

A revision of the western Palaearctic species of *Urophora* Robineau-Desvoidy (Diptera: Tephritidae)

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ABSTRACT. A key is provided to twenty-four western Palaearctic species of *Urophora* Robineau-Desvoidy. The hosts of twenty-three species which attack Asteraceae are listed, including those being used or investigated as possible weed biocontrol agents. The species are divided into four species groups and the differing host relationships and types of galls induced by these groups are discussed. *U. lopholomae* sp.n. and *U. affinis* ssp. *calci-trapae* ssp.n., associated with *Centaurea* (*Lopholoma*) spp. and *C. (Calci-trapa)* spp. respectively, are described. *U. algerica* (Hering) and *U. sjumorum* (Rohdendorf) are both treated as subspecies of *U. quadrifasciata* (Meigen). *U. pontica* is given full specific status and *U. hispanica* is removed from synonymy. The following new synonymies are made (junior synonyms in parentheses): *U. angustifascia* (Hering) (= *Euribia phaeocera* Hering); *U. cardui* (Linnaeus) (= *U. reaumurii* Robineau-Desvoidy, lectotype designated); *U. jaceana* (Hering) (= *E. conyzae* Hering); *U. maura* (Frauenfeld) (= *E. tecta* Hering); *U. mauritanica* Macquart (= *U. lejura* Rondani, *Trypeta macrura* Loew); *U. solstitialis* (Linnaeus) (= *E. sonderupi* Hering, *U. veruata* Rondani); *U. stylata* (Fabricius) (= *E. pia* Hering, *U. vulcanica* Rondani); *U. terebrans* (Loew) (= *E. approximata* Hering, *T. eriolepidis* Loew, *E. manni* Hendel). The possibility that *U. quadrifasciata* is a species complex is discussed; it is also suggested that *U. affinis* and *U. jaceana* represent the morphological extremes of a complex. The misuse of the name *Musca stylata* Fabricius in the genus *Myopites* Blot is noted.

Introduction

The genus *Urophora* includes about 100 species, sometimes known as gall flies, most of which are Palaearctic. However, the genus also includes seven Nearctic species, thirty-two Neotropical species, five Afrotropical species and two Oriental species. This genus is placed in the subfamily

Myopitinae (=Euribiinae, Urophorinae), and, like the related genus *Myopites* Blot, species of known biology induce galls in their hosts, which are members of the plant family Asteraceae (=Compositae). These galls are usually formed within the plant's capitulum (flower or seed head), but *U. cardui* induces a stem gall. The best known example of the genus is the knapweed gall fly (*U. jaceana*), which was the subject of a life-table study (Varley, 1947) which is still

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regarded as a classical example of the life-table technique.

Some *Urophora* species are actual or potential agents for the biological control of composite (Asteraceae) plants of Palaearctic origin that have become noxious weeds in North America (Julien, 1987). The species which have been successfully established are *U. affinis* and *U. quadrifasciata* for *Centaurea* cf. *maculosa* and *C. diffusa*, *U. cardui* for *Cirsium arvense*, and *U. stylata* for *Cirsium vulgare*; two additional species are currently being considered as potential biocontrol agents, namely *U. sirunaseva* for *Centaurea solstitialis*, and *U. solstitialis* for *Carduus acanthoides* and *C. nutans* (Harris, 1984a, b; Harris & Wilkinson, 1984; Peschken, 1984; White & Clement, 1987).

The aims of this paper are to provide a revised key to the European and Mediterranean species of *Urophora*, list the confirmed host-plants of each species, and to discuss possible species complexes. This paper covers all the *Urophora* species known from Europe, and the countries which border the Mediterranean Sea, but excluding Soviet Europe. A second paper is planned (Korneyev & White, in prep.) which will cover the species known from the U.S.S.R. and other Palaearctic areas not covered in this paper. A paper dealing exclusively with the species of relevance to North American weed biocontrol programmes has already been published (White & Clement, 1987). A comprehensive catalogue of published notes on the biology of *Urophora* species is not included; most references of this kind are listed by Hennig (1953, 1968), Ferrar (1987) and White (1988).

Taxonomic history of the Palaearctic *Urophora* species

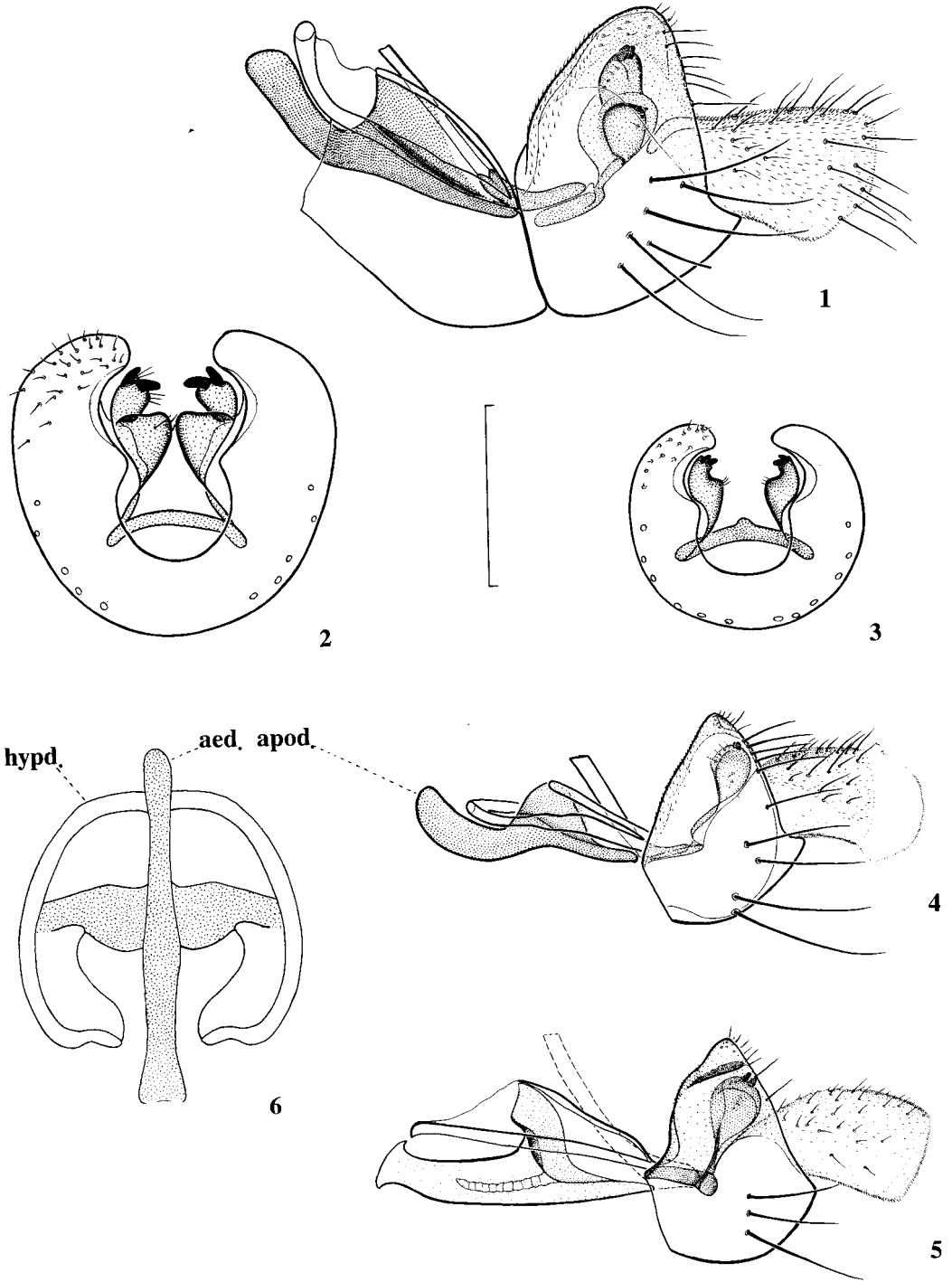
The genus was first named by Meigen (1800) as *Euribia*, to include eighteen unlisted species. Later, *Urophora* was described by Robineau-Desvoidy (1830), who included *Musca cardui* Linnaeus, which was subsequently designated as the type species by Westwood (1840). Between 1835 and 1855 J. Macquart described several Diptera as *Urophora*, most of which are no longer included in the genus, and many of these are now referred to the Platystomatidae and Pyrgotidae. Rondani (1870) described several Italian species of *Urophora*, all of which have

been kept in the genus, and it is his restricted interpretation of the genus which is still applied today. The only named subgenus is *Asimoneura* which was described by Czerny (in Czerny & Strobl, 1909) for the Spanish species, *U. stroblii* Czerny. Between 1909 and 1963 the earlier name of *Euribia* was used by authors such as Hendel (1927) and Hering (1933, 1935, 1937, 1938a, b, 1940, 1941, 1953, 1956, 1961). However, in 1963 the International Commission for Zoological Nomenclature (opinion 678) ruled that the pamphlet of Meigen (1800) be suppressed and all species described as *Euribia* should therefore be placed in *Urophora*. The recent *Catalogue of Palaearctic Diptera* (Foote, 1984) listed sixty-five species, thirty-three of which occur within the area covered by this paper. Since completion of the catalogue a further species has been described from this area by Freidberg (1982); Korneyev (1984, 1985) has added four species from the U.S.S.R., and single species have been described from Japan (Ito, 1983) and Korea (Kwon, 1985). The present paper describes one additional species and a subspecies, and reduces the western Palaearctic list to twenty-five species as a result of new synonyms.

The first key covering a substantial proportion of the genus was produced by Hendel (1927) and this was added to by Hering (1933, 1937, 1938a, b, 1956, 1961). The only modern work on the genus was compiled by Steyskal (1979) who presented separate keys for the Palaearctic and New World species of *Urophora*. However, Steyskal's work was not intended to be a revision and he discussed the need for a thorough revision of the genus. Steyskal (1979) drew attention to the tentative nature of the section of his key that included many of the species of interest for the biocontrol of noxious weeds, such as *U. sirunaseva* and *U. solstitialis*. An interim attempt to resolve this problem was made by White & Clement (1987) who discussed and keyed the species being used or tested as biocontrol agents for introduction into North America.

Taxonomic characters of adult *Urophora*

Traditionally, *Urophora* species have been identified primarily by characteristics of their wing patterns (Figs 65–68), together with femur, palp and antenna colour differences. Hering (1940) was the first author to utilize the shape of



FIGS 1-6. *Urophora* male terminalia. Figs 1-2, *U. cardui*; 1, lateral view of sternite 5, surstyli and aedeagal apodeme (stippled); 2, posterior view of surstyli. Figs 3-4, *U. lopholomae*; 3, posterior view of surstyli; 4, lateral view of surstyli and aedeagal apodeme (stippled). Fig. 5, *U. pontica*, lateral view of surstyli and aedeagal apodeme (stippled). Fig. 6, *U. solstitialis*, dorsal view of hypandrium and aedeagal apodeme (stippled). Scale line=0.2 mm. aed. apod., aedeagal apodeme; hypd., hypandrium.

the apex of the aculeus, or ovipositor piercer, as an aid to species diagnosis, but he seldom used the method in subsequent papers referring to the genus. Steyskal (1979) illustrated the aculeus tip shape for a few species, but not enough to enable the accurate identification of many of the critical species. In this paper, aculeus apex shape is used as a major identification character (Figs 30–64). Most species have very similar male terminalia, with neither the surstyli (Figs 1–5, 7, 8, 10, 11), or the poorly sclerotized aedeagal glans (Figs 12–16) yielding tenable diagnostic characters. However, a few species have well-sclerotized aedeagal glans and male terminalia characters can be used to divide the genus into four species groups; the critical characters are presented in the group diagnoses. Another male character that is sometimes species specific is the shape of the abdominal sternites (Figs 17–22). These vary from being very broad in the stem gall forming *U. cardui* (Fig. 21), to very narrow in *U. angustifascia* and both of the *Echinops* associated species (Figs 19–22). However, other species are very variable and have a sternite shape between those two extremes (Figs 17, 18), although there may sometimes be a deep cleft in the most heavily sclerotized part of sternite 5, sometimes approaching the depth shown in Fig. 22.

Most of the terminology used is that of White (1988) which was based on the system of McAlpine (1981); however, the term distiphallus has been corrected to aedeagal glans (Foote & Steyskal, 1987). The terms primary and secondary aculeus steps are also used; an aculeus with a single pair of preapical steps or shoulders is said to have primary steps only (e.g. Figs 43–45); an aculeus with two pairs of steps has both primary (proximal) and secondary (distal) steps (e.g. Figs 52–55). Following Steyskal (1979), the wing crossbands are named subbasal (covering bm-cu), discal (covering r-m), preapical (covering dm-cu) and apical; see Figs 66–68 for examples with all four crossbands. Measurements were only taken from dissected females, and these are given in the species descriptions, with dimensions of exceptionally small or large individuals given in parentheses; males tend to smaller than females. The following abbreviations are used for measurements:

- AL = Aculeus length (millimeters).
- WL♀ = Wing length of female (millimetres)
- AL/WL = Aculeus length divided by wing length.

Immature stages

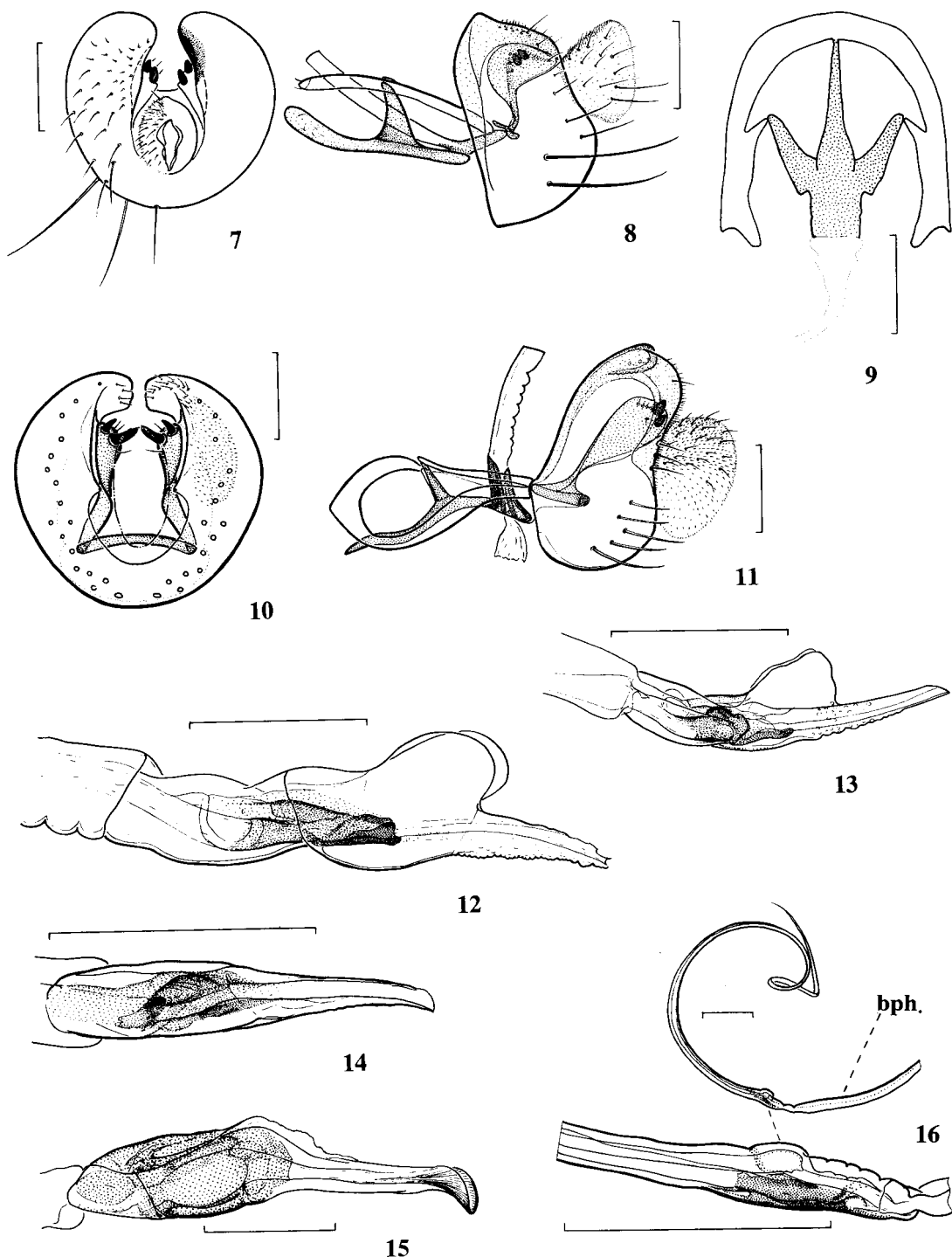
A comprehensive study of larval and pupal stages is beyond the scope of this paper. However, pupal characters for most of the British species of *Urophora* have been tabulated by White (1988). Published larval descriptions are catalogued by Hennig (1968) and Ferrar (1987), and these authors also tabulate some larval characters.

The eggs of many tephritids can be dissected from museum-preserved adult females. Unfortunately this is rarely possible with *Urophora* species, suggesting that their eggs are generally less sclerotized than those of other Tephritidae. Eggs of *U. stigma* and *U. hispanica* were found in dry preserved specimens, but those of *U. affinis* and *U. jaceana* could only be extracted from specimens preserved in alcohol. It was found that the eggs of *U. stigma* are about 0.6 mm long, very broad and have a distinct apical opening (Fig. 24) which is presumed to be a micropyle (see Margaritis, 1985). The eggs of the other species examined are much narrower and 0.6–0.8 mm long (Fig. 23). In the species groups proposed below, *U. stigma* is placed in a different group to the other three species whose eggs were examined, and this suggests that egg structure may differ between the groups.

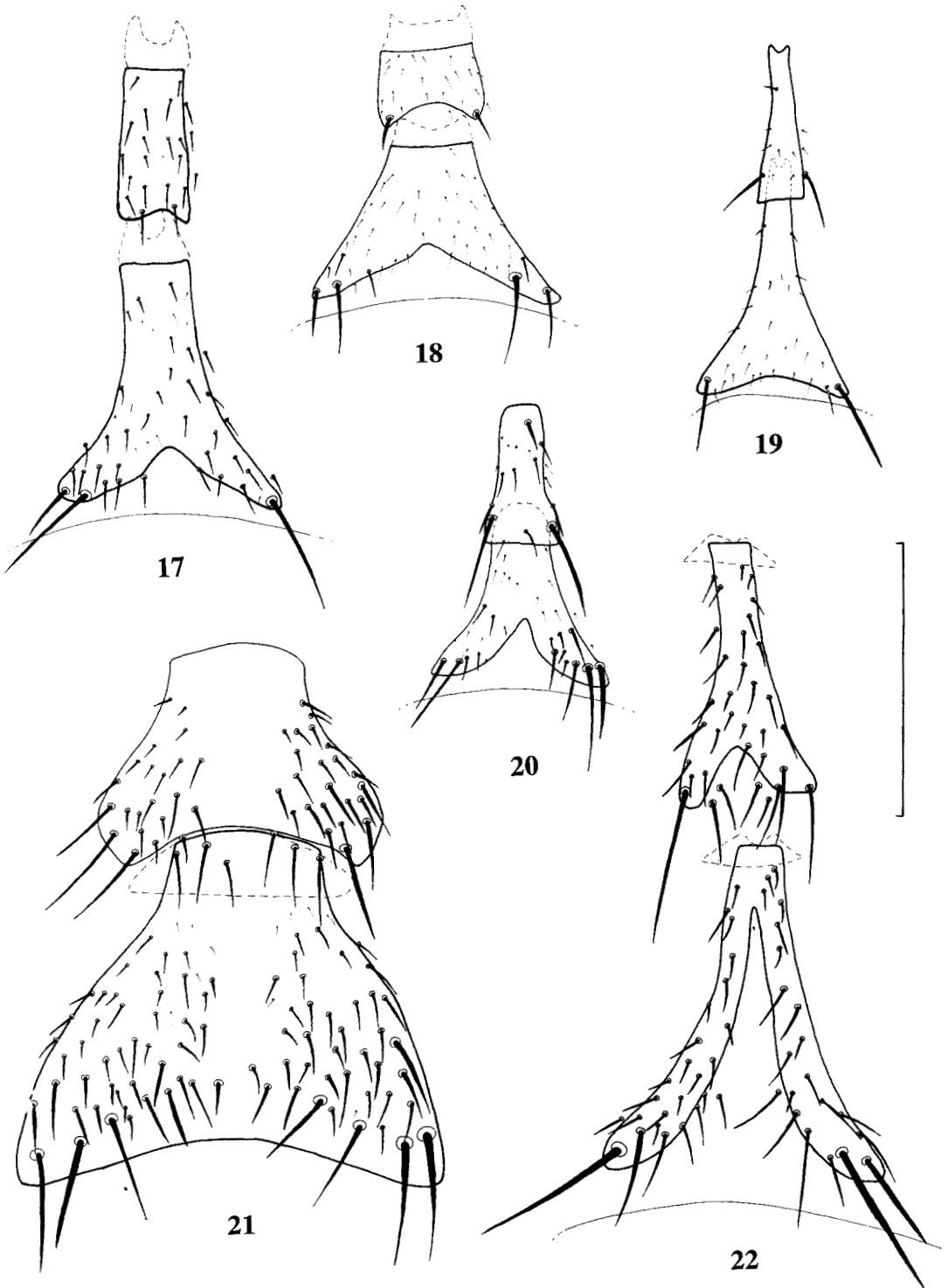
Species groups

The genus was first divided into species groups by Dirlbekova & Dirlbek (1980) who recognized three groups, namely 'stigma', 'cardui' and 'solstitialis', based on types of wing pattern. These authors also presented a key to the 'stigma' species group of *Urophora* which have hyaline rather than patterned wings. However, the present paper rejects this system of species groups in favour of one based on terminalia characters.

