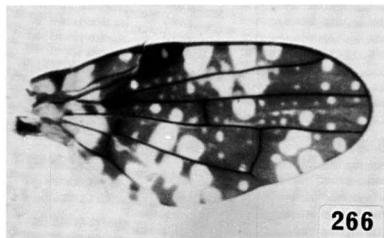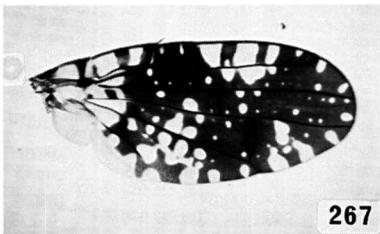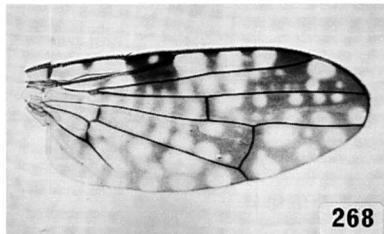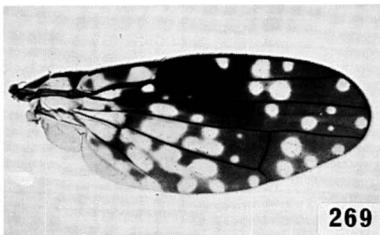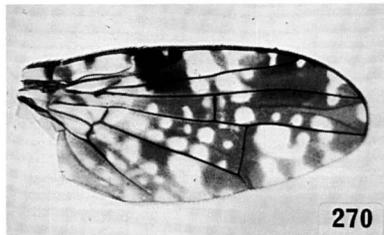
Figs 263–270. Tephritidae; wing pattern reticulate and with a very small hyaline spot at apex of cell r_{4+5}. 263, *Icterica westermanni*, 264, *Oxyna parietina*, 265, *O. nebulosa* (*O. flavipennis* is similar), 266, *Campiglossa argyrocephala*, 267, *C. grandinata*, 268, *Dioxyna bidentis*, 269, *Paroxyna misella* ♂ (most other *Paroxyna* species are similar), 270, *Tephritis vespertina*.
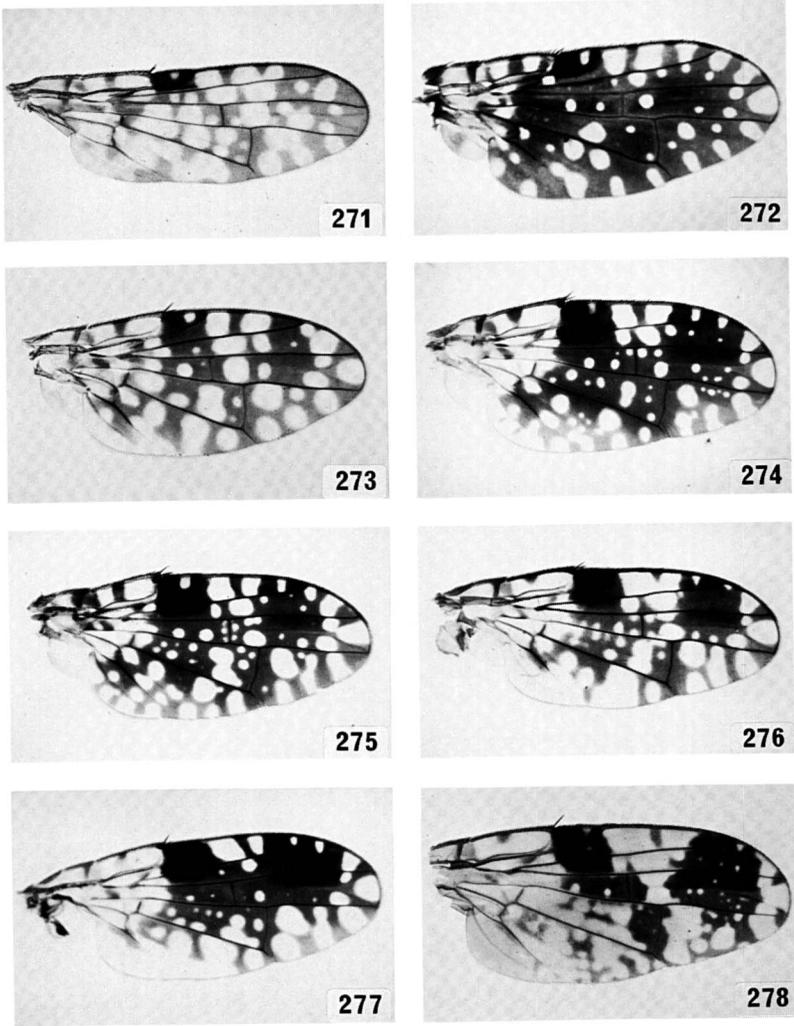
Figs 271–278. Tephritidae. 271, wing pattern reticulate and without a hyaline spot at apex of cell r_{4+5}, *P. plantaginis*. 272–276, wing pattern reticulate and with a hyaline wedge or large spot at apex. 272, *Dithryca guttularis*, 273, *Tephritis praecox*, 274, *T. conura*, 275, *T. ruralis*, 276, *T. leontodontis*, 277, *T. neesii*. 278, wing pattern reticulate and with a preapical hyaline stripe, *Tephritis bardanae*.