Each of the species groups defined in the present paper appears to be associated with a different tribe of the composite subfamily Asteroideae, as follows: group 1 includes all except three of the Palaearctic species and all those of known biology are associated with the Cardueae; group 2 is *U. maura* which is associated with *Inula* species (Inuleae); group 3 includes *U. stroblii* whose host-plant is unknown and most, perhaps all, of the Afrotropical species; group 4 is *U. stigma* which is believed



FIGS 7–16. *Urophora* male terminalia. Figs 7–9, *U. maura*; 7, posterior view of surstyli; 8, lateral view of surstyli and aedeagal apodeme (stippled); 9, dorsal view of hypandrium and aedeagal apodeme (stippled). Figs 10–11, *U. stigma*; 10, posterior view of surstyli; 11, lateral view of surstyli and aedeagal apodeme (stippled). Figs 12–16, lateral view of aedeagal glans; 12, *U. cardui*; 13, *U. lopholomae*; 14, *U. pontica*; 15, *U. stigma*; 16, *U. maura*, showing part of basiphallus (bph.), plus detail of basal part of glans. Scale lines=0.1 mm.



FIGS 17–22. *Urophora* male sternites 4 and 5, ventral view, 17, *U. solstitialis*; 18, *U. affinis*; 19, *U. angustipennis*; 20, *U. pontica*; 21, *U. cardui*; 22, *U. syriaca*. Scale line=0.5 mm.

to attack several species of Anthemideae; other undefined species groups include the New World species. These species groups are not formally named here because many of the eastern Palaearctic species have not been examined. Consequently, the old subgeneric limits are retained here, but they will probably be altered in a forthcoming study of the eastern Palaearctic species by the present authors.

Group 1 (subgenus *Urophora* in part): Species with known hosts are all associated with species of Cardueae (=Cynareae). Some species are known to spend the first larval instar in the egg and emerge as second instars; these are *U. cardui* (Peschken & Harris, 1975), *U. jaceana* (Varley, 1937) and *U. stylata* (Redfern, 1968). Species which are known to emerge as first instar larvae are *U. affinis* and *U. quadrifasciata* (P. Harris, pers. comm.). Of these species, those that hatch as second instar larvae induce multilocular galls, while those that hatch as first instar larvae induce unilocular galls (P. Harris, pers. comm.). Group 1 species of known biology induce a variety of gall types, usually formed of receptacle tissue (Zwölfer, 1983; Harris & Myers, 1984), which engulfs the larval chamber that is situated in the achene or the receptacle (Freidberg, 1984). These galls are lignified and may be multilocular, e.g. *U. jaceana* (Varley, 1947) and *U. stylata* (Harris & Wilkinson, 1984) or unilocular, e.g. *U. affinis* (P. Harris, pers. comm.), *U. jaculata* and *U. sirunaseva* (White & Clement, 1987); often, unilocular galls occur multiply within a single flower head and they can be confused with the true multilocular galls. Conversely, *U. quadrifasciata* forms a papery, non-lignified, gall from the ovary wall (Harris & Myers, 1984). The only species known to form a gall which is not within the capitulum of its host-plant, is *U. cardui* which forms a multilocular stem gall (Lalonde & Shorthouse, 1982) on a narrow range of *Cirsium* species. It is likely that gall-type could be a useful classificatory character, but details of this kind are not yet available for most species. Members of this group are found throughout the Palaearctic region, with a single species in Taiwan, *U. formosana* (Shiraki), and introduced species in North America and Australia.

Group 2 (subgenus *Urophora* in part): *U. maura* is the only known member of this group and it is associated with *Inula* species (Inuleae). Both the male and female terminalia

of *U. maura* show a greater similarity to *Myopites* species than to other *Urophora* species; see illustrations of *Myopites aculeus* and aedeagal glans shapes given by Freidberg (1980) and White (1988). In particular, the aedeagal glans of *U. maura* is a simple long tube with a sclerotized area near its base (Fig. 16), very similar to known *Myopites* species; however, *U. maura* lacks the apical 'cup' shaped structure that is typical of *Myopites* species. Both *U. maura* and members of the closely related genus *Myopites* induce galls in the capitula of species of Inuleae and it is possible that *U. maura* is cladistically at least as closely related to *Myopites* species as it is to other *Urophora* species.

Group 3 (subgenus *Asimoneura* in part): *U. stroblii* is the only confirmed member of this species group, but its biology is unknown. This species has a very long labellum, a black scutellum and hyaline wings. The known Afrotropical species of *Urophora* also have these features and some, possibly all, of them may belong to this group. The only Afrotropical species dissected, *U. petiolata* Munro, was found to be similar to *U. stroblii* in terms of the terminalia characters given in the group diagnosis, although the 'arms' of its aedeagal apodeme were broader. Many of the Afrotropical species are associated with *Vernonia* (Vernonieae) (A. Freidberg, pers. comm.); an exception is the Afrotropical *U. pantomelaena* Bezzi which develops in the capitulum of *Helichrysum setosum* (Inuleae) (Munro, 1926) and this may prove to belong to group 2. It is also likely that *U. shirakii* (Munro) from Taiwan belongs to this species group.

Group 4 (subgenus *Asimoneura* in part): *U. stigma* is the only known member of this species group and it forms a single non-lignified unilocular gall in a capitulum of an *Achillea* species (Anthemideae). Old host records suggest that it may also develop in the capitula of *Anthemis* and *Chrysanthemum*, which is likely because these genera also belong to the composite tribe Anthemideae.

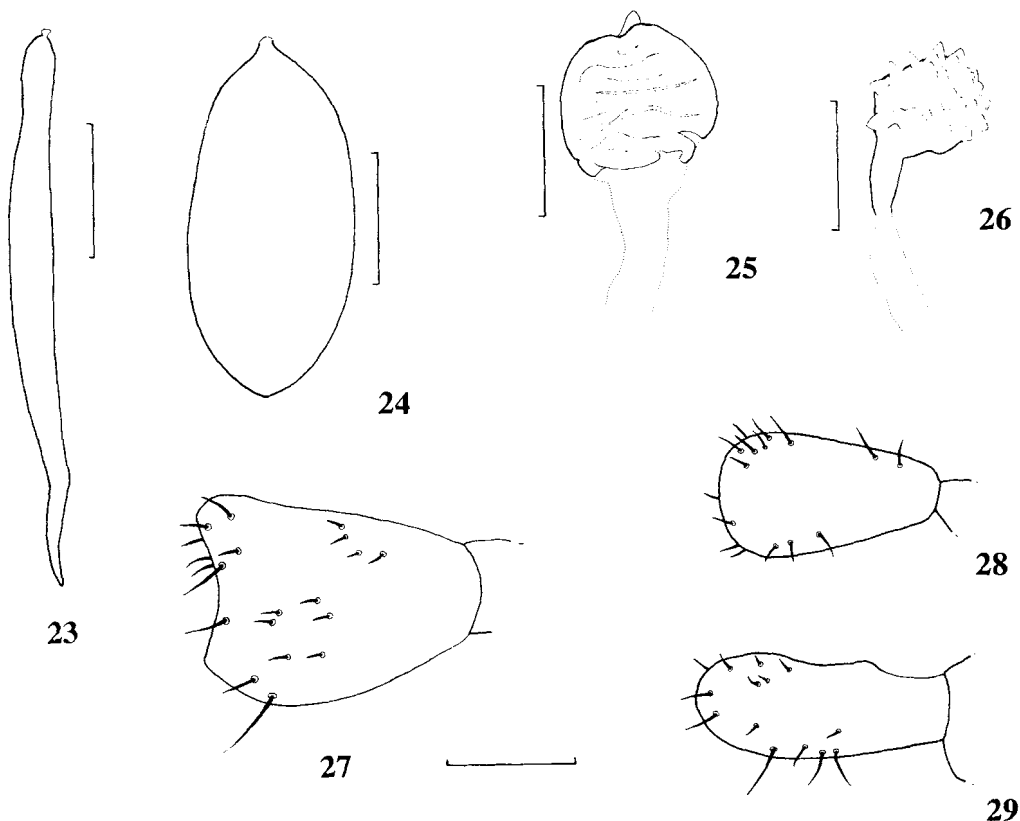
Possible groups 5 onwards: an examination of the New World species of *Urophora* is beyond the scope of this paper. However, an examination of the key and descriptions produced by Steyskal (1979) suggests that none of the species native to the New World belong to the above species groups, and it is likely that all of the New World's native species belong to one or more as yet unrecognized species groups which a future

reviser may decide to regard as separate genera. Little is known of their host-plants, but species of known biology appear to be associated with composite tribes such as Astereae and Heliantheae, neither of which are known host-plant groups for Old World *Urophora* species.

Key to females of western Palaearctic *Urophora* species

The following key uses external characters as far as possible. Host plants are used as key characters so that host-associated specimens of most species can be provisionally identified without the need for dissection. However, identifications made in this way should always be confirmed by dissection of female specimens. The major divisions in the key are based on external characters,

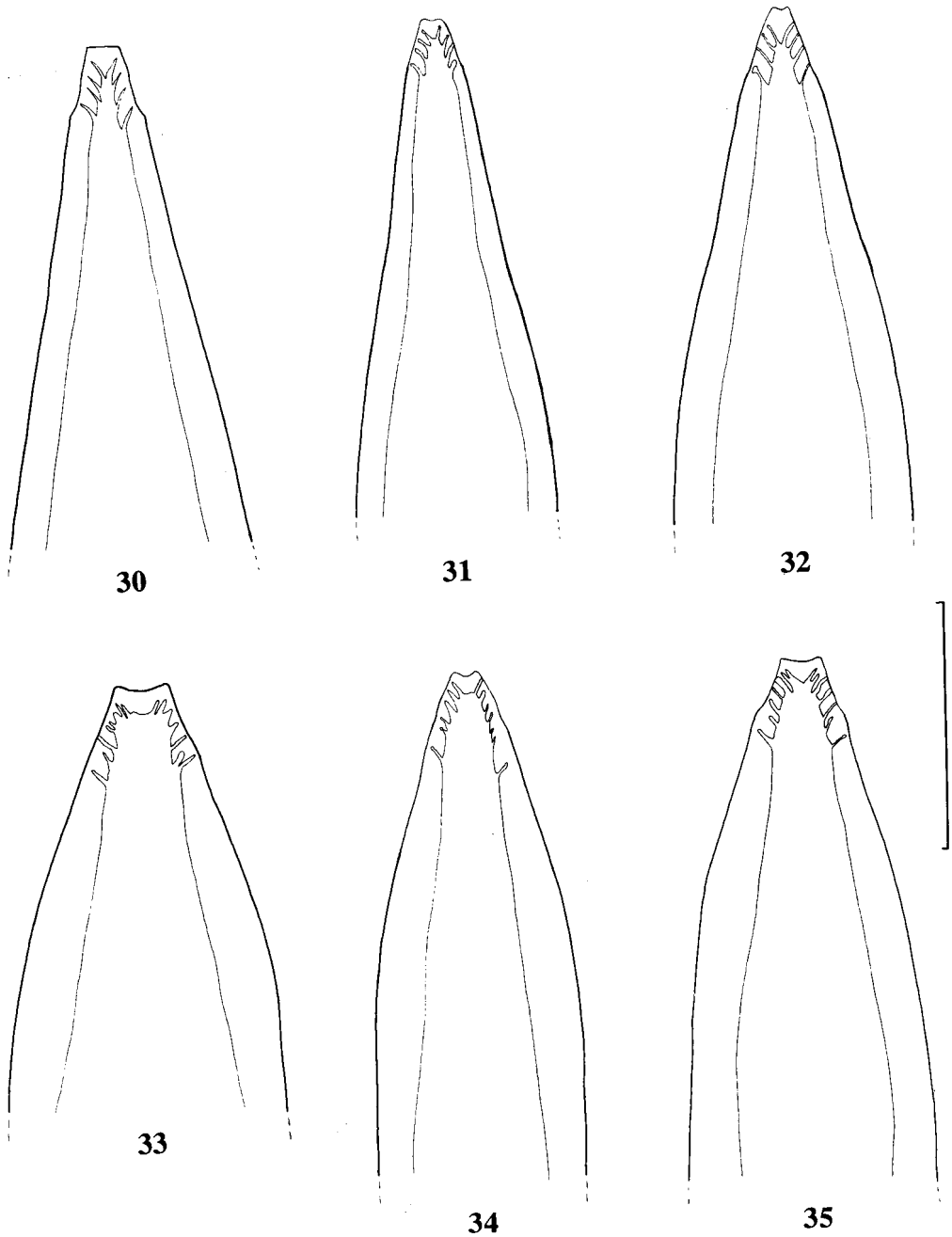
such as wing pattern, and the colour of the first flagellomere and femora. Specimens with aberrant wing patterning are fairly common and these will not run correctly in the following key. However, the alternative method of producing a key to this genus is to use aculeus tip shape characters for the major divisions in the key. Such a key might be slightly more reliable, but it does necessitate dissection of all species, even if they are almost always easily distinguished by simple external characters. Confirmatory characters are given in square brackets and the descriptions should be consulted for other details such as measurements. Identification by aculeus tip shape is facilitated by the figures of the aculeus tips (Figs 30–64) which are grouped according to tip shape. *U. satunini* is not included in the following key because it was not available for study.



FIGS 23–29. Figs 23–24, *Urophora* eggs; 23, *U. hispanica*; 24, *U. stigma*; scale lines=0.2 mm. Figs 25–26, spermathecae; 25, *U. maura*; 26, *U. stigma*; scale lines=0.05 mm. Figs 27–29, lateral views of palpi; 27, *U. syriaca*; 28, *U. pontica*; 29, *U. cardui*; scale line=0.2 mm.

- 1 Labellum about 3 times as long as first flagellomere. [Wings hyaline, at most with a darkened cell sc and a faint trace of an apical crossband.] sg. *ASIMONEURA* 2
- Labellum less than 3 times as long as first flagellomere (usually less than 2 times, except in *Echinops* associated species, which have distinct wing crossbands). [Scutellum yellow, at least centrally, except in very dark specimens of *U. aprica*.] s.g. *UROPHORA* 3
- 2 Scutellum black. [Aculeus, Fig. 63. Spain.] *stroblii*
- Scutellum yellow centrally, black laterally. [Aculeus, Fig. 64. Associated with *Achillea* and perhaps other genera of the tribe Anthemideae, namely, *Anthemis* and *Leucanthemum*. Central Europe, east to Kazakh S.S.R.] *stigma*
- 3 Wing hyaline, sometimes yellow infuscate, but lacking any black or dark brown crossbands. 4
- Wing with distinct black or dark brown crossbands (Figs 65–68). 6
- 4 Femora yellow. Associated with *Inula*. Aculeus pointed, without subapical steps (Fig. 62). Spermathecae sclerotized (Fig. 25). [Central Europe, south-western U.S.S.R.] *maura*
- Femora black, at least in most of basal half. Not associated with *Inula*. Aculeus apex not pointed, with preapical steps (Figs 46, 54). Spermathecae poorly sclerotized (cannot normally be found). 5
- 5 Wing yellow infuscate, at least between veins C and R₄₊₅. Associated with *Cousinia*. Aculeus apex with indistinct secondary steps' (Fig. 46). [Northern Israel.] *hermonis*
- Wing largely colourless, except for cell sc which is yellow, and the costal area which may be slightly darkened. Associated with *Serratula*. Aculeus with distinct secondary steps (Fig. 54). [Southern England.] *spoliata*
- 6 Subbasal crossband absent (Fig. 65), or if present, separated from vein C (costa) by a hyaline area. 7
- Subbasal crossband present and connected to vein C (Figs 66–68) 9
- 7 Aculeus without preapical steps (Fig. 37), or with indistinct steps (Fig. 36). [Associated with *Mantisalca* and some *Centaurea* species. Preapical and apical crossbands usually separate. Southern France, Spain] *hispanica*
- Aculeus with distinct primary steps (Figs 45, 56–59). 8
- 8 Aculeus with ill-defined secondary steps (Figs 56–59). Associated with some *Centaurea* species, mainly belonging to subgenera *Acrolophus* and *Calcitrapa*. Wing usually with a rudimentary subbasal crossband. Preapical and apical crossbands usually separate. [Central Europe, east to Afghanistan; introduced to western North America.] *affinis*
- Aculeus without secondary steps (Fig. 45). Associated with some *Cirsium*, *Carduus* and *Galactites* species. Wing usually without any trace of a subbasal crossband. Preapical and apical crossbands usually joined. [Throughout most of the Palaearctic region; introduced to western North America; accidentally established in Australia.] *stylata*
- 9 Discal and preapical crossbands joined, from midway between veins M and CuA₁, to hind margin of wing (Fig. 68). [Large, wing more than 3.5 mm long. Each femur usually black in basal two-thirds, sometimes with a pale stripe along posterior side, rarely predominantly orange. Forms a stem gall on some species of *Cirsium*. Aculeus short in comparison to body size; less than 0.4 times as long as wing (Fig. 43). First flagellomere orange. Western and central Europe, the Balkans, east to Kazakh S.S.R.; introduced to western North America.] *cardui*
- Discal and preapical crossbands separate (Figs 66, 67). 10
- 10 Each femur dark brown or black, at least in the basal two-thirds, at most with a stripe of dark orange (some individuals of *U. terebrans* only) 11
- At least some femora predominantly orange, at most marked with black areas, often streaked with black. [First flagellomere orange or yellow.] 18
- 11 Wing base black. Associated with *Echinops*. Palpi black and broad (Figs 27, 28). [Aculeus pointed, without any preapical steps (Fig. 41). First flagellomere dark orange or grey, at least on outer side. Femora dark orange to black.] 12
- Wing base yellow or hyaline. Not associated with *Echinops*. Palpi yellow, usually darkened to orange apically (except for some *U. angustifascia* which are darkened to black apically), and narrower (similar to Fig. 29). 13
- 12 Large, wing more than 3.5 mm long, aculeus more than 2.0 mm long. Palpi shaped as Fig. 27. Proximal edge of preapical crossband sinuate, usually meeting vein C almost opposite r-m crossvein. [Northern Israel, Lebanon, western Syria.] *syriaca*
- Small, wing less than 3.5 mm long, aculeus less than 2.0 mm long. Palpi shaped as Fig. 28. Proximal edge of preapical crossband concave, meeting vein C about half way between the r-m and dm-cu crossveins. [Southern Europe and southern U.S.S.R.] *pontica*
- 13 First flagellomere usually grey or black, at least on outer side; if first flagellomere yellow or orange (some forms of *U. quadrifasciata*) then basal scutellar setae based at the margin of the black

- and yellow areas, and aculeus apex truncate and without any distinct preapical steps (Figs 31–35). Subbasal and discal crossbands joined between veins C and R_{4+5} , between C and R_1 , or between R_1 and R_{4+5} (Fig. 67). Cell c black, at least in distal two-thirds 14
- First flagellomere yellow or orange. Subbasal and discal crossbands usually separated by a yellow or hyaline area (similar to Fig. 66); if subbasal and discal crossbands joined (some *U. aprica*) then basal scutellar setae based in the black lateral areas of the scutellum, and aculeus apex with distinct preapical steps (Figs 48, 49). Cell c hyaline, or at most darkened centrally (except some *U. aprica*). 16
- 14 Separation of discal and preapical crossbands along vein R_{4+5} about 2.5 times as great as breadth of preapical crossband on R_{4+5} . Cell c hyaline in at least basal third. Subbasal and discal crossbands only joined between veins C and R_1 . Associated with *Cousinia*. Aculeus apex pointed (Fig. 40). [First flagellomere black. Turkey to Afghanistan.] *angustifascia*
- Separation of discal and preapical crossbands along vein R_{4+5} less than breadth of the preapical crossband on R_{4+5} . Cell c entirely black. Subbasal and discal crossbands joined between C and R_{4+5} . Not associated with *Cousinia*. Aculeus apex truncate (Figs 30–35) 15
- 15 Subbasal crossband reaching hind margin of wing. Associated with *Ptilostemon*. [Aculeus, Fig. 30. First flagellomere black, Crete.] *neuenschwanderi*
- Subbasal crossband not reaching hind margin of wing. Associated with *Centaurea*. [Aculeus, Figs 31–35. Western Palaearctic, east to Pakistan; introduced to western North America; accidentally established in Australia.] .. *quadrifasciata*
- 16 Associated with large thistles. Large, female wing length more than 4.0 mm, aculeus length more than 2.0 mm (Fig. 55). Yellow area on disc of scutellum broad, basal scutellar setae usually based at the margin of the yellow and black areas. [Known hosts are *Cirsium eriophorum*, *C. vulgare*, *Onopordon* sp., and probably *Carlina vulgaris* and *Cynara cardunculus*. Southern and central Europe.] *terebrans*
- [Some aberrant individuals of *U. solstitialis* have dark femora and these may be confused with *U. terebrans*. However, these individuals usually have the basal scutellar setae based within the black lateral areas of the scutellum and they are only known to be associated with *Carduus defloratus*. Furthermore, the aculeus is usually shorter and the section between the primary and secondary steps usually longer than in *U. terebrans* (Fig. 53). See the redescrptions of these species for further details.]
- Associated with knapweeds or cornflower (*Centaurea*). Small, female wing length less than 4.0 mm, aculeus length less than 2.0 mm. Yellow area on disc of scutellum narrow, basal scutellar setae usually on a black ground. 17
- 17 Aculeus without secondary steps; distance between primary steps and apex less than breadth of aculeus section beyond primary steps (Fig. 47). Only known to be associated with *Centaurea* subgenus *Lopholoma*, e.g. *C. sadleriana* and probably *C. scabiosa*. [Austria, Hungary and south-western U.S.S.R.] *lopholomae*
- Aculeus with secondary steps (Figs 48, 49), which are not always very distinct (Fig. 48); distance between primary steps and apex longer than breadth of aculeus section beyond primary steps (Figs 48, 49). Associated with *Centaurea* subgenus *Cyanus*. [France, Italy, Sweden, Turkey and south-western U.S.S.R.] *aprica*
- 18 Associated with *Carthamus*. Aculeus pointed and with primary steps only; apex pointed (Fig. 42). [Mediterranean area.] *mauritanica*
- Not associated with *Carthamus*. Aculeus usually not pointed; if aculeus pointed, then without any preapical steps (*U. jaculata*, Figs 38, 39); if aculeus with primary steps only (*U. congrua*), then apex truncate (Fig. 44). 19
- 19 Associated with *Carduus* or *Cirsium*. Aculeus section distal to primary steps elongate (Figs 44, 53); secondary steps, if present, separated from preapical steps by a greater distance than the breadth of the aculeus between the primary and secondary steps (Fig. 53). 20
- Associated with *Centaurea*. Aculeus section distal to primary steps less elongate (except in *U. sp.* near *cuspidata*, Fig. 51); secondary steps often absent (Figs 38, 39), or if present, either indistinct (Figs 48, 60, 61), or separated from primary steps by a distance which is less than the breadth of the aculeus between the primary and secondary steps (Figs 49, 50, 52). 21
- 20 Aculeus without secondary steps (Fig. 44). [Associated with *Cirsium erisithales*. Austria.] *congrua*
- Aculeus with secondary steps (Fig. 53). [Throughout the western Palaearctic region.] *solstitialis*
- 21 Aculeus with very prominent preapical steps and a deep apical notch (Figs 50, 51); aculeus usually more than 3.0 mm long. 22
- Aculeus usually without such prominent preapical steps, or an apical notch (Figs 38, 39, 52, 60, 61) (except *U. aprica*, Figs 48, 49); aculeus usually less than 2.5 mm long. 23
- 22 Associated with *Centaurea* subgenus *Lopholoma*. Aculeus with secondary steps (Fig. 50). [Northern, western and central Europe, east to central Asia.] *cuspidata*
- Associated with *Centaurea (Cyanus) depressa*. Aculeus without secondary steps (Fig. 51). [Turkey.] indet. species near *cuspidata*



FIGS 30–35. *Urophora* aculeus apices that are truncate and lack distinct preapical steps, dorsal views; 30, *U. neuenschwanderi*; 31, *U. quadrifasciata quadrifasciata*; 32, *U. quadrifasciata sjumorum*. Figs 33–35, *U. quadrifasciata algerica*; 33, Algerian form; 34, western Mediterranean form on *Centaurea aspera*; 35, Italian form on *C. nicaeensis*. Scale line=0.1 mm.

- 23 Associated with *Centaurea* subgenus *Cyanus*. At least hind-femora predominantly black. Aculeus with a distinct apical notch (Figs 48, 49). Yellow area on disc of scutellum narrow, basal scutellar setae usually on a black ground. [See couplet 17.]
..... *aprica*
- Not associated with *Centaurea* subgenus *Cyanus*. All femora predominantly orange, at most striped black. Aculeus without a distinct apical notch (Figs 38, 39, 52, 60, 61). Yellow area of scutellum broader, basal scutellar setae usually based at the margin of the yellow and black areas. 24
- 24 Associated with *Centaurea* subgenus *Jacea*. Large, wing length usually more than 3.5 mm. Aculeus with indistinct secondary steps (Figs 60, 61). Femora usually striped with black. [Northern, western and central Europe; accidental established in eastern North America.]
..... *jaceana*
- [Some aberrant individuals of *U. affinis* which are associated with *Centaurea* subgenus *Calcitrapa*, will run to *U. jaceana*.]
- Associated with *Centaurea* subgenus *Solstitiaria*. Small, wing length usually less than 3.5 mm. Aculeus either without any preapical steps (Figs 38, 39), or with distinct secondary steps (Fig. 52). Femora orange. 25
- 25 Aculeus apex pointed; without preapical steps (Figs 38, 39). Separation of discal and preapical crossbands along vein R_{4+5} about equal to breadth of preapical crossband along R_{4+5} . [Italy, Greece.] *jaculata*
- Aculeus apex truncate; with distinct primary and secondary secondary steps (Fig. 52). Separation of discal and preapical crossbands along vein R_{4+5} about twice breadth of preapical crossband along R_{4+5} (except in specimens found in Crete, some areas of Turkey and Israel). [North-eastern Greece, Turkey, south-western U.S.S.R. northern Israel.] *sirunaseva*

Materials

Unless otherwise stated, only type and dissected specimens are listed under material examined; where relevant an indication is given of the number of additional undissected specimens seen and specimens without host data were only listed if they added substantially to the distribution information. Data for specimens collected outside of the western Palaearctic area are included if they add to existing knowledge of a species distribution. Full data are not given for non-type specimens, but these data are available from the senior author.

Specimens were examined from the following collections: British Museum (Natural History),

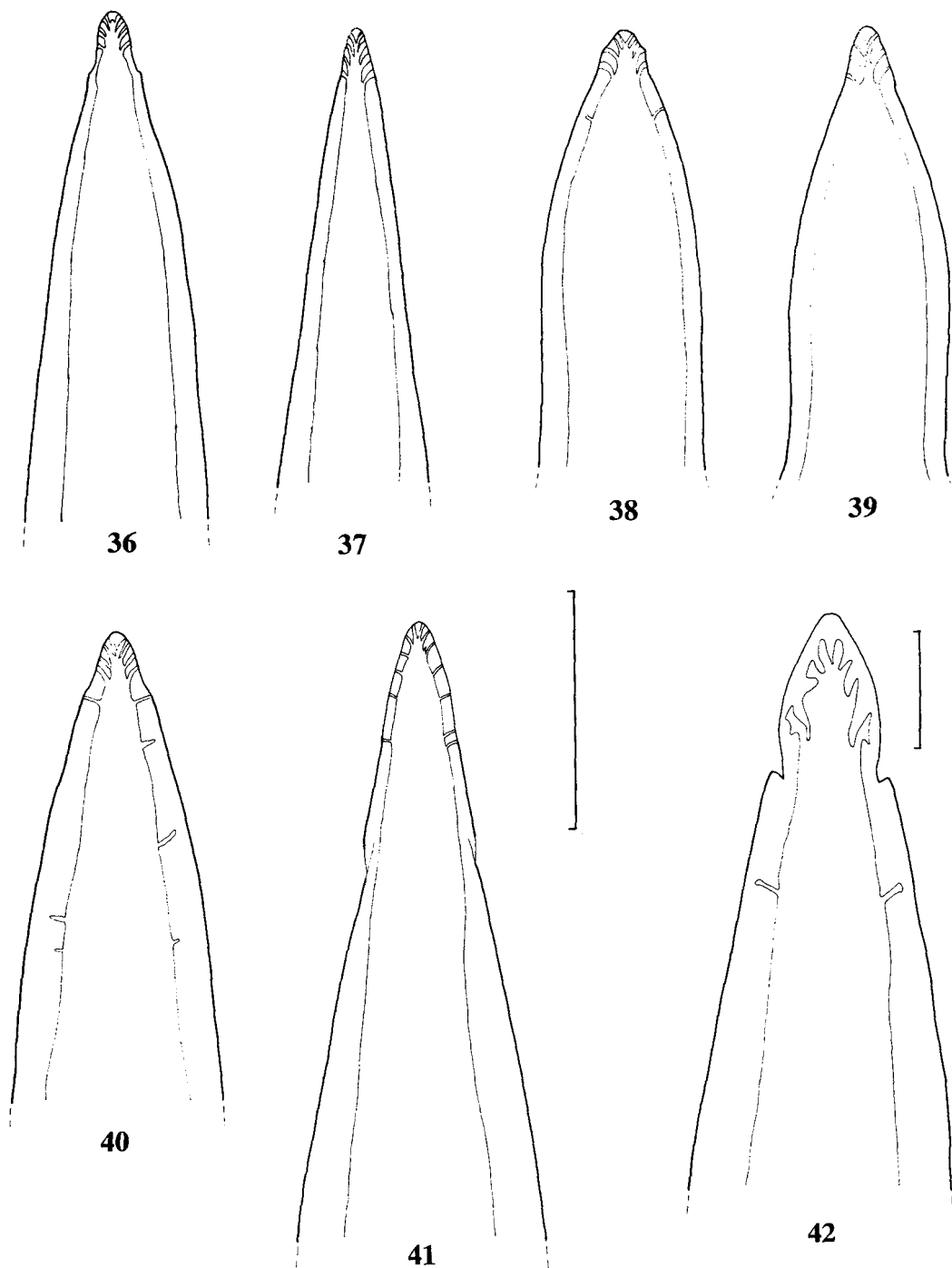
London, England (BMNH); Agriculture Canada, Regina, Canada (ACR); Linnean Society, London (LS); Lehrstuhl für Tierökologie, Universität Bayreuth, B.R.D. (LTUB); Muséum d'Histoire Naturelle, Lille, France (MHNL); Muséum National d'Histoire Naturelle, Paris, France (MNHNP); Museo Zoologico dell'Università degli Studi di Firenze, Florence, Italy (MZF); Naturhistorisches Museum, Vienna, Austria (NHMV); National Museum of Ireland, Dublin, Republic of Ireland (NMID); Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS); All-Union Institute of Biocontrol for Plant Protection, Kishinev, U.S.S.R. (IBPPK); Staatliches Museum für Naturkunde, Stuttgart, B.R.D. (SMNS); Tel Aviv University, Israel (TAU); Termesztudományi Múzeum, Budapest, Hungary (TMB); University Museum, Oxford University, England (UMO); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); Zoological Institute, Soviet Academy of Sciences, Leningrad, U.S.S.R. (ZIL); Zoologisches Museum, Humboldt Universität, Berlin, D.D.R. (ZMHB); Zoological Museum, Moscow, U.S.S.R. (ZMM); Zoologisk Museum, Universitetet i Bergen, Norway (ZMUB); Zoologisk Museum, Universitets Copenhagen, Denmark (ZMUC).

Genus *Urophora* Robineau-Desvoidy

Urophora Robineau-Desvoidy, 1830: 769. Type species: *Musca cardui* Linnaeus, 1758: 600, designated by Westwood, 1840: 149, who refers to the lectotype illustrated by Reaumur, 1738; Plate 45, Fig.14 [Westwood types validated by ICZN, opinion 71].

Euribia Meigen, 1800: 36. Type species: *Musca cardui* Linnaeus, 1758: 600, designated by Hendel, 1927: 49 [Meigen, 1800 generic names suppressed by ICZN, opinion 678].

Generic diagnosis. The genus *Urophora* may be separated from other genera of Myopitinae by the following combination of characters (Steyskal, 1979; White & Clement, 1987): Proboscis elongate, with narrow reflexed labella; vein M ending at or close to wing tip.



FIGS 36–42. *Urophora* aculeus apices that are pointed, dorsal views. Figs 36–41, without distinct steps; 36–37, extremes of form in *U. hispanica*; 38–39, extremes of form of *U. jaculata*; 40, *U. angustifascia*; 41, *U. pontica* (*U. syriaca* is very similar); scale line=0.1 mm. Fig. 42, *U. mauritanica*, which has distinct preapical steps; scale line=0.02 mm.

Subgenus *Urophora* Robineau-Desvoidy*Euribia* (*Euribia*); Hendel, 1927: 38.*Urophora* (*Urophora*); Foote, 1984: 140.

Subgeneric diagnosis. Lower facial margin not protruding; fold of proboscis and palpi not extending beyond oral margin; labellum 1–2.5 times as long as first flagellomere; scutellum yellow centrally, with lateral black margins.

***Urophora* species group 1**

Group diagnosis. Labellum usually about 1.5 times as long as first flagellomere, except for species associated with *Echinops* (*U.pontica* and *U.syriaca*) in which it is about 2.5 times as long as first flagellomere. Scutellum yellow, black at sides. Aedeagal glands reduced to a narrow membranous sac, with no heavily sclerotized areas (Figs 12–14). ‘Arms’ of aedeagal apodeme broadly joined to hypandrium (Figs 1, 4–6). Spermathecae not sclerotized (it is not usually possible to find them).

Comments. It is possible that a careful study of male terminalia characters might allow some further division of this group. For example, the only stem gall former is also the only species with remarkably broad male sternites (Fig. 21). Similarly, some of the species with pointed aculei (Figs 40, 41), also have very narrow male sternites (Figs 19–22) and the aedeagal glands of *U.pontica* and *U.syriaca* (Fig. 14) differ from other species (typically as in Figs 12, 13). *U.pontica* and *U.syriaca* are the only species associated with *Echinops*, and they also differ from other species by having very broad palpi (Figs 27, 28), a longer labellum, and by the black basal area of their wings. These data suggest that the two *Echinops* associated species could be regarded as a distinct species group, and that would concord with a recent cladistic study of the tribes of Asteraceae (Bremer, 1987) which places *Echinops* in a separate tribe (*Echinopsidae*) from the *Cardueae*.

Urophora affinis* (Frauenfeld)Trypeta affinis* Frauenfeld, 1857: 541.*Urophora affinis* (Frauenfeld); Zwölfer, 1965: 138; Steyskal, 1979: 14; Foote, 1984: 140.

Comments. The only available specimen which is almost certainly a syntype of *U.affinis* is

a male, so it cannot be confirmed that it is the species which attacks *Acrolophus* in Central Europe. However, a female which is likely to be a syntype, was dissected and the identity of this species is assumed to have been confirmed by examination of that specimen. *Urophora affinis* is here divided into two subspecies, which not only differ in their morphology, but also in their distributions and host associations. The two subspecies may be separated using the following key:

- 1 Wing length (♀) usually less than 3.4 mm. Aculeus length usually less than 1.9 mm, without deep primary steps (Figs 56, 57). Associated with *Centaurea* subgenus *Acrolophus*. Central and eastern Europe, and Turkey. *affinis affinis*
- Wing length (♀) usually more than 3.4 mm. Aculeus length usually more than 1.9 mm, with deep primary steps (Figs 58, 59). Associated with *Centaurea* subgenus *Calcitrapa*. Middle East and Turkey. *affinis calcitrapae*

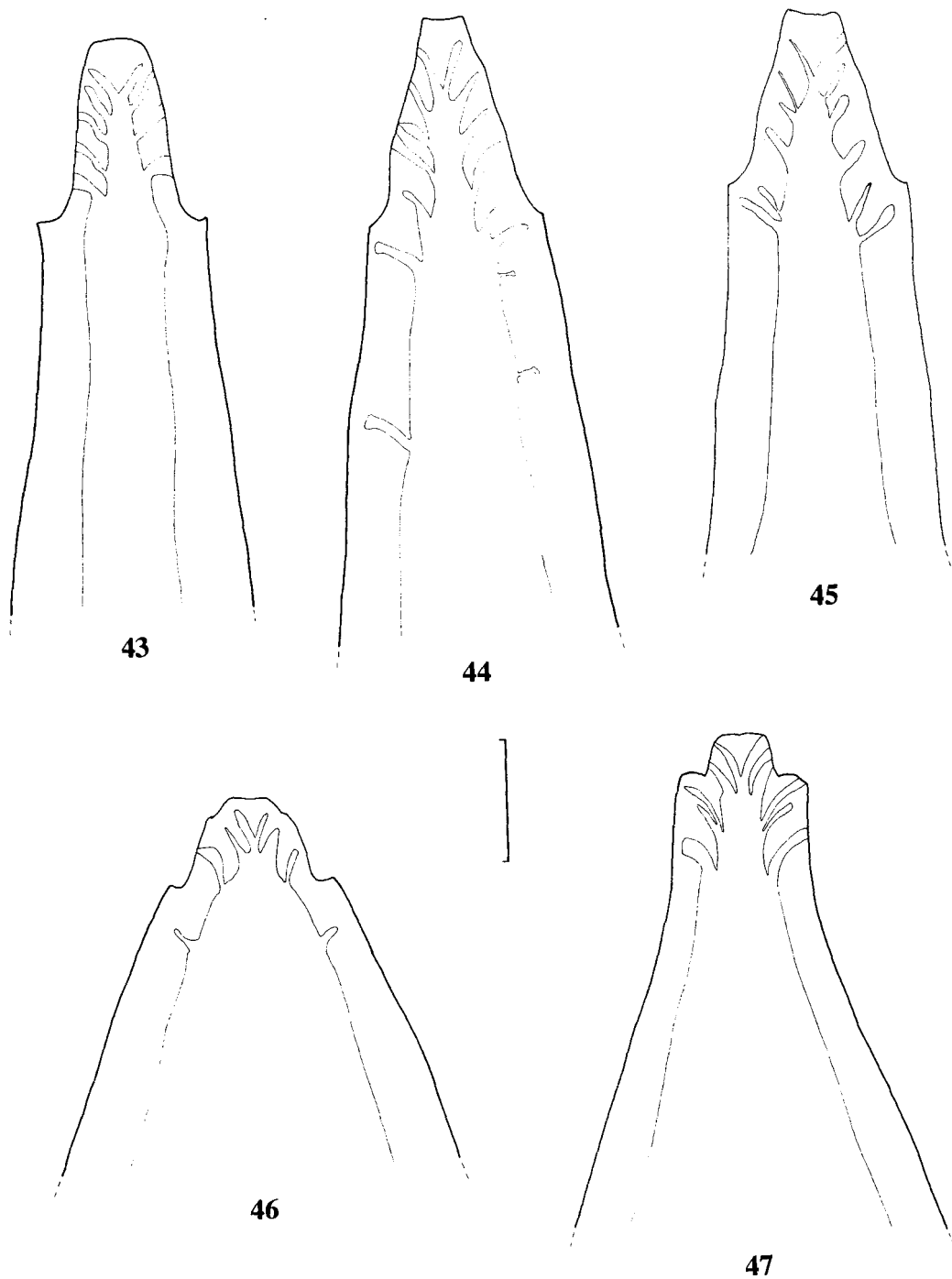
***Urophora affinis affinis* (Frauenfeld) stat.n.**

(Figs 18, 56, 57)

Urophora algira Macquart, 1843; Zwölfer, 1965: 140 [misidentification].

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U.cardui*; gena about 0.3–0.4 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange. Wing: base hyaline; subbasal crossband absent, or represented by a faint mark extending between veins R_1 and A_1 ; discal crossband sometimes broken into spots; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 3–4 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands separate. Terminalia: aculeus apex, Figs 56, 57; ♂ sternite 4 and 5, Fig. 18. WL♀=2.5–3.4 mm; AL=1.2–1.9(–2.1) mm; AL/WL=0.45–0.60.

Biology. This small subspecies is only known to attack *Centaurea* subgenus *Acrolophus* in the



FIGS 43–47. *Urophora* aculeus apices that have distinct preapical steps, dorsal views; 43, *U. cardui*; 44, *U. congrua*; 45, *U. stylata*; 46, *U. hermonis*; 47, *U. lopholomae*. Scale line=0.02 mm.

area covered by this paper. However, in the Ukrainian S.S.R. it has been reared from *Centaurea (Phalolepis) sterilis*, a species which is known to hybridize with some *Acrolophus* species (J. Dostal, in Moore *et al.*, 1976), for example *C. diffusa* and *C. maculosa*, both of which are known hosts of *U. affinis* ssp. *affinis*. This subspecies emerges from its egg as a first instar larva and the larvae induce unilocular galls within the host capitulum (P. Harris, pers. comm.).

Comments. *U. affinis* and *U. jaceana* have very similar aculeus tip shapes and the possibility that these two species are very closely related is discussed later in this paper. This subspecies has been established in North America as a bio-control agent for *Centaurea diffusa* and *Centaurea* sp. near *maculosa* (Harris & Myers, 1984; Piper, 1985).

Syntype, GERMANY (as 'Deutschland' in original description): 1♂ (bearing a handwritten label 'Frflid 1856') (NHMV). *Possible syntypes*, 2♀ (1 dissected), 2♂ (not dissected): no label data (NHMV). Other material, '*Centaurea arenaria*: 1♀, Romania, Hanu Conachi (not reared) (BMNH). *C. cariensis*: 1♀ (aculeus tip broken, so determination not confirmed), Turkey, Elmali-Finike Road (BMNH) [plant det. by G. Wagenitz]. *C. diffusa*: 4♀, 1♂, Romania, four localities (LTUB, BMNH). *C. maculosa*: 9♀, Austria, three eastern localities (BMNH); 1♀, Czechoslovakia, Moravia, near Nickolberg, Hocheck (BMNH); eggs, 4♀, France, two Alsace localities (BMNH); 1♀, 1♂, Germany, Upper Rhine, Bamlach (BMNH); 5♀, Hungary, five localities (BMNH). *C. paniculata*: 1♀, France, Tavel, Remouline (LTUB) [the host may be a misidentification of *C. leucophaea*: which has recently been confirmed as occurring in this area by G. Wagenitz]. *C. sivasica*, 1♀, Turkey, Gelendorf (BMNH). *C. sterilis*: 1♀, U.S.S.R., Ukrainian S.S.R., Crimea (ACR). *C. virgata*, 1♀, Turkey, Nigde, SW of Bor (USNM).

Biological control establishments: *C. diffusa*, Canada, British Columbia, samples from Grand Forks, Killiney Beach, Midway, Pritchard, Summerland and Okanagan Falls (BMNH); U.S.A., Washington State, samples from Entiat and Swauk Pass (BMNH). *C. cf. maculosa*, Canada, British Columbia, samples from Castlegar, Chase, Nelson, Salmo and Wasa (BMNH).

Urophora affinis calcitrapae ssp.n.

(Figs 58, 59)

Description. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.4 times eye height, labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on the margin of the central yellow and marginal black area, or based within the black area; femora orange. Wing: base hyaline; subbasal crossband usually extending between veins R_1 and A_1 , rarely between C and A_1 ; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1–3 times as broad along vein R_{4+5} as breadth of preapical crossbands on vein R_{4+5} ; preapical and apical crossbands separate. Terminalia: aculeus apex, Figs 58, 59. WL♀3.3–4.4 mm; AL=1.9–2.4 mm; AL/WL=0.45–0.65.

Diagnosis. *U. affinis calcitrapae* differs from the nominal subspecies in being larger and having deeper primary aculeus steps.