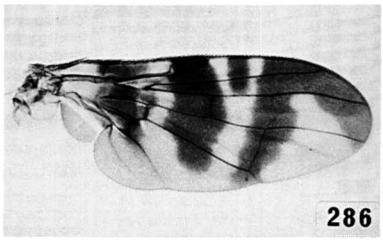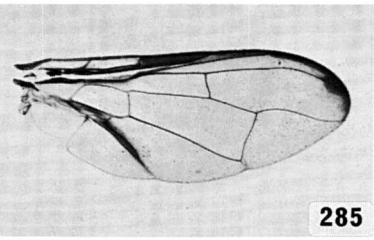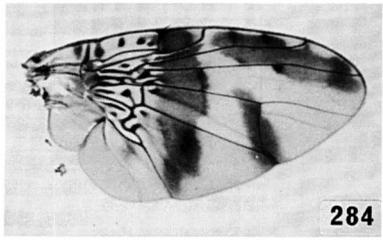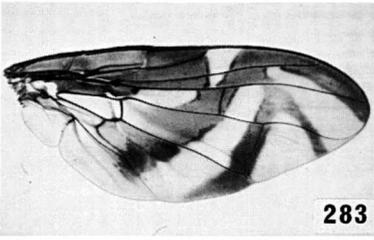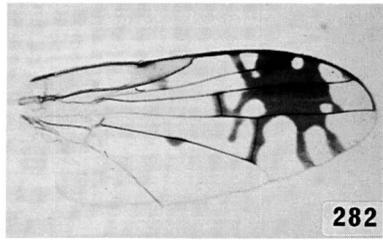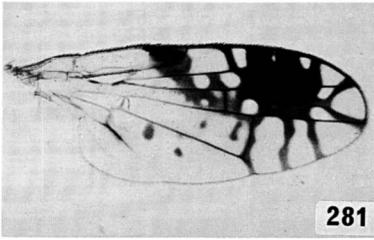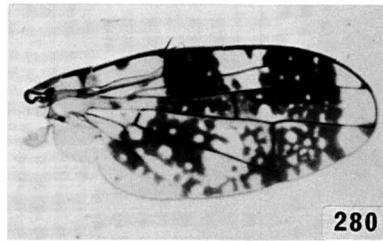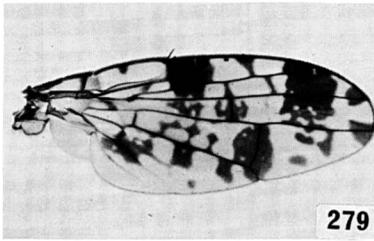
Figs 279–286. Tephritidae. 279–280, wing pattern reticulate and with a preapical hyaline stripe. 279, *T. hyoscyami,* 280, *Tephritis formosa.* 281, wing with an apical star-shaped mark and a hyaline wedge at apex, *T. cometa.* 282, wing with an apical star-shaped mark and a preapical hyaline stripe, *Trupanea stellata* (*T. amoena* is similar). 283–285, non-British species sometimes imported in fruit. 283, *Anastrepha obliqua,* 284, *Ceratitis capitata,* 285, *Dacus ciliatus,* 286, *Rhagoletis cerasi.*

Index to host-plant taxa

Names in *italics* are synonyms. Page numbers in **bold** refer to pupal keys and lists of associated tephritids.

Index to tephritids and other insect taxa

Names in *italics* are synonyms. Page numbers in **bold** refer to descriptive details of adults and host lists; numbers in *italics* refer to pages with figures.

132