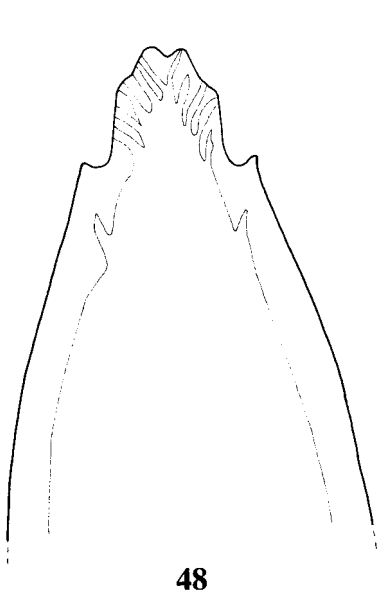
Biology. This subspecies is only known to attack species of *Centaurea* subgenus *Calcitrapa* and it is known from several countries between Turkey and Iran.

Comment. It is possible that the two 'subspecies' of *U. affinis* are distinct species, and the evidence for this is given in the discussion

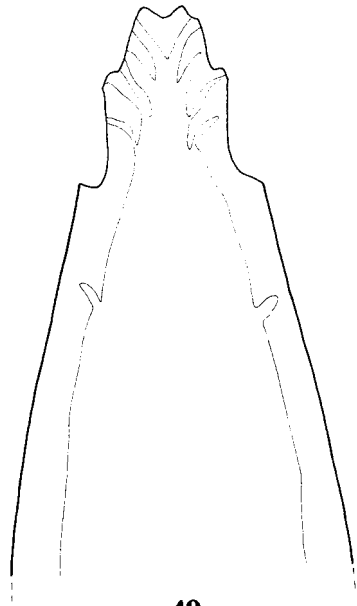
Material examined

Holotype, ♀, ex *Centaurea iberica*, ISRAEL: Mount Hermon, 1600 m, 2.vii.1986 (emerged by 17.ix.1986) (*Freidberg*) (BMNH); not dissected, but aculeus tip exposed.

Paratypes. Ex *C. calcitrapa*, TURKEY: 3♀, 1.5 km N Balikesir, 20.vii.1984 (emerged by 24.v.1985) (*Rosenthal*) (USNM); 4♀, Burdur, 61 km N Antalaya, 19.vii.1984 (emerged 3.x.1985) (*Rosenthal*) (USNM); 2♀, 37 km E Erzincan, 29.vii.1984 (emerged by 24.v.1985) (*Rosenthal*) (USNM); 4♀+, 10 km N Erzurum, 29.vii.1984 (emerged by 24.v.1985) (*Rosenthal*) (USNM). Ex *C. hyalolepis*, ISRAEL: 1♂, 1♀, Benot Ya'aqov Bridge, 7.v.1987 (emerged by 1.vi.1987) (*White, Freidberg*) (BMNH). Ex *C. iberica*, ISRAEL: 2♀, Mount Hermon, Majdel Chams, 22.vi.1969 (reared) (*Kugler*) (BMNH); 1♀, Mount Hermon, 1700 m,



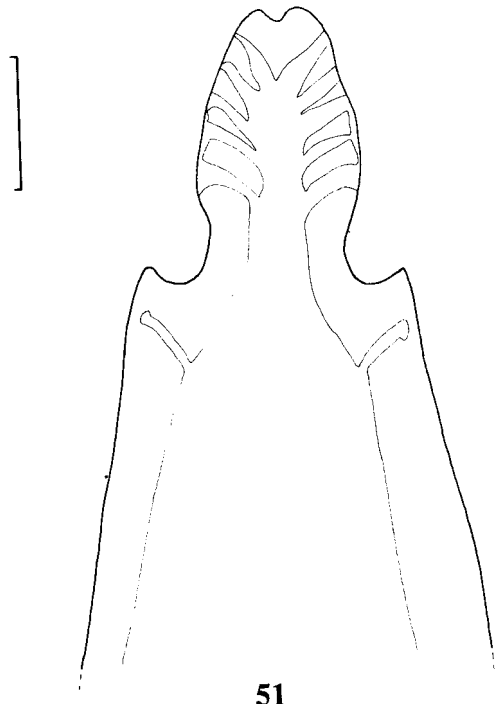
48



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FIGS 48–51. *Urophora* aculeus apices that have distinct preapical steps, dorsal views; 48–49, extremes of form of *U. aprica*; 50, *U. cuspidata*; 51, indet. species near *U. cuspidata*. Scale line=0.02 mm.

16.vi.1977 (swept) (*Freidberg*) (BMNH); 1 ♀, Mount Hermon, 19.v.1981 (swept) (*Furman*) (BMNH); 5 ♂ (not dissected), 9 ♀ (not dissected), Mount Hermon, 1600 m, 2.vii.1986 (emerged by 17.ix.1986) (*Freidberg*) (BMNH); 1 ♂, 6 ♀, Mount Hermon, 700–1400 m, 6.v.1987 (swept) (*White, Freidberg*) (BMNH); 1 ♀, Mount Meiron, 14.v.1974 (swept) (*Nachbar*) (BMNH); 1 ♀, Mount Meiron, 30.iv.1981 (swept) (*Kaplan*) (BMNH); 7 ♀, Mount Meiron, Kefar Shammai, 5.v.1987 (swept) (*White, Freidberg*) (BMNH); 4 ♀, Mount Meiron, Sasa, 5.v.1987 (swept) (*White, Freidberg*) (BMNH). On *C. procurrans*, ISRAEL: 1 ♀, Herzliya, 3.v.1987 (swept from a large pure stand of plant) (*White Freidberg*) (BMNH).

Non-type material, no host data: 1 ♀, Egypt, Carnac (BMNH); 1 ♀, Lebanon, Becharre, Cedern (BMNH).

Urophora angustifascia (Hering) (Figs 19,40)

Euribia angustifascia Hering, 1956: 83.

Euribia phaeocera Hering, 1961: 319 *syn.n.*

Urophora angustifascia (Hering); Steyskal, 1979: 9; Foote, 1984: 141.

Redescription. Head: first flagellomere black; palpi orange in specimens from Turkey and Israel, but darkened to grey or black apically in specimens from Iran and Afghanistan; palpi shape similar to *U. cardui*; gena about 0.3 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta based on the central yellow area; marginal black area of scutellum very narrow; femora black, except for extreme apex which is orange. Wing: base hyaline or yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossband joined between veins C and R₁; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 2.5 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between C and R₂₊₃ or R₄₊₅. Terminalia: aculeus apex, Fig. 40. ♂ sternites 4 and 5, Fig. 19. WL ♀ = 3.3–3.6 mm; AL = 2.0–2.6 mm; AL/WL = 0.60–0.75.

Biology. *U. angustifascia* has been reared from *Cousinia hermonis* in northern Israel (Freidberg, 1974b). *U. angustifascia* is also known from

Turkey, Iran and Afghanistan and *Cousinia* is a very diverse genus in these areas (Wagenitz, in Davis, 1975; Wagenitz, 1980), so it is likely that *Cousinia* species are the normal hosts of this species. Furthermore, *U. angustifascia* belongs to a Middle-Eastern species group all of which have a pointed aculeus and black femora, and the only other member of this group with a recorded host is *U. melanocera* (Hering), which is also associated with a *Cousinia* species (Korneyev, 1983).

Comments. *U. angustifascia* and *U. phaeocera* were separated by Hering (1961) and Steyskal (1979) largely on the basis of palpi colour differences. These two nominal species have identical aculeus shapes and they are very similar in all other respects, so they are here assumed to be conspecific. Should a future reviser find good evidence that they are in fact distinct species, it should be noted that both Hering (1961) and Steyskal (1979) erroneously reversed the palpi colours of these nominal species in their keys.

Material examined

Holotype, ♀, *E. angustifascia*, IRAN: Baluchistan, Iranshar; not located. *Paratype*, *E. angustifascia*, IRAN: ♀ (not dissected), data as holotype (BMNH). *Holotype*, ♂ (not dissected), *E. phaeocera*, ISRAEL: (TAU). Other material: 1 ♂, 1 ♀, Turkey, Adana, Karatas (BMNH); 1 ♀, Afghanistan, Badakschan (BMNH).

Urophora aprica (Fallén) (Figs 48, 49)

Tephritis aprica Fallén, 1820: 7.

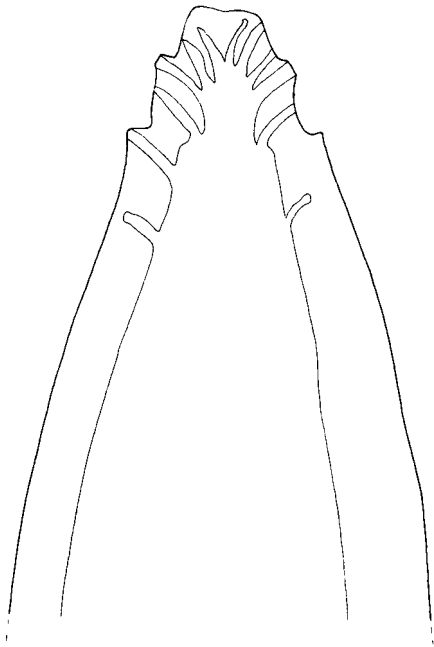
? *Urophora brunicornis* Robineau-Desvoidy, 1830: 772.

Urophora centaureae (Fabricius, 1794); Robineau-Desvoidy, 1830: 772 [misidentification].

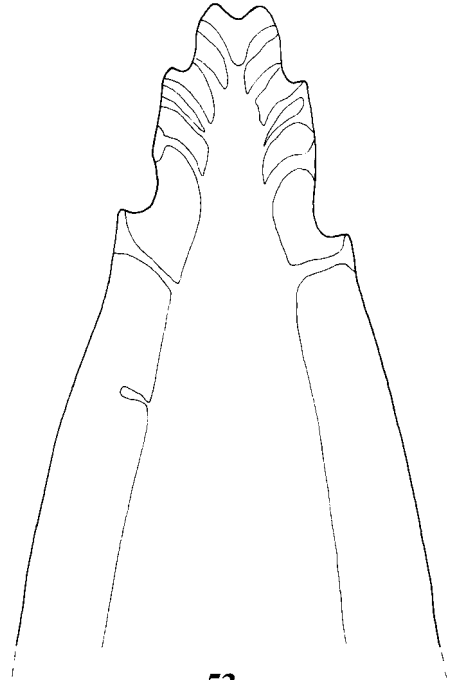
Urophora scutellata Rondani, 1970: 15, 21.

Urophora aprica (Fallén); Foote, 1984: 141.

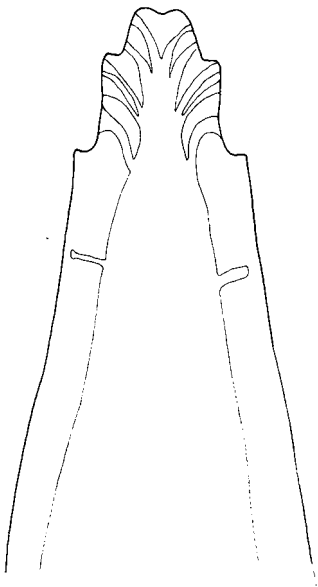
Redescription. Head: posterior half of frons often grey, anterior half orange; first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.4–0.6 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely



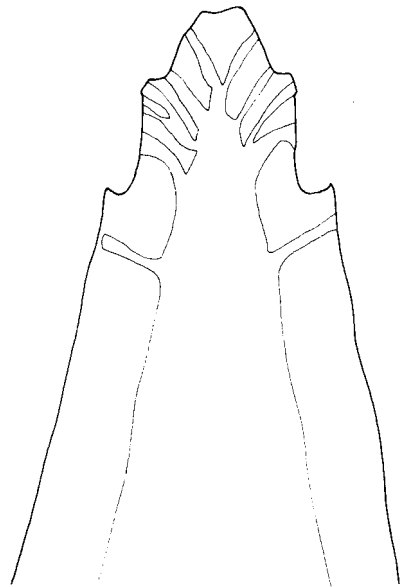
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54



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FIGS 52–55. *Urophora* aculeus apices that have distinct preapical steps, dorsal views; 52, *U. sirunaseva*; 53, *U. solstitialis*; 54, *U. spoliata*; 55, *U. terebrans*. Scale line=0.02 mm.

yellow; basal scutellar seta based within the broad marginal black area, except in some Turkish specimens; femora black, at least in basal two-thirds orange apically, except in Turkish specimens which have extensive orange areas on at least the fore- and mid-femora. Wing: base yellow; subbasal crossband extending between veins C and A_1 ; subbasal and discal crossbands separated by a narrow yellow area, but sometimes joined between veins C and R_{4+5} ; discal and preapical crossbands separated; hyaline area between preapical and discal crossbands 1–1.5 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands joined between C and R_{4+5} . Terminalia: aculeus apex, Figs 48, 49. WL ♀ = 2.6–3.8 mm; AL = 1.2–2.2 mm; AL/WL = 0.40–0.57.

Biology. This species has been reared from *Centaurea* (*Cyanus*) *depressa* in Turkey and swept from the very closely related *C. (C.) cyanus* in France.

Comments. The name *U. aprica* has been misapplied to small specimens of *U. terebrans* (previously known as *U. approximata*) and to *U. lopholomae*. Although it is a Fallén species, Hering (1938b) actually described *U. approximata* as a new species for what he thought was the 'aprica' of Fallén and then gave a key to separate it from the 'aprica' of Loew. The lectotype is mould covered and in a delicate state. Consequently, it was not dissected, but its external features are sufficiently distinct as to leave little doubt about the identity of this species. *U. brunicornis* was described within Robineau-Desvoidy's (1830) description of *U. centaureae* suggesting that it is likely to be a synonym of *U. aprica*.

Material examined

Lectotype, ♀ (designated by Persson, 1958; not dissected), *T. aprica*, SWEDEN: (NRS). **Paralectotype**, *T. aprica*, 1♂ (not dissected), SWEDEN: ('Westrogothia, Uplandia, Scaniae') no label data (NRS). **Possible paralectotype**, *T. aprica*, SWEDEN: 1♀, no label data (Westermann) (ZMUC). **Syntype**, *U. scutellata*, ITALY: 1♀, Brescia (as 'in montuosis agri brixienensis') no label data (Tacchetti) (MZP). Other material, *Centaurea cyanus*: 4♀, 4♂, France, four southern localities (not reared, but no other likely hosts at the sites, thirteen not dissected)

(BMNH). *C. depressa*: 3♀, Turkey, three localities (BMNH). No host data: 1♀, U.S.S.R., Ukrainian S.S.R., near Borshchev ('Krzywce, kr. Borszczow') (BMNH).

Other type data

Syntypes, *U. brunicornis*, probably FRANCE: presumed lost.

***Urophora cardui* (Linnaeus)** (Figs 1, 2, 12, 21, 29, 43, 68)

Musca cardui Linnaeus, 1758: 600.

Scatophaga flexuosa Germar, in Ahrens, 1814: 25.

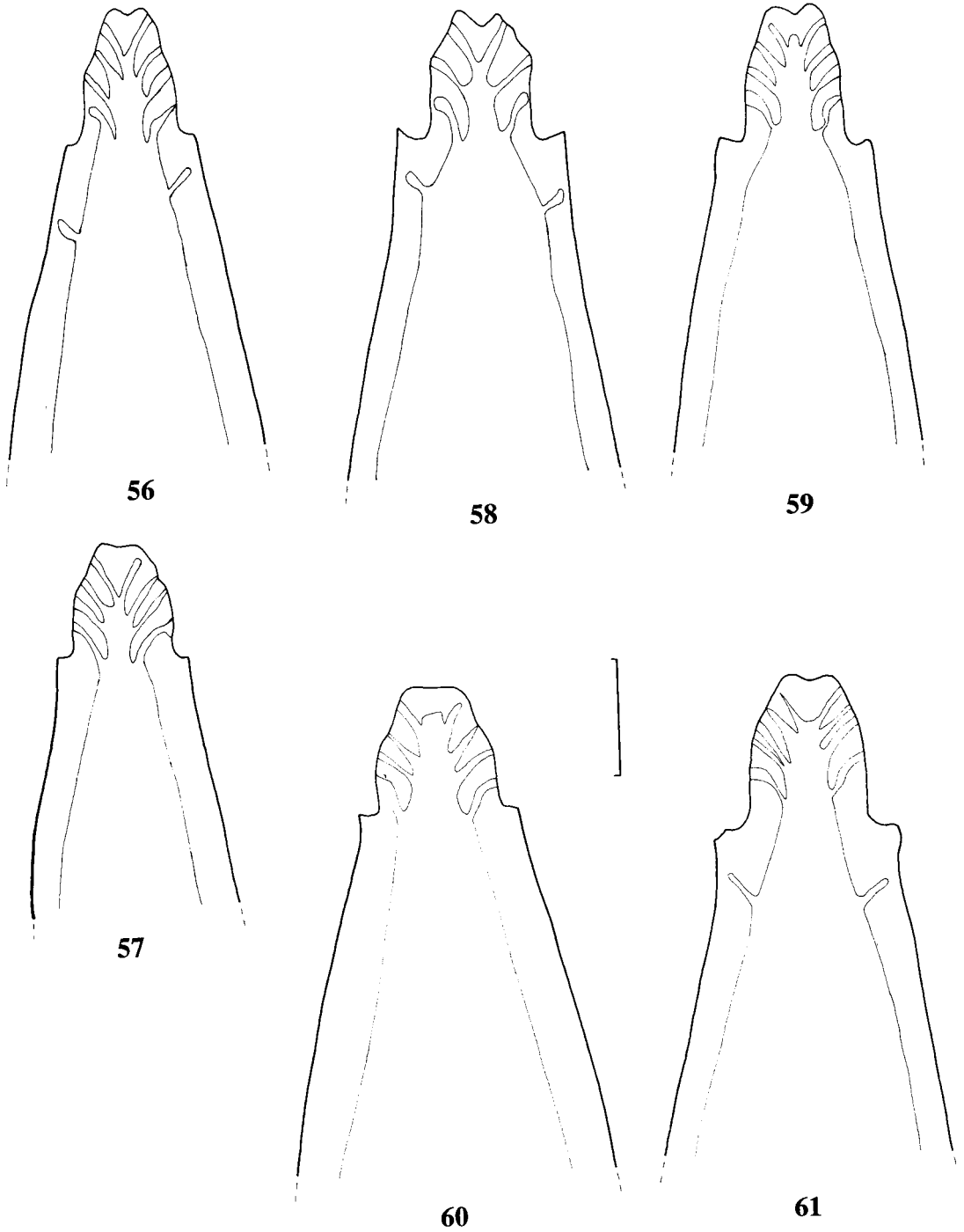
Urophora reaumurii Robineau-Desvoidy, 1830: 770 **syn.n.**

? *Urophora sonchi* Robineau-Desvoidy, 1830: 771.

Urophora cardui (Linnaeus); Steyskal, 1979: 12; Foote, 1984: 141.

Redescription. Head: first flagellomere orange; palpi orange; palpi shape, Fig. 29; gena about 0.25–0.5 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow or orange; basal scutellar seta on or near margin of central yellow and marginal black area; femora usually black in basal two-thirds, sometimes black and orange striped, rarely dark orange. Wing: Fig. 68; base yellow; subbasal crossband extending between veins C and hind margin of wing; subbasal and discal crossbands joined between veins C and R_{4+5} ; discal and preapical crossbands joined between middle of cell dm and hind margin of wing; hyaline area between preapical and discal crossbands, measured along vein R_{4+5} , approximately equal in breadth to preapical crossband on vein R_{4+5} ; preapical and apical crossbands joined between C and R_{4+5} . Terminalia: aculeus apex, Fig. 43; ♂ terminalia, Figs 1, 2, 12. ♂ sternites 4 and 5, Fig. 21. WL ♀ = 4.9–5.4 mm; AL = 1.7–1.9 mm; AL/WL = 0.30–0.40.

Biology. *U. cardui* is only known to attack *Cirsium arvense* and *C. creticum*. The larvae emerge from the egg in the second instar and they induce a multilocular stem gall. No other *Urophora* species is known to induce a stem gall



FIGS 56–61. Aculeus apices of the *Urophora affinis* and *U.jaceana* species complex, dorsal views; 56–57, extremes of form of *U.affinis* ssp. *affinis*; 58–59, extremes of form of *U.affinis* ssp. *calcitrapae*; 60–61, extremes of form of *U.jaceana*. Scale line=0.02 mm.

and it has the shortest aculeus length to wing length ratio of any European species. However, the eastern Palearctic species *U. misakiana*, *U. bicoloricornis* and *U. hoenei* each have a similarly short aculeus, which is almost identical to *U. cardui* in its apical shape. Unfortunately, the biology of these species is unknown, but they may also prove to be stem gall formers.

Comments. The lectotype of *U. cardui* (designated by White, 1987), is only known through an illustration (Reaumur, 1738), and the same illustration is referred to in the original description of *U. reaumurii*; the lectotype of *U. cardui* is here designated as the lectotype of *U. reaumurii*, so these nominal species are objective synonyms. Although this lectotype, and the syntypes of other synonyms have all been lost, Reaumur (1738) illustrates both the morphology and biology of *U. cardui* in great detail and there is no doubt that it refers to the species which forms stem galls on *Cirsium arvense*. *U. cardui* has been established at a few sites in Canada and the U.S.A. for the biocontrol of *Cirsium arvense* (Peschken *et al.*, 1982; Piper, 1985; Story, 1985b).

Material examined

Cirsium arvense: 3♀, 1♂, England, three localities (BMNH); 1♀, France, Caen (BMNH); 1♀, Germany, Berlin (BMNH); 1♀, Hungary, Velence (BMNH). *C. creticum*: 1♂, 2♀, Greece, Kavalla (BMNH). No host data: 1♀, Yugoslavia, Macedonia, Lake Ochrid, (BMNH).

Type data

Lectotype. ♀, *M. cardui*, ex *Carduus* (originally included the thistles now known as *Cirsium*), LOCALITY UNKNOWN: illustrated by Reaumur (1738: Plate 45, Fig. 14) and designated by White (1987); presumed lost. **Syntype.** *S. flexuosa*, AUSTRIA: presumed lost. **Lectotype.** ♀, *U. reaumurii*, ex *Carduus*, LOCALITY UNKNOWN: Robineau-Desvoidy (1830: 770) refers to syntypes illustrated by Reaumur (1738) and one of these specimens is the lectotype of *M. cardui* Linnaeus; this same specimen (Reaumur, 1738: Plate 45, Fig. 14) is here designated as the lectotype of *U. reaumurii* Robineau-Desvoidy; presumed lost. **Syntypes.** *U. sonchi*, on *Sonchus*, LOCALITY UNKNOWN: presumed lost.

Urophora congrua Loew (Fig. 44)

Urophora congrua Loew, 1862: 74; Steyskal, 1979: 9; Foote, 1984: 141.

Redescription. Head: first flagellomere orange; palpi orange; palpi shape similar to *U. cardui*; gena about 0.3–0.4 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange, often extensively marked with black, sometimes with fore- and hind-femora almost entirely black in basal half. Wing: base hyaline; subbasal crossband extending between veins C and A₂; subbasal and discal crossbands joined between veins C and R₄₊₅; discal and preapical crossbands joined between C and R₄₊₅; hyaline area between preapical and discal crossbands 0.75–1.5 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between veins C and R₄₊₅. Terminalia: aculeus apex, Fig. 44. WL♀ = 4.4–5.4 mm; AL = 2.2–2.8 mm; AL/WL = 0.45–0.55.

Biology. This species attacks the capitula of *Cirsium erisithales* (Zwölfer, 1965).

Comments. The aculeus tip shape of *U. congrua* (Fig. 44) is very similar to that of *U. stylata* (Fig. 45), suggesting that these two species associated with *Cirsium* species may be closely related, or similarly adapted for oviposition in the capitula of that genus.

Material examined

Presumed syntypes. AUSTRIA: 1♂ (not dissected), 1♀ (aculeus tip broken) (no label data) (Egger) (ZMHB); the original description implies that many more syntypes from Bavaria and Austria were examined by Loew, but these have not been located. Other material, *Cirsium erisithales*: 12♀, 2♂, Austria, three localities (SMNS, ZMUC).

Urophora cuspidata (Meigen) (Fig. 50)

Trypeta cuspidata Meigen, 1826: 328.
Urophora cuspidata (Meigen): Steyskal, 1979: 22; Foote, 1984: 141.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange

apically; palpi shape similar to *U. cardui*; gena about 0.3–0.4 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area, except in alpine specimens (associated with *Centaurea alpestris*) which have a broader black margin to the scutellum so that the basal seta is based within the black area; femora orange, usually striped black. Wing: base yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossband separated by a yellow area; discal crossband often reduced to spots in British specimens, sometimes reduced to a single mark along the r-m crossvein; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1.5–2 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands usually joined between C and

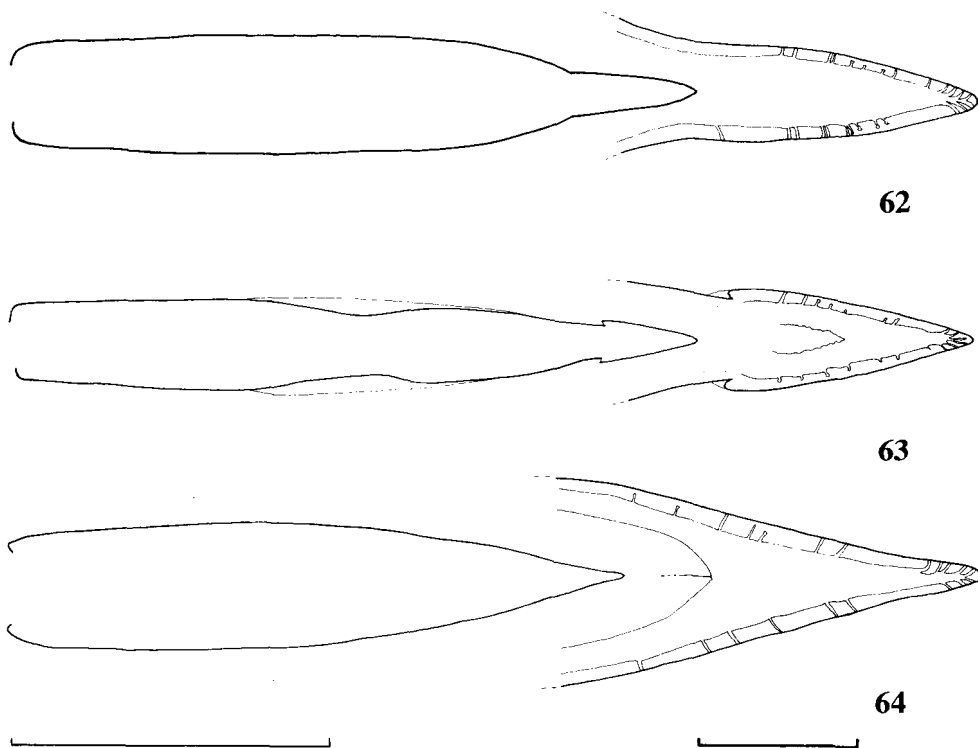
R₂₊₃, sometimes separate. Terminalia: aculeus apex, Fig. 50. WL ♀ = 4.0–6.0 mm; AL = (2.8–) 3.1–4.2 mm; AL/WL = 0.55–0.75.

Biology. Attacks the capitula of *Centaurea* subgenus *Lopholoma* species and the larvae induce multilocular galls within the capitulum.

Comments. Although the only possible syntype could not be positively identified because its ovipositor is broken, the size and wing pattern of this specimen is typical of the species associated with *Centaurea* subgenus *Lopholoma*.

Material examined

Presumed syntype, ♀ (aculeus tip missing, not dissected), LOCALITY UNKNOWN: (MNHNP). Other material, *Centaurea alpestris*: 2 ♀, Switzerland, two localities in the Bernese Oberland (not reared, but no other likely hosts at sites, thirteen not dissected) (BMNH). *C. collina*: 1 ♀, France, Aix en Provence (LTUB). *C. scabiosa*: 2 ♀, Austria, Hornstein (not reared)



FIGS 62–64. Aculei of *Urophora* species groups 2–4, dorsal views with apex details; 62, *U. maura*; 63, *U. strobilii*; 64, *U. stigma*. Scale line for aculeus = 0.5 mm; scale line for aculeus tip = 0.1 mm.

(BMNH); 2♀, 1♂, England, two southern localities (BMNH); 10♀, 1♂, France, four southern localities (not reared) (BMNH); 1♀, Germany, Naumberg on Saale (BMNH). No host data: 2♀, Norway, Akershus, Berum, Ostoya (ZMUB).

***Urophora* species nr *cuspidata* (Meigen)**

(Fig. 51)

Diagnosis. Similar to *U.cuspidata*, except in the following: femora orange; subbasal crossband extending between veins C and A₂, sometimes almost reaching hind margin of wing; hyaline area between preapical and discal crossbands 1–2 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between C and R₂₊₃. Terminalia: aculeus apex, Fig. 51. WL♀=4.7–4.9 mm; AL=3.5 mm; AL/WL=0.70–0.75.

Biology. Two females of this species have been reared from the capitula of *Centaurea* (*Cyanus*) *depressa*.

Comment. The deep apical notch and primary steps of this species (Fig. 51) indicate that it is probably a very close relative of *U.cuspidata* (Fig. 50), but the section beyond the primary steps is very elongate and it lacks the distinct secondary steps of *U.cuspidata*. A single male of *Terellia colon* (Meigen), or a very closely related species, was also reared from the same collection of *C.depressa* capitula. *T.colon*, like *U.cuspidata*, is normally only associated with *Centaurea* subgenus *Lopholoma*; this implies that *C.depressa* is probably very similar to *Lopholoma* species in terms of the characteristics that are of importance to these tephritids. This *Urophora* species is not formally described here because the aculeus tip shape could only be studied on one specimen and the possibility that this is simply an aberrant *U.cuspidata* cannot be discounted.

Material examined

Centaurea depressa: 2♀ (1 with aculeus tip broken off). Turkey, Konya, Beysehir, junction of roads to Konya, Isparta and Seydesehir, 17.vii.1984 (emerged by 15.v.1985) (*Rosenthal*) (USNM).

***Urophora hermonis* Freidberg** (Fig. 46)

Urophora hermonis Freidberg, 1974a: 49.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U.cardui*; gena about 0.4 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; area of scutum adjoining postpronotal lobe and notopleuron yellow; basal scutellar seta based within the central yellow area; femora black in basal half, then mostly orange. Wing: lacking crossbands; orange infusate, usually more deeply orange anterior to vein R₄₊₅ than rest of wing. Terminalia: aculeus apex, Fig. 46. WL♀=4.6–5.0 mm; AL=3.4–3.8 mm; AL/WL=0.70–0.80.

Biology. Induces galls in the capitula of *Cousinia hermonis* (Freidberg, 1974b).

Material examined

Holotype, ♂ (not dissected), ex *Cousinia hermonis*, ISRAEL: Mount Hermon, 28.vi.1971 (reared) (Freidberg) (TAU). *Paratypes*, ex *C.hermonis*, ISRAEL: 21♀, 39♂, (none dissected), Mount Hermon, 1971–73 (Freidberg) (BMNH). Other material, 1♂, 2♀, from the type locality (BMNH).

***Urophora hispanica* Strobl** (Figs 23, 36, 37)

Urophora (affinis ?ssp.) *hispanica* Strobl, 1906: 358.

Urophora affinis (Frauenfeld, 1857); Zwölfer, 1965: 141 [misidentification].

Urophora sp. nr *affinis* (Frauenfeld, 1857); Zwölfer, 1965: 146 [misidentification].

Urophora algira Macquart, 1843; auctt. (in part) [misidentifications].

Redescription. Egg, Fig. 23. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U.cardui*; gena about 0.3 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta based in yellow area, or at margin of central yellow and marginal black

area; femora yellow or orange. Wing: base hyaline; subbasal crossband extending between veins R_1 and A_1 , or absent; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1.5–2 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands separate. Terminalia: aculeus apex, Figs 36, 37. WL ♀ = 2.7–3.5 mm; AL = 1.4–1.9 mm; WL/AL = 0.45–0.60.

Biology. *Urophora hispanica* attacks several distantly related species of Centaureinae, namely *Mantisalca salmantica* and starthistles belonging to the *Centaurea* subgenera *Seridia*, *Solstitiaria* and possibly *Calcitrapa*.

Comments. The syntypes of *U. hispanica* could not be examined, but it was described as being very similar to *U. affinis*, and the type locality is in coastal north-eastern Spain. The only species known from the western mediterranean coastal area, which resembles *U. affinis*, is this species which attacks *Mantisalca* and starthistles. Consequently, the name *U. hispanica* is assumed to apply to this species. This species has previously been misidentified as *U. affinis* and

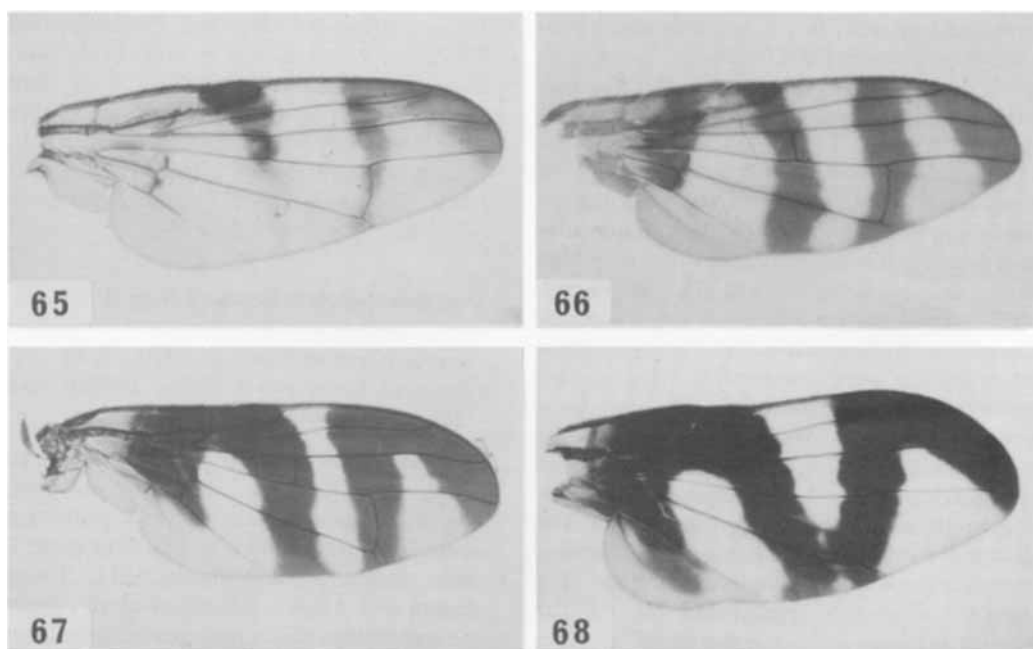
U. algira. The latter species was described from a male which was 2 lines (4.2 mm) long. As males of *U. hispanica* are only about 3 mm long it is unlikely that the name *U. algira* applies to this species.

Material examined

Centaurea aspera: 9 ♀, 2 ♂, France, nine southern localities (BMNH, LTUB, SMNS); 1 ♀, Spain, Granada, Lobres (not reared) (BMNH). *C. calcitrapa*: 1 ♀, France, Vaucluse, Chateauneuf de Pape (not reared) (SMNS). *C. melitensis*: 7 ♀, France, Herault, Frontignan (LTUB, SMNS). *Mantisalca salmantica*: eggs, 5 ♀, France, four southern localities (BMNH, LTUB, SMNS).

Type data

Syntypes, SPAIN: 3 ♂, 1 ♀, Gerona Province, Malgrat de Mar (as 'Malgrat', data from original publication only) (presumed to be in the collections of Strobl which are housed in the Benedictine Monastery at Admont, Austria); not examined.



FIGS 65–68. *Urophora* wing pattern types; 65, *U. stylata*, lacks subbasal crossband; 66, *U. jaceana*, subbasal and discal crossbands separate; 67, *U. quadrifasciata*, subbasal and discal crossbands joined; 68, *U. cardui*,

***Urophora jaceana* (Hering)** (Figs 60, 61, 66)

Euribia conyzae Hering, 1933: 309 **syn.n.** [ICZN case 2680].

Euribia jaceana Hering, 1935: 169.

Euribia solstitialis (Linnaeus, 1758); auctt. pre 1935 (in part) [misidentification].

Urophora solstitialis (Linnaeus, 1758); auctt. pre 1935 (in part) [misidentification].

Urophora jaceana (Hering, 1935); Steyskal, 1979: 20; Foote, 1984: 142.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.4–0.6 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange, often with black areas or streaks. Wing: Fig. 66; base hyaline to yellow; subbasal crossbands extending between veins C and A₁, or C and A₂; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1–3 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands usually joined between C and R₂₊₃, or C and R₄₊₅, but sometimes separate. Terminalia: aculeus apex, Figs 60, 61. WL ♀ = 3.2–4.6 mm; AL = 2.0–2.6 mm; AL/WL = 0.50–0.70.

Biology. *U. jaceana* attacks the capitula of knapweeds belonging to *Centaurea* subgenus *Jacea* in which it induces a lignified multilocular gall of receptacle tissue (Varley, 1947), and the larvae emerge during the second instar (Varley, 1937). In southern France a population of *Urophora* which were morphologically identical to *U. jaceana* were swept off *C. (Acrolophus) spinabadia* at a site where no subgenus *Jacea* could be found. *Acrolophus* species are the normal hosts of *U. affinis affinis*, which has an identical aculeus tip shape to *U. jaceana*, suggesting that these may be closely related species. The possibility that *U. affinis affinis* and *U. jaceana* are simply the morphological extremes of a complex of closely related and very similar species, is discussed later in this paper.

Comments. *U. conyzae* is the oldest available name for the knapweed gall fly. However, the

name *U. jaceana* is well known because of the life-table study of this species carried out by Varley (1947), which is still quoted to students of population ecology. Consequently, an application has been made to the International Commission for Zoological Nomenclature to have the name *U. jaceana* given precedence over *U. conyzae* by any authors who regard them as synonyms (Case 2680). *U. jaceana* is also known from North America where it has been accidentally established since before 1923 (Shewell, 1961).

Material examined

Syntypes, *E. jaceana*, ex *Centaurea jacea*, GERMANY / POLAND border: 1 ♀, River Oder at Crossen, 3.vii.1934 (reared) (Hering) (BMNH); 7 ♂, 7 ♀ (none dissected), same locality, 10.vi.1934–21.vi.1935 (Hering) (BMNH). **Syntypes, *E. conyzae*, in cop on *Inula conyza*, FRANCE:** 1 ♀, 1 ♂ (not dissected), Paris, Lardy, 18.vii.1932 (not reared) (Hering?) (BMNH). Other material, *Centaurea jacea*: 5 ♀, France, Pyrenees-Oriental, Font-Romeu (BMNH); 2 ♂, 3 ♀, Germany, same data as syntypes (BMNH); 1 ♀, Hungary, Pilis, Dobogoko (not reared) (BMNH). *C. nigra*: 9 ♀, 18 ♂, England, seven localities (BMNH). *C. phrygia*, 1 ♀, Austria, Eisenstadt (SMNS). *C. spinabadia*: 8 ♀, France, Pyrenees Oriental, Collioure, Tour Madeloc (not reared, but no other likely host at site, 45 not dissected) (BMNH) [Plant determined by G. Wagenitz]. No host data: 2 ♀, Norway, Akershus, Berum, Ostoya (ZMUB); 1 ♀, Romania, Transylvania (BMNH); 2 ♀, Scotland, Badenoch & Strathspey, Grantown (BMNH).

***Urophora jaculata* Rondani** (Figs 60, 61, 66)

Urophora jaculata Rondani, 1870: 14, 18.

Urophora sirunaseva (Hering, 1938b); auctt. [misidentification].

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.4 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora

orange. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₂; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separated; hyaline area between preapical and discal crossbands about 0.75 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between C and R₄₊₅. Terminalia: aculeus apex, Figs 38, 39. WL ♀ = 3.2–3.5 mm; AL = 1.5–2.0 mm; AL/WL = 0.50–0.60.

Biology. *U.jaculata* attacks *Centaurea solstitialis* in Italy and in mainland Greece, except in the north-east where this plant is attacked by *U.sirunaseva*. *U.jaculata* induces lignified unilocular galls in the capitulum of *C.solstitialis* (White & Clement, 1987) and it has also been swept from another member of *Centaurea* subgenus *Solstitiaria*.

Comment. This species used to be confused with *U.sirunaseva* and all references to that species in pre-1987 weed biocontrol literature actually refer to *U.jaculata* (White & Clement, 1987).

Material examined

Lectotype, ♀ (designated by White & Clement, 1987), ITALY: no label data, but distribution given in original description as Parma countryside and more southern provinces (MZP). Other material, *Centaurea* ? *napifolia*: 2 ♀, Italy, Catanzaro (not reared) (SMNS). *C.solstitialis*: 4 ♀, Greece three mainland localities (BMNH); 8 ♀, 2 ♂, Italy, five localities from Rome to Sicily (BMNH).

Urophora lopholomae sp.n. (Figs 3, 4, 13, 47)

Urophora aprica (Fallén, 1820); auctt. partim [misidentification].

Description. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U.cardui*; gena about 0.3 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta usually based within the black marginal area of the scutellum, sometimes on the margin of the central yellow and marginal

black area; femora black, except at apex. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands about 0.75 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between C and R₄₊₅. Terminalia: aculeus apex, Fig. 47; ♂ terminalia, Figs 3, 4, 13. WL ♀ = 3.4–3.8 mm; AL = 1.6–1.7 mm; AL/WL = 0.40–0.45.

Diagnosis. This species is easily distinguished from other *Urophora* species, including the superficially similar *U.aprica*, by its characteristic aculeus tip shape (Fig. 47).

Biology. The type host of *U.lopholomae* is *Centaurea sadleriana*, but a single male which is probably this species was swept from a plant identified as *C.scabiosa*. These two plants are very closely related species of subgenus *Lopholoma*, and it is possible that the plant identified as the common and widespread *C.scabiosa* was also *C.sadleriana*.

Comment. This species has previously been confused with *U.aprica*.

Material examined

Holotype, ♀, ex *Centaurea sadleriana*, HUNGARY: Budapest, 21.v.1934 (reared) (Aczel) (BMNH).

Paratypes, ex *Centaurea sadleriana*, HUNGARY: 4 ♂ (2 not dissected), 1 ♀, Budapest, 21.v.1934 (reared) (Aczel) (BMNH).

Non-type material, *C. ?scabiosa*: 1 ♂ (not dissected), Austria, Hornstein Chalk Quarry (not reared) (BMNH); 1 ♂, U.S.S.R., Moldavian S.S.R., Kishinev (IBPPK). No host data; 1 ♀, Austria, Mödling (Franz) (private coll. H. Franz).

Urophora mauritanica Macquart (Fig. 42)

?*Urophora algira* Macquart, 1843: 378.

Urophora mauritanica Macquart, 1851: 259.

Trypeta macrura Loew, 1855: 40 **syn.n.**

Urophora lejura Rondani, 1870: 14, 19 **syn.n.**

?*Urophora sejuncta* Becker, 1907: 390.

Urophora sp. nr *solstitialis* (Linnaeus, 1758); Zwölfer, 1965: 146 [misidentification].

Urophora macrura (Loew, 1855); Foote, 1984: 143.

Urophora sibynata Rondani, 1870; auctt. [misidentification].

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.3–0.4 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange, with a black stripe on at least the forefemur. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands usually 1.5–2 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅, but up to 4 times in some areas of North Africa; preapical and apical crossbands separate, or joined, often as far as vein R₄₊₅; preapical and apical crossbands reduced to spots in some areas of North Africa. Terminalia: aculeus apex, Fig. 42. WL ♀ (2.9–)3.5–5.6 mm; AL=(2.5–)3.3–5.4(–6.0) mm; AL/WL=0.75–1.00(–1.10).

Biology. In *Carthamus arborescens*, *U. mauritanica* induces lignified multilocular galls. It also attacks the capitula of other *Carthamus* species, but it has not been recorded from the commercially grown safflower, *C. tinctorius* L.

Comments. The oldest name which may apply to this species is *U. algira*. However, its type was not found amongst Macquart material in either MNHNP or UMO, and it is probably in MHNL, where most of the surviving Macquart material is badly mould damaged. The name *U. algira* has previously been applied to *U. hispanica*, but the described size of the male of *U. algira* is larger than *U. hispanica*. The only large species which is known from Algeria is the *Urophora* species associated with *Carthamus*. The oldest name which definitely applies to this species is *U. mauritanica*, and *U. macrura* and *U. lejura* are synonyms. *U. sejuncta* from Tunisia is probably a synonym of *U. mauritanica* because it is the only large *Urophora* species known from North Africa.

Material examined

Syntype, *U. mauritanica*, ALGERIA: 1 ♀, no label data (UMO). **Syntypes**, *T. macrura*, GREECE: 1 ♀ (not dissected but aculeus tip exposed), 1 ♂ (not dissected) (*Kiesenwetter*) (ZMHB). **Syntypes**, *U. lejura*, ITALY: 1 ♀, 4 ♂ (not dissected), Apennine mountains near Parma (as 'Apenninis montuosis ditionis parmensis') no label data (MZP). Other material, *Carthamus arborescens*: 6 ♀, 2 ♂, Spain, single localities in Granada and Malaga provinces (BMNH). *C. lanatus*: 3 ♀, France, three southern localities (LTUB, BMNH). *C. tenuis*: 2 ♀, Israel, two localities (BMNH). No host data: 1 ♀, Cyprus, Zakaki (BMNH); 1 ♀, Italy, Sardinia, Gairo (BMNH); 1 ♀, Yugoslavia, Macedonia, Prespa Geul, Otesevo (BMNH); 2 ♀, Libya, Tripolitania, Homs (BMNH); 1 ♀, Malta (BMNH); 1 ♀, Morocco, Ito (BMNH); 2 ♀, Algeria, Dazinville (BMNH).

Other type data

Syntype, *U. algira* (♂ only, mentioned in description), ALGERIA: (presumed to be in MHNL); not available for examination. **Syntypes**, *U. sejuncta*, TUNISIA: near Tunis, v.1906 (*Becker*); not located.

Urophora neuenschwanderi Freidberg (Fig. 30)

Urophora neuenschwanderi Freidberg, 1982: 56.

Redescription. Head: first flagellomere black, sometimes dark orange on inner side; palpi yellow, darkening to orange or grey apically; palpi shape similar to *U. cardui*; gena about 0.3 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a fine tomentum which does not obscure the underlying cuticle; postpronotal lobe yellow laterally, but black on the medial side of the postpronotal seta; basal scutellar seta on or near margin of central yellow and marginal black area; femora black, except for the apex which is orange. Wing: base yellow; subbasal crossband extending between vein C and the hind margin; subbasal and discal crossbands joined from C to R₄₊₅; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands less than half as broad along vein

R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands joined from C to R_{4+5} . Terminalia: aculeus apex, Fig. 30. WL ♀ = 3.5–3.6 mm; AL = 2.2 mm; AL/WL = 0.60–0.65.

Biology. *U. neuenschwanderi* attacks the capitula of *Ptilostemon* species, belonging to the section of the genus that are shrubs, rather than herbs. It is only known from Crete and the type host is *Ptilostemon gnaphaloides* (Freidberg, 1982), but there is also a single rearing record from *Staelhelia arborea* (Neuenschwander & Freidberg, 1983); *S. arborea* forms part of the same chasmophytic plant community as the shrubby *Ptilostemon* species and this record probably represents an oviposition error by *U. neuenschwanderi*. *U. neuenschwanderi* is only known from Crete and its competition with other species attacking the same host is discussed by Neuenschwander (1984).

Material examined

Holotype, ♀ (not dissected), ex *Ptilostemon gnaphaloides*, GREECE: Crete, Chania Province, Aerinos, 18.vi.1980 (emerged 16.v.1981) (Neuenschwander) (TAU). **Paratypes**, ex *P. gnaphaloides*, GREECE: 3♂ (one labelled allotype, none dissected), 2♀, Crete (TAU). Other material, *P. chamaepeuce*: 1♂, 2♀, Greece, Crete, Nio Horio (not reared, but no other likely host at site) (BMNH).

***Urophora pontica* Hering stat.n.** (Figs 5, 14, 20, 28, 41)

Euribia dzieduszyckii pontica Hering, 1937: 244.
Urophora dzieduszyckii Frauenfeld, 1867;
auctt. [misidentification].

Redescription. Head: gena sometimes black below the eye; first flagellomere dark orange to grey; palpi black; palpi, Fig. 28; gena about 0.4–0.5 times eye height; labellum about 2–2.5 times length of first flagellomere. Thorax: scutum with a fine tomentum which does not obscure the underlying cuticle; postpronotal lobe yellow laterally, and black on the medial side of the postpronotal seta; basal scutellar seta on or near margin of central yellow and marginal black area; femora dark orange to black, except for apex which is black. Wing: base black; subbasal

crossband extending between veins C and A_1 ; subbasal and discal crossbands joined between C and R_{4+5} ; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 0.75–1 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands joined, usually to R_{4+5} . Terminalia: aculeus apex, Fig. 41; ♂ terminalia, Figs 5, 14; ♂ sternites 4 and 5, Fig. 20. WL ♀ = 2.6–3.0 mm; AL = 1.1–1.3 mm; AL/WL = 0.35–0.45.

Biology. Attacks the capitula of *Echinops* species.

Comments. Previous authors have called this species *U. dzieduszyckii*, but that name refers to a much larger species whose female was described as having a wing length of 4.4 mm. Specimens from France were regarded as the nominal subspecies of *U. dzieduszyckii* by Hering (1937), who described subspecies *pontica* from near Volgograd, because it lacked the abnormally long fore coxae of his nominal subspecies. Hering (1937) described the nominal subspecies as having the fore coxae as long as the fore femur. In fact, Hering's own specimens (BMNH) have the fore coxae 0.7–0.8 (3♂) and 0.8 (1♀) times as long as the fore femur, and the specimens labelled as 'paratype ssp. *pontica*' in the BMNH have the fore coxae 0.6 (1♀, 1♂) times as long as the fore femur (this is typical of all other *Urophora* species); an additional specimen from Turkey has a ratio of 0.8 (1♀). These data suggest that there may be a tendency towards abnormally long fore coxae in Mediterranean and western European individuals of this species, but the evidence is tenuous and there is no good reason to give any of these poorly known populations subspecific status.

Material examined

Syntypes, U.S.S.R.: 1♀ (not dissected), 1♂ (not dissected), Russian SFSR, near Volgograd, Sarepta (*Becker 36581*) (♂ BMNH, ♀ ZMHB); specimens labelled as types, but not listed in original description, 2♀ (one in BMNH dissected), Sarepta (*Becker 33610* and *42081*) (BMNH, ZMHB). Other material, *Echinops ritro*: 1♀, 1♂ (neither dissected), France, Vaucluse, Chateau neuf du Pape (LTUB). *Echinops* sp.: 2♂, 2♀, France, Aveyron, Peyreleau (BMNH); 1♀ (not dissected), Turkey, Bandirma (BMNH).

***Urophora quadrifasciata* (Meigen)**

Trypeta quadrifasciata Meigen, 1826: 331.
Urophora dejeanii Robineau-Desvoidy, 1830: 772.
Urophora quadrifasciata (Meigen, 1826); Steyskal, 1979: 15; Foote, 1984: 143.

Comments. *Urophora quadrifasciata* is a very variable species and two forms of aculeus shape can be distinguished (Figs 31, 32, & 33–35). One of these forms can be further divided by differences in aculeus length. The resulting three forms each attack non-overlapping ranges of host-plants and have some geographic separation. There is some rather circumstantial evidence that *U. quadrifasciata* is a species complex, and this is presented in the discussion. With the evidence available at present, it would be unwise to attempt to distinguish true species within this possible complex. However, the three morphologically distinct forms may be regarded as subspecies and these are separated by the following key:

- 1 Aculeus margins swollen before apex; each margin is not parallel to the lumen wall (Figs 33–35). [AL=1.9–3.0 mm. Aculeus apex at least 8 µm wide. Western Mediterranean area. Associated with *Centaurea aspera* in France and Spain (aculeus apex width 8–12 µm; Fig. 34); *C. nicaeensis* in southern Italy (aculeus apex width 14–16 µm; Fig. 35); also known from Algeria (aculeus apex width 20 µm; Fig. 33).] *quadrifasciata algerica*
- Aculeus margins not swollen before apex; each margin roughly parallel to the lumen wall (Figs 31, 32). [Aculeus apex at most 10 µm wide, usually less than 8 µm.] 2
- 2 Aculeus usually less than 2.0 mm long (AL=1.3–2.1 mm); sample means less than 2.0 mm (Fig. 31). Associated with knapweeds (mostly *Centaurea* subgenera *Acrolophus* and *Jacea*) and *Centaurea solstitialis*. *quadrifasciata quadrifasciata*
- Aculeus usually more than 2.0 mm long (1.8–3.0 mm); sample means greater than 2.0 mm (Fig. 32). Associated with *Centaurea* subgenus *Calcitrapa*, namely *C. calcitrapa* in Turkey, and *C. iberica* in Israel and Pakistan; specimens without host data have been found in Armenian S.S.R., Cyprus, Iran and Turkmen S.S.R.). .. *quadrifasciata sjumorum*

***Urophora quadrifasciata quadrifasciata* (Meigen) stat.n.** (Figs 31, 67)

Redescription: Head: first flagellomere yellow to black; on *Centaurea arenaria* grey in 62% of specimens examined, yellow in 25% and black in 6% (n=8); on *C. diffusa* grey in 83%, black in 11%, yellow in 6% (n=19); on *C. maculosa* grey in 73%, black in 22%, yellow in 5% (n=56); on *C. nigra* grey in 53%, black in 47% (n=34); on *C. solstitialis* grey in 82%, black in 18% (n=9); palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.25–0.3 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a fine tomentum which does not obscure the underlying cuticle; basal scutellar-seta on or near margin of central yellow and marginal black area; femora black, except at extreme apex. Wing: Fig. 67; base yellow; subbasal crossband extending between veins C and A₁ or between C and A₂; subbasal and discal crossbands joined between C and R₄₊₅; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands usually about 0.75–1.5 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands joined between C and R₄₊₅. Terminalia: aculeus apex, Fig. 31. WL ♀=2.2–3.0 mm; AL=1.3–2.1 mm; aculeus apex breadth 4–10 µm; AL/WL=0.55–0.75.

Biology. *U. quadrifasciata quadrifasciata* attacks the capitula of *Centaurea* species belonging to subgenera *Acrolophus*, *Cyanus*, *Jacea*, *Phalolepis* and *Solstitiaria*. In *Acrolophus* species which are adventive in Canada, this subspecies of *U. quadrifasciata* induces a thin non-lignified gall, formed from the wall of an ovary (Harris & Myers, 1984), and the larvae emerge in the first instar (P. Harris, pers. comm.). Sobhian & Zwölfer (1985) describe the gall of *U. quadrifasciata* in *Centaurea solstitialis* as 'a gall in the ovary and later [the larva] feeds within a transformed achene the seed coat of which is inflated'. This reference to an inflated seed coat suggests that the galls examined by Harris & Myers (1984) and Sobhian & Zwölfer (1985) may differ in structure, but this has not been confirmed.

Comments. *U. quadrifasciata quadrifasciata* is established in North America on *Centaurea* sp. near *maculosa* and *C. diffusa* (Harris & Myers, 1984; Piper, 1985; Story, 1985a).

Material examined

Syntypes. *T. quadrifasciata*, GERMANY: 1♂ (not dissected), 1♀ (not dissected), ('Mühlheim am Rhein') no label data (MNHN). Other material, *Centaurea alba*: 2♀, Italy, Rome (BMNH). *C. arenaria*: 1♂, 9♀, Romania, Hanu Conachi (BMNH). *C. cariensis*: 2♀, Turkey, two localities (BMNH) [plants det. by G. Wagenitz]. *C. cyanus*: 2♀, Greece, Agios Prodromos (BMNH). *C. diffusa*: 2♀, Greece, Macedonia, 9.5 km W Veria (BMNH); 10♀, Romania, two localities (not reared) (BMNH). *C. jacea*: 2♀, Germany, Naumberg on Saale (BMNH). *C. maculosa*: 45♀, Austria, three eastern localities (BMNH); 11♀, Hungary, three localities (BMNH, TMB); 5♀, Romania, Iasi Socola (BMNH). *C. nigra*: 41♀, England, Surrey, Riddlesdown (BMNH). *C. sivasica*: 2♀, Turkey, two localities (BMNH) [plants det. by G. Wagenitz]. *C. solstitialis*: 1♂, 6♀, Italy, Rome (BMNH); 1♀, Greece, Kozani (not reared) (BMNH). *C. virgata*: 1♀, Turkey, Konya (BMNH) [plant det. by G. Wagenitz]; 1♀, Turkey, Nigde, SW Bor (USNM). No host data: 1♀, Australia, New South Wales, Nara-been West (BMNH).

Other type data

Syntypes, *U. dejeanii*, FRANCE: presumed lost.

Biological control establishments: *C. diffusa*, Canada, British Columbia, samples from Grand Forks, Killiney Beach, Midway, Summerland and Okanagan Falls (BMNH); U.S.A., Washington State, samples from Entiat, Quincy, Swauk Pass, Wakefield and Wenatchee (BMNH). *C. cf. maculosa*, Canada, British Columbia, samples from Castlegar, Chase, Nelson, Salmo and Wasa (BMNH).

***Urophora quadrifasciata algerica* (Hering) stat.n. (Figs 33–35)**

Euribia algerica Hering, 1941: 52.

Urophora algerica (Hering, 1941); Steyskal, 1979: 15; Foote, 1984: 140.

Redescription. First flagellomere grey ($n=15$ off *C. aspera*), except in 12% of specimens off *C. nicaeensis*, black ($n=9$); aculeus apex, Figs 33–35; WL♀=2.4–3.8 mm; AL=1.9–3.0 mm;

apex breadth at least 8 µm (see key); AL/WL=0.60–0.80; other details as nominal subspecies.

Biology. The known hosts of *U. quadrifasciata algerica* are starthistles belonging to the *Centaurea* subgenera *Seridia* and *Solstitaria*.

Comments. Hering (1941) described *Urophora algerica* on the basis of two male specimens, so it is not possible to confirm the identity of this nominal species. However, its wing pattern is typical of *U. quadrifasciata*, although Hering (1941) compared it to *U. congrua*. The only available female specimen from Algeria which has a 'quadrifasciata' type wing is clearly related to the southern Italian *Urophora quadrifasciata* population which attacks *Centaurea nicaeensis* and this implies the identity of *U. algerica*.

Material examined

Holotype, ♂ (not dissected), ALGERIA: between Blida and Medea, 7.viii.1884 (*Quedenfeldt*) (ZMHB); one wing of the holotype, mounted on a slide (BMNH); specimen labelled as a type and mentioned in original description, but not listed as a type, ITALY: Calabria (*Erber*) (ZMHB). Other material, *Centaurea aspera*: 2♂, 18♀, Spain, Granada Prov., Lobres (not reared) (BMNH). *C. nicaeensis*: 7♀, Italy, two Puglia localities (BMNH). No host data: 1♀, Algeria (BMNH).

***Urophora quadrifasciata sjumorum* (Rohdendorf) stat.n. (Fig. 32)**

Euribia sjumorum Rohdendorf, 1937: 144.

? *Euribia armeniaca* Hering, 1937: 245.

Urophora sjumorum (Rohdendorf, 1973); Steyskal, 1979: 15; Foote, 1984: 144.

Redescription. First flagellomere yellow in 60%, grey in 40% of specimens ($n=17$); aculeus apex, Fig. 32; WL♀=2.6–4.1 mm; AL=2.0–3.0 mm; AL/WL=0.65–0.85; other details as nominal subspecies.

Biology. *U. quadrifasciata sjumorum* has been reared from the capitula of plant species belonging to *Centaurea* subgenus *Calcitrapa* in Turkey, Israel and Pakistan; specimens were also examined from Cyprus and Iran, and the types of *U. sjumorum* and its probable synonym were

collected in Turkman S.S.R. and Armenian S.S.R.

Comments. It is clear from the original description of *U.sjumorum* that it is a form of *U.quadrifasciata* with a long ovipositor; its type locality indicates that it is almost certainly the form associated with *Centaurea* subgenus *Calcitrapa*. Hering (1937) describes *U.armeniaca* as being similar to *U.hoenei*, which is a Chinese species that is closely related to *U.cardui*, but he says the ovipositor is longer than the abdomen. The available slide mounted wing labelled as 'armeniaca' in the Hering collection (BMNH) has the typical pattern of *U.quadrifasciata*; its size (WL=4.1 mm), long ovipositor and type locality, indicated that it is also most likely to be this subspecies of *U.quadrifasciata*.

Material examined

Presumed syntype (could be part of holotype or paratype), *E.armeniaca*, U.S.S.R.: wing on slide, Armenian S.S.R. (BMNH). Other material, *Centaurea calcitrapa*: 4♀, Turkey, two localities (USNM). *C.hyalolepis*: 1♂, 4♀, Israel, Benot Ya'aqov Bridge (BMNH). *C.iberica*: 1♂, 21♀, Israel, Mount Hermon (BMNH). No host data: 5♀, Cyprus, Cherkes (BMNH); 1♀, Pakistan, Mingosa (BMNH).

Other type data

Holotype, ♀, *E.sjumorum*, U.S.S.R.: Turkmen S.S.R.; not located. *Holotype*, ♀, *E.armeniaca*, U.S.S.R.: Armenian S.S.R. (in coll. 'Hermann, Erlangen'); not located. *Paratype*, *E.armeniaca*, U.S.S.R.: 1♀, data as holotype (presumed to be with holotype).

Urophora satunini (Zaitzev)

Euribia satunini Zaitzev, 1945: 379.

Urophora satunini (Zaitzev, 1945); Foote, 1984: 144.

Comments. The syntypes of this nominal species were not located and the original description, written in Georgian, was not available in any library accessible to us. Consequently this species is not included in the key. It was described from north-east Turkey, close to the border with Armenian S.S.R., and it is hoped

that it will be possible to include *U.satunini* in a later paper which will cover the Soviet species (Korneyev & White, in prep.).

Type data

Syntypes, TURKEY: Kars District, Lake Chaldyr; not located.

Urophora sirunaseva (Hering) (Fig. 52)

Euribia sirunaseva Hering, 1938b: 397.

Urophora algira Macquart, 1843; Steyskal, 1979: 17 [misidentification].

Urophora sirunaseva (Hering, 1938b); Steyskal, 1979: 18; Foote, 1984: 144.

Redescription. Head: First flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U.cardui*; gena about 0.3 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a tomentum which barely obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands usually about 2 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅, except in Crete and Israel where the separation is only about equal to the breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands separate, except in Crete and Israel where they are joined almost to R₄₊₅. Terminalia: aculeus apex, Fig. 52. WL♀=(2.6–)2.9–3.7 mm; AL=1.4–2.1 mm; AL/WL=0.50–0.65.

Biology. *U.sirunaseva* attacks the capitula of plants belonging to *Centaurea* subgenus *Solstitiaria*. In north-eastern Greece, Turkey, Moldavian S.S.R., Ukrainian S.S.R. and northern Israel it is associated with *C.solstitialis*, and in Crete it attacks the closely related *C.idaea*. In both of these hosts the larvae induce lignified unilocular galls, which often occur multiply.

Comment. Records of this species from Italy and other areas of Greece refer to *U.jaculata*; this misidentification caused confusion to the

weed biocontrol programme against *C. solstitialis* in North America (White & Clement, 1987).

Material examined

Syntypes, ex *Centaurea solstitialis*, U.S.S.R.: 1♂, 1♀ (neither dissected), Moldavian S.S.R., Bendery (as 'Tighina') (BMNH); the following specimens labelled 'paratypes', but not listed in the original description: 3♂ (not dissected), 4♀ (not dissected), 1♀, same data as syntypes (BMNH). Other material, *Centaurea calcitrapa*: 2♀, Turkey, Samsun, 18 km E Merzifon (USNM) [also on *C. solstitialis* at this site; possibly a data label error or an aberrant host]. *C. idaea*: 1♂, 2♀, Greece, Crete (BMNH). *C. solstitialis*: 10♀, 1♂, Greece, Kos and two north-eastern localities (BMNH); 2♀, Israel, Hermon Reserve, Har Dov (BMNH); 35♀, Turkey, thirteen localities (USNM); 1♀, U.S.S.R., Ukrainian S.S.R. near Odessa, Velikodolynskoe (ZMM).

Urophora solstitialis (Linnaeus)

(Figs 6, 17, 53)

Musca solstitialis Linnaeus, 1758: 601.

Musca dauci Fabricius, 1787: 353.

Trupanea leucacanthi Schrank, 1803: 141.

Dacus hastatus Fabricius, 1805: 276.

Trypeta pugionata Meigen, 1826: 330.

? *Urophora femoralis* Robineau-Desvoidy, 1830: 770.

Urophora veruata Rondani, 1870: 14, 18 **syn.n.**

Urophora sibynata Rondani, 1870: 14, 18.

Euribia sonderupi Hering, 1940: 1 **syn.n.**

Urophora sp. nr *approximata* (Hering, 1938b); Zwölfer, 1965: 95 [misidentification].

Urophora solstitialis (Linnaeus, 1758); Steyskal, 1979: 14; Foote, 1984: 144.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.4–0.5 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area, except in some individuals from mountain areas which

have the setae based within the marginal black area; femora orange with dark stripes, except in some individuals from mountain areas which have extensive black marks on the femora and in some cases almost completely black femora. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₁; subbasal and discal crossbands separated by a yellow area; discal and preapical crossbands separated; hyaline area between preapical and discal crossbands about 2 times as broad along vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅; preapical and apical crossbands separate, or sometimes joined, but rarely beyond R₁. Terminalia: aculeus apex, Fig. 53; aedeagal apodeme, Fig. 6. WL♀ = (2.7–)3.0–4.8 mm; AL = (1.7–)2.3–3.9 mm; AL/WL = 0.60–0.90; the specimens from Denmark (reared from *Cirsium*) are at the lower end of the size range.

Biology. *U. solstitialis* normally attacks the capitula of some *Carduus* species, namely *C. acanthoides*, *C. crispus* and *C. nutans*, in which the larvae induce lignified multilocular galls (White & Clement, 1987). In the mountain areas of the Jura, the Alps and southern Germany, a form with dark femora and broad black margins to the scutellum has been found associated with *C. defloratus*; there is no evidence that this is not conspecific with other *Carduus* associated populations and the dark coloration may be the effect of cold winter diapause; such an effect has been experimentally induced in some butterflies such as *Pieris brassicae* (Gardiner, 1979). Furthermore, alpine populations of *U. cuspidata* have similar broad black margins to the scutellum. *U. sonderupi* is here regarded as a synonym of *U. solstitialis*, although it was apparently reared from *Cirsium vulgare*, rather than from a species of *Carduus*; this unusual host association is detailed in the discussion.

Comments. No female syntype of *U. solstitialis* could be located, but Linnaeus described this species as being *Carduus* associated and its identity is assumed from that information (White, 1987). Similarly, the types of *U. dauci*, *U. leucacanthi* and *U. femoralis* were unavailable for study, and the types of *U. hastatus* and *U. pugionata* were too frail to be dissected; for nomenclatorial stability these nominal species, whose types have the typical wing pattern and size of *U. solstitialis*, were all assumed to be synonyms of *U. solstitialis*. Both *U. veruata* and *U. sibynata* have the

typical aculeus tip shape and wing pattern of the species which attacks *Carduus* and they are also assumed to be that species. *U. sonderupi* also has this aculeus tip shape and wing pattern, but it was apparently reared from *Cirsium vulgare*.

Material examined

Presumed syntype, M. solstitialis, on *Carduus* ♂, LOCALITY UNKNOWN: (LS). *Syntype, M. dauci*, SWEDEN: represented only by a pin (ZMUC). *Syntype, D. hastatus*, DENMARK: 1 ♀ (not dissected) (ZMUC). *Presumed syntypes, T. pugionata*, LOCALITY UNKNOWN: 1 ♂, 1 ♀ (neither dissected) (MNHNP). *Syntypes, U. veruata*, ITALY: 2 ♀, in the Appennines near Parma (as 'in Appenino parmensi'), no label data (MZP). *Syntype, U. sibynata*, ITALY: 1 ♀, sub-Appennine parts of Parma district and Piedmont (as 'subappenino ditionis parmensis, et in pedemontio'), no label data (MZP). *Syntype, E. sonderupi*, ex *Cirsium vulgare*, DENMARK: Falster, Nørre Alslev, 10.viii.1940 (reared); not located; specimens labelled 'type ♂' (from Maribo), 'type ♀' (from Maribo) and 'paratype' (from Maribo) (BMNH), are not syntypic because they do not match the data in the original publication; 1 ♂, 3 ♀ from Nørre Alslev are dated 22.vi.1941 which is 8 months after the description was published; specimens erroneously labelled as types, Lolland, Maribo, 29.iii-1.iv.1935 and 12.vii-22.viii.1940 ('in flor. -Galle') (*Sonderup*) (BMNH); 1 ♀, Maribo, 24.viii.1940 (? reared) (*Sonderup*) (BMNH). Other material, *Carduus acanthoides*: 3 ♀, Austria, Soltenau (not reared) (BMNH); 2 ♀, Germany, Upper Palatinate, near Regensburg (BMNH). *C. crispus*, 1 ♀, France, Alsace, Hirtzfelden (BMNH). *C. defloratus*: 1 ♀, Austria, Tirol, Ötztal, Zwieselstein (SMNS); 7 ♀, Switzerland, Jura and three localities in Valais (BMNH, SMNS, ZMUC). *C. nigrescens*: 1 ♂, 1 ♀, France, Herault, Salvat (BMNH). *C. nutans*: 1 ♀, England, Surrey, Banstead Downs (BMNH); 4 ♀, 1 ♂, France, three localities (BMNH); 1 ♀, Germany, Neuenberg (BMNH); 1 ♀, Turkey, Erzurum (USNM); 1 ♀, U.S.S.R., Ukrainian S.S.R. (ZIL). *Cirsium helenioides*: 2 ♀, Switzerland, Valais, Gletch (SMNS). No host data: Form with dark femora, known to be associated with *Carduus defloratus*, 1 ♀, Germany, Alterburg (BMNH).

Other type data

Syntypes, T. leucacanthi, 'Ingolstadt': believed lost.

Urophora spoliata (Haliday) (Fig. 54)

Tephritis spoliata Haliday, 1838: 186.

Urophora spoliata (Haliday, 1838); Steyskal, 1979: 12; Foote, 1984, 144.

Redescription. Head: first flagellomere orange; palpi orange; palpi shape similar to *U. cardui*; gena about 0.3 times eye height; labelum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta usually based within the marginal black area; each femur mostly black, but often not on all faces, even in the basal half. Wing: without crossbands; cell sc yellow; rest of wing hyaline. Terminalia: aculeus apex, Fig. 54. WL ♀ = 3.2 mm; AL = 1.7–2.0 mm; AL/WL = 0.50–0.65.

Biology. *U. spoliata* attacks the capitula of *Serratula tinctoria* in a small area of southern England; there are no confirmed records from any other areas.

Material examined

Probable syntype, ENGLAND: 1 ♀ (not dissected), Hants, Isle of Wight (no label data) (NMID). Other material, *Serratula tinctoria*: 1 ♂, England, Hants, Leckford (BMNH); several other reared specimens from Leckford and Cranmore, Isle of Wight, seen (BMNH), but not dissected; 3 ♀, 1 ♂, not reared, dissected.

Urophora stylata (Fabricius) (Figs 45, 65)

Musca stylata Fabricius, 1775: 785.

Trupanea cirsii Schrank, 1808: 140.

Musca jacobaeae Panzer, 1805: 22.

Urophora venabulata Rondani, 1870: 14, 17.

Urophora vulcanica Rondani, 1870: 13, 15 **syn.n.**

Euribia pia Hering, 1938a: 244 **syn.n.**

Urophora stylata (Fabricius, 1775); Steyskal, 1979: 13; Foote, 1984: 144.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.25–0.4 times eye height; labellum about 1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora orange. Wing: Fig. 65; base hyaline; subbasal crossband absent, or rarely extending between veins R_1 and A_1 ; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1.5–2 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} ; preapical and apical crossbands usually joined, sometimes to just below R_1 . Terminalia: aculeus apex, Fig. 45. WL♀=(2.7)–4.0–5.3 mm; AL=2.3–3.4 mm; AL/WL=0.50–0.75.

Biology. This species probably occurs throughout the Palaearctic region, and it has been found in Pakistan. It attacks the capitula of *Cirsium* species in most of Europe, and it has been swept from a *Cirsium* species in Japan. However, in the Mediterranean area it has been found associated with *Carduus* and *Galactites* species (Neuenschwander & Freidberg, 1983). In *Cirsium vulgare* its larvae induce a multilocular gall (Harris & Wilkinson, 1984) and its larvae emerge during the second instar (Redfern, 1968).

Comments. The type of *U. stylata* lacks an abdomen, so even if it is a female the identity cannot be confirmed. However, the type locality is England, and the wing pattern of the available syntype is typical of the species which attacks *Cirsium vulgare* in England. The identity of the available syntypes of *U. venabulata* was confirmed by examination of the aculeus apex. *U. pia* was described by Hering (1938a) from a single male which was collected at the same locality, and by the same collector, as typical specimens of *U. stylata*, and *U. pia* is probably only an aberrant *U. stylata* that differs from typical specimens by having a partly formed subbasal crossband. Similarly, *U. vulcanica* could only be identified by its wing pattern and no syntypes of *U. cirsii* or *U. jacobaeae* could be located; these species were regarded as synonyms of *U. stylata* to maintain nomenclatorial stability. The eastern Palaearctic species *U. sachalinensis* (Shiraki), *U. japonica* (Shiraki) and *U. campes-*

tris Ito are very similar to *U. stylata*, and their status will be discussed in a later paper (Korneyev & White, in prep.). *U. stylata* has been established in North America for the biocontrol of *Cirsium arvense* (Harris & Wilkinson, 1984; Piper, 1985). The name *Musca stylata* Fabricius 1775, has also been used for a species of the related genus *Myopites* Blot, normally known as '*M. stylatus* (Fabricius, 1794)'; Fabricius (1794) gives *Musca stylata* as a redescription from his work of 1775. Only *Urophora stylata* fits the original description of *Musca stylata* which was described from England, an area from which the species known as '*Myopites stylatus*' is not known to occur (White, 1988); this *Myopites* species should therefore be known by its synonym *Myopites limbardae* Schiner, 1864.

Material examined

Syntype *Musca stylata*, ENGLAND: 1 (no abdomen) ('in Angliae nemoribus') no label data (ZMUC). **Syntypes**, *U. venabulata*, ITALY: 3♂ (not dissected), 5♀ (not dissected, but 2 with exposed aculeus), 2 (no abdomens), ('in tota Italia') no label data (MZP). **Syntype**, *U. vulcanica*, ITALY: 1♂, (not dissected), near Vesuvius ('prope Vesuvium'), no label data (MZP). **Holotype**, ♂ (not dissected), *E. pia*, FRANCE: Lot, Douelle, ix.1934 (*Lhomme*) (BMNH). Other material, *Carduus pycnocephalus*: 1♀, Spain, Granada Province, 4 km S Velez de Benaudalla (not reared, but no other likely host at site, 12♂ not dissected) (BMNH). *Cirsium arvense*: 1♀, Austria, Burgenland, Apetlon (SMNS); 2♀, France, Tarascon (SMNS). *C. eriophorum*: 1♀, France, Caen (BMNH); 2♀, Germany, Beuron (BMNH). *C. vulgare*: 5♀, 1♂, England, four southern localities (BMNH). No host data: 1♀, Australia, New South Wales, Narabeen West (BMNH); 1♀, Czechoslovakia, Eastern Bohemia, Tachov-Halze (BMNH); 1♀, Hungary, Budapest, Budajeno (BMNH); 1♂, 1♀, Israel, Haifa (BMNH); 1♀, Pakistan, Abbottabad (BMNH); 1♀, Japan, Honsyu, Akita, Yuze (BMNH); 1♀, Romania, Muldau, Botosani (BMNH); 1♀, Turkey, Bursa, 10 km S Karacabey (BMNH).

Other type data

Syntypes, *T. cirsii*, 'Ingolstadt': believed lost. **Syntypes**, *M. jacobaeae*, LOCALITY UNKNOWN: believed lost.

***Urophora syriaca* (Hendel)** (Figs 22, 27)

? *Urophora dzieduszyckii* Frauenfeld, 1867: 498.

Euribia syriaca Hendel, 1927: 49.

Euribia erichschmidti Hering, 1953: 2.

Urophora syriaca (Frauenfeld, 1867); Steyskal, 1979: 9; Foote, 1984: 145.

Redescription. Head: first flagellomere dark orange to grey; palpi black; palpi shape, Fig. 27; gena about 0.3–0.6 times eye height; labellum about 1.5–2.5 times length of first flagellomere. Thorax: scutum with a fine tomentum which does not obscure the underlying cuticle; postpronotal lobe yellow laterally, black on the medial side of the postpronotal seta; basal scutellar seta on or near margin of central yellow and marginal black area; femora black, except at extreme apex. Wing: base black; subbasal crossband extending between veins C and A₁ or A₂; subbasal and discal crossbands joined between C and R₄₊₅; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands up to 2 times as broad below vein R₄₊₅ as breadth of preapical crossband on vein R₄₊₅, but narrower than preapical crossband above R₄₊₅; preapical and apical crossbands joined from C to R₄₊₅. Terminalia: aculeus apex similar to Fig. 41; ♂ sternites 4 and 5, Fig. 22. WL ♀ = 3.8–4.3 mm; AL = 2.4–2.7 mm; AL/WL = 0.55–0.75.

Biology. *U. syriaca* is only known from the Lebanon, plus nearby areas of Syria and Israel. In northern Israel it has been reared from an *Echinops* species (Kugler & Freidberg, 1975).

Comments. The oldest available name that may apply to this species is *U. dzieduszyckii*, but this nominal species has no type locality and the female from which it was described could not be located. Previous authors, such as Hendel (1927) and Foote (1984), give the type locality of *U. dzieduszyckii* as being Poland. This is an error caused by the fact that Frauenfeld (1867) was sent the specimen by M. Nowicki of Krakow, Poland. Frauenfeld also acknowledges W. Dzieduszycki, who was presumably the collector, and notes that Dzieduszycki was a supporter of a museum in Lemberg, now in Latvian S.S.R. Hendel (1927) examined the type of *U. dzieduszyckii*, and even presents a photograph of its wing. Frauenfeld described the species as being larger than *U. eriolepidis* (a synonym of *U. tere-*

brans), and as having a wing length of 4.4 mm. It is just possible that *U. dzieduszyckii* is an aberrant *U. cardui* found in Latvian S.S.R., but the wing photograph presented by Hendel (1927) and its large size, suggest that *U. dzieduszyckii* is more likely to be the *Echinops* associated species found in the Middle East. There is little doubt that the holotypes of *U. syriaca* and *U. erichschmidti* also represent this *Echinops* associated species, which is here referred to as *U. syriaca* as that is the oldest confirmed name.

Material examined

Holotype, ♀ (not dissected), *E. syriaca*, SYRIA: (NHMV). **Holotype**, ♂ (not dissected), *E. erichschmidti*, SYRIA: 5 km from Tartus, 'Nahr el Houssaine' (BMNH). Other material, *Echinops* sp.: 1 ♀, Israel, Mount Meiron, Kefar Shammai (not reared) (BMNH); 1 ♀, 2 ♂, without any host data, from Israel, also dissected.

Other type data

Holotype, ♀, *U. dzieduszyckii*, LOCALITY UNKNOWN: not found; however Hendel (1927) figures its wing.

***Urophora terebrans* (Loew)** (Fig. 55)

Trypeta terebrans Loew, 1850: 53.

Trypeta eriolepidis Loew, 1856: 52 **syn.n.**

Euribia manni Hendel, 1927: 45 **syn.n.**

Euribia approximata Hering, 1938b: 398 **syn.n.**

Urophora aprica (Fallén, 1820); auctt. partim [misidentification].

Urophora terebrans (Loew, 1850); Steyskal, 1979: 17; Foote, 1984: 145.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*; gena about 0.2–0.5 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar seta on or near margin of central yellow and marginal black area; femora black, at least in basal two-thirds, sometimes with dark orange stripes. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A₁ or A₂; subbasal and discal

crossbands separated by a yellow area; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 0.5–1.0 times as broad along vein R_{4+5} as breadth of preapical crossband on vein R_{4+5} , with the broadest separation in Pyrenean populations and the narrowest in Austrian; preapical and apical crossbands joined, usually to, or almost to R_{4+5} . Terminalia: aculeus apex, Fig. 55. $WL\text{♀}=4.0\text{--}5.3$ mm; $AL=2.6\text{--}4.9$ mm; $AL/WL=0.55\text{--}1.00$.

Biology. *U. terebrans* has been reared from the capitula of *Cirsium eriophorum*, *C. vulgare* and *Onopordum*, and swept from *Carlina vulgaris* and *Cynara cardunculus*. All of these species have a very large capitulum, the smallest being *Carlina vulgaris* (15–30 mm), and the largest *Cynara cardunculus* (40–60 mm) (size data from Moore *et al.*, 1976). Other *Urophora* species each have a shorter aculeus than *U. terebrans* and most attack plants with a relatively smaller capitulum.

Comments. Previous authors, for example Steyskal (1979), separated *U. terebrans* and *U. eriolepidis* on the basis of the relative breadth of the hyaline area between the discal and preapical wing crossbands; however, this appears to be geographic variation in a single species. Specimens from Germany, including the syntypes of *U. approximata*, are smaller than *U. terebrans* from other areas, but they have the same aculeus tip shape and they attack the same host as *U. terebrans* in the Pyrenees; these differences are probably also explained by geographic variation. Hendel (1927) described *U. manni* because he said it had 3–4 pairs of frontal setae, rather than the usual 2 pairs. In fact the type specimens each differ in the number of frontals on each side of their heads, and the paralectotype was found to have the typical aculeus tip shape of *U. terebrans*. Consequently, it is assumed that the types of *U. manni* are simply aberrant specimens of *U. terebrans*.

Material examined

Syntypes, *T. terebrans*, [FRANCE/SPAIN ?] ‘die Pyrenäen’: 1 ♀ (aculeus tip broken) (*Kiesewetter*) (ZMHB). **Syntypes**, *T. eriolepidis*, AUSTRIA: 1 ♀ (not dissected), 1 ♂ (not dissected), Carinthia (according to Foote, 1984; original description not available) (ZMHB). **Lectotype**, ♂ (not dissected; designated by

Hardy, 1968), *E. manni*, AUSTRIA: no label data (NHMV). **Paralectotype**, *E. manni*, AUSTRIA: 1 ♀, no label data (NHMV). **Syntypes**, *E. approximata*, *Cirsium eriophorum*, GERMANY: 1 ♂, 1 ♀, ‘Beuron (Alb.)’, iii.1937 (*Ziegenhagen*) (BMNH). Other material, *Carlina vulgaris*: 1 ♀, Poland, Hohe Tatra, Hohlenhain (not reared) (BMNH). *Cirsium eriophorum*: 2 ♀, France, Pyrenees, Forges d’Abel (not reared) (BMNH); 2 ♀, Germany, Thüringen, Mühlhausen (reared from receptacle gall) (BMNH). *C. vulgare*: 1 ♀, [unknown country], Pomáz (BMNH). *Cirsium* sp., 2 ♀, Greece, Peloponissos, Taigetos Mountains, 2 km W of pass between Sparta and Kalamata (USNM). *Cynara cardunculus*: 4 ♀, Italy, Catanzaro (not reared) (LTUB, SMNS). *Onopordum* sp.: 1 ♂, 2 ♀, Italy, near Rome, west of Manziana (BMNH). No host data: 1 ♀, Austria, Styria, Mixnitz (BMNH); 1 ♀, Yugoslavia, Macedonia, Scardus Mountains, Popova Sapka (BMNH).

Urophora species group 2

Group diagnosis. Labellum about 1–1.5 times as long as first flagellomere. Scutellum yellow, black at sides. Female T6 shiny centrally, tomentose laterally. Spermathecae well sclerotized and ridged (Fig. 25). Aedeagal apodeme with narrow ‘arms’ (Figs 8, 9). Aedeagal glands reduced to a long membranous tube with a distinct basal sclerite (Fig. 16).

***Urophora maura* (Frauenfeld)** (Figs 7–9, 16, 25, 62)

Trypeta maura Frauenfeld, 1857: 550.

Euribia tecta Hering, 1940: 2. **syn.n.**

Urophora maura (Frauenfeld, 1857); Steyskal, 1979: 11; Foote, 1984: 143.

Redescription. Head: first flagellomere orange; palpi yellow, darkening to orange apically; palpi shape similar to *U. cardui*, but slightly narrower; gena about 0.2–0.3 times eye height; labellum about 1–1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe often largely yellow, but sometimes mostly black with a small yellow spot just posterior to postpronotal seta; basal scutellar seta based within the central yellow

area of the scutellum; femora orange. Wing: without crossbands; entirely hyaline except for yellow cell sc. Terminalia: aculeus, Fig. 62; spermatheca, Fig. 25. ♂ terminalia, Figs 7–9, 16. WL♀=2.9 mm; AL=1.1–1.2 mm; AL/WL=0.40–0.45.

Biology. *U. maura* has been reared from the capitula of *Inula britannica*, *I. hirta* and *I. oculus-christi*, according to Frauenfeld (1857, 1863). Mihályi (1960) also records it from *Lensifolia*, and Richter (1970) lists *I. salicina* as a host, but there is no indication of the original source of this record. Although no reared specimens were examined, there is no reason to doubt the association with *Inula*. The records of *U. maura* associated with *Acroptilon repens* (L.) DC. (Tyurebaev, 1981; Watson & Harris, 1984) probably refer to either *U. xanthippe* (Munro) or *U. impicta* (Hering).

Comment. The holotype of *U. tecta* was dissected and its aculeus shape was found to be typical of *U. maura*. No tenable differences were found between these nominal species and they are therefore regarded as synonyms.

Material examined

Syntypes, *T. maura*, AUSTRIA: 1♂ (not dissected), Vienna ('Mauer nächst Wien'), no label data (NHMV). **Holotype**, ♀, *E. tecta*, FRANCE: Lot, Douelle, ix.1934 (*Lhomme*) (BMNH). Other material, *Inula montana*: 1♀, France, Aveyron (not reared) (BMNH). *I. ensifolia*: 1 puparium, adult apparently lost, Hungary, Budapest (TMB). No host data, 1♀, 1♂, Austria, Ost.-Hainleite (BMNH); 1♀, France, Angouleme (BMNH).

Subgenus *Asimoneura* Czerny

Asimoneura Czerny, in Czerny & Strobl, 1909: 253. Type species: *Asimoneura stroblii* Czerny, in Czerny & Strobl, 1909: 253, by monotypy.

Euribia (*Asimoneura*); Hendel, 1927: 38.

Urophora (*Asimoneura*); Foote, 1984: 145.

Subgeneric diagnosis. Lower facial margin protruding; fold of proboscis and palpi extending beyond oral margin; labellum about 3 times as long as first flagellomere.

Urophora species group 3

Group diagnosis. Labellum about 3 times as long as first flagellomere. Scutellum black. Spermathecae not sclerotized (it is not possible to find them). Aedeagal glans reduced to a narrow membranous sac, with no heavily sclerotized area. 'Arms' of aedeagal apodeme narrowly joined to hypandrium (similar to Fig. 9).

Urophora stroblii (Czerny) (Fig. 63)

Asimoneura stroblii Czerny, in Czerny & Strobl, 1909: 253.

Euribia (*Asimoneura*) *stroblii* (Czerny, 1909); Hendel, 1927: 48.

Urophora (*Asimoneura*) *stroblii* (Czerny, 1909); Foote, 1984: 146.

Redescription. Head: first flagellomere black; palpi yellow; labellum about 3 times length of first flagellomere. Thorax: postpronotal lobe black; scutellum black; femora and tibia black; tarsi yellow. Wing: without crossbands; cell sc yellow; rest of wing hyaline. Terminalia: aculeus, Fig. 63. WL♂=2.0 mm; WL♀=2.4 mm; AL=1.08 mm; AL/WL=0.45.

Biology. *U. stroblii* is the only *Urophora* species included in this paper for which there is no available biological data.

Material examined

Syntypes, SPAIN: 1♂, 1♀, Gerona Province, Monistrol, 14–22.v.1907 (data from original publication, no label data) (*Strobl*) (NHMV).

Urophora species group 4

Group diagnosis. Labellum about 3 times as long as first flagellomere. Scutellum yellow, black at sides. Female T6 tomentose. Spermathecae well sclerotized and covered in warty tubercles (Fig. 26). Aedeagal apodeme with narrow 'arms' (Fig. 11; similar to Fig. 9). Aedeagal glans largely comprised of a well-sclerotized basal section with a narrow membranous extension (Fig. 15).

***Urophora stigma* (Loew)** (Figs 10, 11, 15, 24, 26, 64)

? *Musca placida* Müller, 1764: 85.

Trypeta stigma Loew, 1840: 156.

Trypeta unimaculata Roser, 1840: 60.

Euribia (Asimoneura) stigma (Loew, 1840);
Hendel 1927: 47.

Urophora (Asimoneura) stigma (Loew, 1840);
Foote, 1927: 145.

Redescription. Egg, Fig. 24. Head: first flagellomere orange; palpi orange; palpi shape similar to *U. cardui*; gena about 0.2–0.3 times eye height; labellum about 3 times length of first flagellomere. Thorax: scutum with a fine tomentum which does not obscure the underlying cuticle; postpronotal lobe usually largely yellow; basal scutellar seta based within the marginal black area which is usually very broad; femora orange; last 2 segments of tarsi black. Wing: without crossbands; cell sc black; rest of wing hyaline. Terminalia: aculeus, Fig. 64; spermatheca, Fig. 26. ♂ terminalia, Figs 10, 11, 15. WL♂ = 2.6 mm; WL♀ = 3.2–3.3 mm; AL = 1.0–1.1 mm; AL/WL = 0.3–0.35.

Biology. *U. stigma* has been reared from the capitula of some *Achillea* species. There are also old records from some other Anthemideae, namely *Anthemis arvensis*, *A. cotula* and *Leucanthemum vulgare* (Schlechtendel, 1891), but none of these records have been confirmed. In *Achillea nobilis* the larvae induce a non-lignified unilocular gall in the capitulum, which appears to be formed from the ovary wall in a similar manner to the gall of *U. quadrifasciata* in some *Centaurea* subgenus *Acrolophus* species.

Material examined

Presumed syntypes, *T. stigma*, POLAND: 1♂ (not dissected), Silesia (Scholtz) (ZMHB); **LOCALITY UNKNOWN:** 1♂ (not dissected), labelled '626' (ZMHB). **Syntypes, *T. unimaculata*, GERMANY:** 1 (no abdomen) (SMNS); possible syntypes or author determined specimens: 1♀, 1♂ (neither dissected) (SMNS). Other material, *Achillea millefolium*: 1♂, Germany, Süd-Kyffhauser (BMNH). *A. nobilis*: 1♂ (not dissected), 1 gall, probably Austria (NHMV). No host data, eggs, 2♀, 1♂, France, three southern localities (BMNH).

Other type data

Syntypes, *M. placida*, DENMARK: destroyed during Nelson's bombardment of Copenhagen.

Discussion

Many of the *Urophora* species described in this paper are very variable in characters such as size and wing pattern. Previous authors, such as Hendel (1927) and Hering (1937, 1938a, b, 1940, 1961), accepted some mere varietal forms as distinct species. For example, *U. terebrans* and *U. approximata* were distinguished by the relative lengths of their ovipositors, despite the fact that both of these nominal species attack the same host and there is no evidence to suggest that the longer ovipositor of *U. terebrans* is anything other than an allometric artefact of its larger body size. Loew (1856), and all subsequent authors, distinguished *U. terebrans*, from the Pyrenees, and *U. eriolepidis*, from Austria, by the relative separation of their discal and preapical crossbands, although there is no other distinct difference between these two nominal species. Similarly, Hendel (1927) separated *U. manni* from other *Urophora* species because he said it has three, rather than two pairs of frontal setae. In fact the lectotype of *U. manni* has three frontal setae on one side of its head, and two on the other, and it is clearly an aberrant individual of *U. terebrans*. These earlier authors were unaware of allometry, they did not have large enough collections with which to detect geographic variation in wing patterns, and they often failed to detect aberrant chaetotaxy. They also lacked the benefit of our present knowledge of host-plant relationships, which was largely founded upon the work of Zwölfer (1965), and they were unaware of the taxonomic value of the aculeus tip shape. In this paper *U. eriolepidis*, *U. manni* and *U. approximata* are all placed in synonymy with *U. terebrans* because there is no good evidence to suggest that they are distinct species, although it would be unwise to discount such a possibility entirely. A similar approach was taken in the interpretation of all the species covered by this paper. Consequently, the nomenclatural confusion caused by such ill-founded nominal species as *U. manni* should have been overcome. However, some of the so-called 'species' described in this paper may in

fact be groups of very closely related species that cannot be easily distinguished morphologically. The possible species complexes will now be discussed.

In central Europe *U. affinis* subspecies *affinis* and *U. jaceana* are only known to attack species of the *Centaurea* subgenera *Acrolophus* and *Jacea*, respectively. These two *Urophora* species are superficially quite different in appearance, as they differ in both size and wing pattern, but they share an almost identical aculeus tip shape (Figs 56–61) which suggests that they may be closely related species. In central Europe they are never found on each other's range of hosts and there is little doubt that they are distinct species in that area. However, individuals that are morphologically identical to *U. jaceana* have been found on a species of *Acrolophus* on the Mediterranean coast of France. Furthermore, flies which are the size of *U. jaceana*, but with the wing pattern of *U. affinis*, are found attacking species of the subgenus *Centaurea* (*Calcitrapa*) in Turkey and the Middle East, and these populations are named here as *U. affinis* subspecies *calcitrapae*. A few specimens reared from *Acrolophus* species in Turkey were examined, and found to be typical of subspecies *affinis*. The discovery of both subspecies in an area of sympatry, suggests that the two 'subspecies' may in fact be distinct species. However, the only Turkish specimens of subspecies *affinis* were not from sites where subspecies *calcitrapae* was found, so there is no evidence that the two subspecies are distinct when they occur together at a single site. Consequently, the two forms of *U. affinis* should be treated as subspecies until more conclusive evidence is obtained to support their separation. Similarly, the flies from southern France, which were found on *Centaurea* (*Acrolophus*) *spinabadia*, are unlikely to be genetically typical *U. jaceana*, as that species has never been found associated with such closely related plant species as *C. (A.) maculosa*, although *C. maculosa* has been well surveyed by several weed biocontrol specialists. These data suggest that central European *U. affinis* subspecies *affinis* and *U. jaceana* may simply be the morphological extremes of a series of at least four groups of populations, some or all of which may be reproductively isolated and therefore distinct species.

Urophora quadrifasciata, as delimited in this paper, has the longest host list of any species of

Urophora, although all of its confirmed hosts belong to a single genus, namely *Centaurea*. R. D. Wild (unpublished CIE report, 1987) showed that populations associated with different hosts and geographic areas are morphometrically distinct. In this paper, three groups of populations are regarded as subspecies, each of which occurs within a section of the total distribution, and has a host list which does not overlap with the host lists of the other two subspecies. At the extreme ends of the variation in the aculeus tip shape of *U. quadrifasciata* are Central European individuals of the nominal subspecies (Fig. 31), and the single available Algerian female of *U. quadrifasciata algerica* (Fig. 33). Between these two extremes, every conceivable intermediate form of aculeus shape has been found. However, *U. quadrifasciata algerica* could be further subdivided according to geographical origin or host (Figs 33–35), and there is some tentative biological evidence that some populations of the nominal subspecies cannot attack some of the hosts listed for that subspecies. *U. quadrifasciata quadrifasciata* is widespread on adventive species of *Acrolophus* in North America, but it rarely attacks *C. (Jacea) nigra*, although that is a heavily attacked plant in Europe. Similarly, it has spread into the North American range of *C. solstitialis*, but it has not yet been recorded as attacking that plant, although that is a host of the nominal subspecies in Europe. Without biological evidence, such as the results of host choice tests, combined with the discovery of morphometric differences between sympatric populations, there is no good reason to regard any of the populations here referred to as *U. quadrifasciata* as anything other than forms of a single polytypic species. However, appropriate study may show that this so-called 'species' is actually a complex of several species, some or all of which only attack a very narrow range of closely related *Centaurea* species.

Urophora stylata attacks more than one host-plant genus, but it shows no obvious variation which correlates with the host differences. No detailed morphometric analysis has been carried out, but there is no indication that *U. stylata* populations associated with *Cirsium* species in central Europe are morphologically different from Mediterranean populations associated with *Carduus* and *Galactites*.

Urophora solstitialis attacks *Carduus* species

throughout most of its range, but from the Danish islands of Lolland and Falster there are some reared series from *Cirsium vulgare*. This plant has been well surveyed in many areas of Europe by Zwölfer (1965), and by several subsequent weed biocontrol specialists, but no further finds of *U. solstitialis* have been made on it. However, there is a single record of specimens identical to normal *U. solstitialis* reared from *Cirsium helenioides* in Switzerland (leg. Zwölfer). The Danish specimens are smaller than typical *Carduus* associated specimens of *U. solstitialis* and they were described as a separate species called *U. sonderupi* by Hering (1940). It is possible that *U. sonderupi* is a distinct species, but this is unlikely as it has never been found again on *Cirsium vulgare*. It is also possible that the host-plant was a misidentified *Carduus* species, possibly *C. acanthoides* or *C. crispus*, but that does not explain why the specimens were unusually small. It is also possible that *Cirsium vulgare* is the normal host of *U. solstitialis* in Scandinavia, as that area has not been well surveyed. No obvious conclusion can be drawn from these possibilities and *U. sonderupi* is here regarded as a synonym of *U. solstitialis* because there is no good evidence that it is a distinct species.

U. hispanica and *U. terebrans* are very variable species, both of which appear to have an ecologically determined host range. *U. hispanica* attacks species of Centaureinae which have a spinose bract appendage, and which current botanical classifications separate into two genera, namely *Mantiscalca* (previously *Centaurea (Microlonchus)*), and the *Centaurea* subgenera *Calcitrapa*, *Seridia* and *Solstitiaria*. All of the species attacked by *U. hispanica* are component parts of plant communities which grow adjacent to each other in coastal western Mediterranean areas. This suggests that the flies associated with these plants are probably a single species which has a preference for particular habitats, as well as plant type. Similarly, *U. terebrans* attacks thistles with large capitula, regardless of whether they are *Carlina*, *Cirsium*, *Cynara* or *Onopordon* species. One of the largest forms, and the smallest form of *U. terebrans*, both attack *Cirsium eriophorum*; the large form is found in the Pyrenees and the small form in Germany (formerly known as *U. approximata*). In all respects other than size these two populations, plus *Urophora* specimens that have been

found on *Onopordon*, *Cynara* and *Carlina*, lack any differences other than size, and there is no evidence that they are not conspecific.

The main aim of this study was to revise the species concepts and nomenclature of western Palaearctic *Urophora* species so that a new key could be produced and a meaningful host-plant list compiled. In any genus of monophagous or oligophagous insects it is impossible to be certain about the true limits of species that show host-related variation, unless very expensive and detailed studies are undertaken of each of the potential species complexes. This revision has stopped short of actually attempting detailed studies of each possible species complex. As a compromise, the available evidence suggesting that some of the 'species' described here may actually be species complexes has been presented, and these data should be taken into account when using the host list (see appendix) as a reference source for selecting potential weed biocontrol agents.

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Appendix

Host plants of western Palaearctic Urophora species

Plant nomenclature follows Moore *et al.* (1976) for European taxa, Feinbrun-Dothan (1978) for Israel and Davis (1975) for Turkey. The large genus *Centaurea* is divided into the subgenera proposed by J. Dostál (in Moore *et al.*, 1976). Host records that have not been confirmed by the examination of reared material are followed by a note or reference in square brackets. Unconfirmed records of doubtful validity are not included. Single rearing records that do not fit the normal host range of a species are marked 'aberrant host?' to draw attention to the possibility that they may only be hosts in a single area or the result of a few individuals of a large population ovipositing on the 'wrong' plant.

Host plant

Urophora sp.

Family Asteraceae (=Compositae)

Subfamily Asteroideae

Tribe Inuleae

Inula L. (samphire)

britannica L.

hirta L.

oculus-christi L.

ensifolia L.

montana L.

salicina L.

maura [Frauenfeld, 1857, 1863]

maura [Frauenfeld, 1857, 1863]

maura [Frauenfeld, 1857, 1863]

? *maura*

maura [not reared]

maura [Richter, 1970]

Tribe Anthemideae

Anthemis L. (chamomile)

arvensis L.

cotula L.

stigma [Schlechtendal, 1891]

stigma [Schlechtendal, 1891]

Achillea L. (yarrow)

millefolium L.

nobilis L.

stigma

stigma

Leucanthemum Miller (ox-eye daisy)

vulgare Lam.

stigma [Schlechtendal, 1891]

Tribe Cardueae (=Cynareae)
Subtribe Carduinae

<i>Cynara</i> L. (globe artichoke)	
<i>cardunculus</i> L.	<i>terebrans</i> [not reared]
<i>Cousinia</i> Cass.	
<i>hermonis</i> Boiss.	<i>angustifascia</i> [Freidberg, 1974b]
<i>hermonis</i>	<i>hermonis</i>
<i>Arctium</i> L. (burdock)	
<i>lappa</i> L.	? <i>solstitialis</i> [Zwölfer, 1965; aberrant host ?]
<i>minus</i> Bernh.	? <i>solstitialis</i> [Zwölfer, 1965; aberrant host ?]
<i>Galactites</i> Moench (some thistles)	
<i>tomentosa</i> Moench	<i>stylata</i> [Neuenschwander <i>et al.</i> , 1983; aberrant host ?]
<i>Onopordon</i> L. (some thistles)	
sp.	<i>terebrans</i>
<i>Cirsium</i> Miller (some thistles)	
<i>arvense</i> (L.) Scop.	<i>cardui</i>
<i>arvense</i>	<i>stylata</i>
<i>creticum</i> (Lam.) D'Urv.	<i>cardui</i>
<i>creticum</i>	<i>stylata</i> [Neuenschwander & Freidberg, 1983]
<i>eriphorum</i> (L.) Scop.	<i>stylata</i>
<i>eriphorum</i>	<i>terebrans</i>
<i>erisithales</i> (Jacq.) Scop.	<i>congrua</i>
<i>helenioides</i> (L.) Hill	<i>solstitialis</i> [aberrant host ?]
<i>pannonicum</i> (L. fil.) Link	<i>stylata</i> [Zwölfer, 1965]
<i>phyllocephalum</i> Boiss. & Bl.	<i>stylata</i> [Kugler & Freidberg, 1975]
<i>vulgare</i> (Savi) Ten.	<i>solstitialis</i> [error or aberrant host ?]
<i>vulgare</i>	<i>stylata</i>
<i>vulgare</i>	<i>terebrans</i>
<i>Ptilostemon</i> Cass.	
<i>chamaepeuce</i> (L.) Less.	<i>neuenschwanderi</i> [not reared]
<i>gnaphaloides</i> (Cyr.) Soják	<i>neuenschwanderi</i>
<i>Carduus</i> L. (some thistles)	
<i>acanthoides</i> L.	<i>solstitialis</i>
<i>acanthoides</i>	<i>stylata</i> [Zwölfer, 1965]
<i>crispus</i> L.	<i>solstitialis</i> [not reared]
<i>defloratus</i> L.	<i>solstitialis</i>
<i>nigrescens</i> Vill.	<i>solstitialis</i>
<i>nutans</i> L.	<i>solstitialis</i>
<i>personata</i> (L.) Jacq.	<i>solstitialis</i> [Zwölfer, 1965]
<i>pycnocephalus</i> L.	<i>stylata</i> [Neuenschwander & Freidberg, 1983]
	Subtribe Centaureinae
<i>Serratula</i> L. (saw-wort)	
<i>tinctoria</i> L.	<i>quadrifasciata quadrifasciata</i> [Zwölfer, 1965]
<i>tinctoria</i>	<i>spoliata</i>
<i>Mantisalca</i> Cass. (some knapweeds)	
<i>salmantica</i> (L.) Briq. & Cavillier	<i>hispanica</i>

Centaurea L.sg. *Lopholoma* (Cass.) Dobroc (some knapweeds)

<i>alpestris</i> Hegetschw.	<i>cuspidata</i> [not reared]
<i>collina</i> L.	<i>cuspidata</i>
<i>sadleriana</i> Janka	<i>lopholomae</i>
<i>scabiosa</i> L.	<i>cuspidata</i>
<i>scabiosa</i>	? <i>lopholomae</i> [not reared]
<i>scabiosa</i>	<i>quadrifasciata quadrifasciata</i> [Zwölfer, 1965]

sg. *Acrolophus* (Cass.) Dobroc (some knapweeds)

<i>arenaria</i> Bieb. ex Willd.	<i>affinis</i>
<i>arenaria</i>	<i>quadrifasciata</i>
<i>cariensis</i> Boiss.	<i>affinis affinis</i>
<i>cariensis</i>	<i>quadrifasciata quadrifasciata</i>
<i>diffusa</i> Lam.	<i>affinis affinis</i>
<i>diffusa</i>	<i>quadrifasciata quadrifasciata</i>
<i>maculosa</i> Lam.	<i>affinis affinis</i>
<i>maculosa</i>	<i>quadrifasciata quadrifasciata</i>
<i>paniculata</i> L. // <i>leucophaea</i> Jordan	<i>affinis affinis</i>
<i>pinetorum</i> Hub.-Mor.	<i>quadrifasciata quadrifasciata</i> [D. Schroeder, pers. comm.]
<i>sivasica</i> Wagenitz	<i>affinis affinis</i>
<i>sivasica</i>	<i>quadrifasciata quadrifasciata</i>
<i>spinabadia</i> Bubani ex Timb. Lagr.	? <i>jaceana</i> [not reared]
<i>spinosa</i> L.	<i>affinis affinis</i> [Neuenschwander & Freidberg, 1983]
<i>virgata</i> Lam.	<i>affinis affinis</i>
<i>virgata</i>	<i>quadrifasciata quadrifasciata</i>

sg. *Calcitrapa* (Heinster ex Fabr.) Hayek (some star thistles)

<i>calcitrapa</i> L.	<i>affinis calcitrapae</i>
<i>calcitrapa</i>	<i>hispanica</i> [not reared]
<i>calcitrapa</i>	<i>sirunaseva</i> [aberrant host ?]
<i>calcitrapa</i>	<i>quadrifasciata sjumorum</i>
<i>calcitrapa</i>	<i>stylata</i> [Neuenschwander <i>et al.</i> , 1983; aberrant host ?]
<i>iberica</i> Trev. ex Spreng.	<i>affinis calcitrapae</i>
<i>iberica</i>	<i>quadrifasciata sjumorum</i>
<i>hyalolepis</i> Boiss.	<i>affinis calcitrapae</i>
<i>hyalolepis</i>	<i>quadrifasciata sjumorum</i>
<i>procurrans</i> Sieb. ex Spreng.	<i>affinis calcitrapae</i> [not reared]

sg. *Seridia* (Juss.) Czerep. (some starthistles)

<i>aspera</i> L.	<i>hispanica</i>
<i>aspera</i>	<i>quadrifasciata algerica</i> [not reared]
? <i>napifolia</i> L.	<i>jaculata</i> [not reared]

sg. *Solstitaria* (Hill) Dobroc (some starthistles)

<i>idaea</i> Boiss. & Heldr	<i>sirunaseva</i>
<i>melitensis</i> L.	<i>hispanica</i>
<i>nicaeensis</i> All.	<i>quadrifasciata algerica</i>
<i>solstitialis</i> L.	<i>jaculata</i>
<i>solstitialis</i>	<i>quadrifasciata quadrifasciata</i>
<i>solstitialis</i>	<i>sirunaseva</i>

sg. *Phalolepis* (Cass.) Dobrocz. (some knapweeds)

alba L.

quadrifasciata quadrifasciata

sg. *Jacea* (Miller) Hayek (some knapweeds)

jacea L.

jaceana

jacea

quadrifasciata quadrifasciata

nigra L.

jaceana

nigra

quadrifasciata quadrifasciata

nigrescens Willd.

quadrifasciata quadrifasciata [Zwölfer, 1965]

phrygia L.

jaceana

sg. *Cyanus* (Miller) Hayek (cornflowers)

cyanus L.

aprica [not reared]

cyanus

quadrifasciata quadrifasciata

depressa Bieb.

aprica

depressa

cf. *cuspidata*

Carthamus L. (some thistles)

arborescens L.

mauritanica

lanatus L.

mauritanica

tenuis (Boiss. & Bl.) Bornm.

mauritanica

Staehelina L.

arborea Schreber

neuenschwanderi [Neuenschwander *et al.*, 1983;
aberrant host?]

Subtribe Carlininae

Carlina L. (carline thistle)

vulgaris L.

terebrans [not reared]

Subtribe Echinopsidinae

Echinops L. (globe thistle)

ritro L.

pontica

sp.

syriaca [Kugler & Freidberg, 1975]