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) (=*Euribiaphaeocera* Hering); *U.cardui* (Linnaeus) (=*U.reaumurii* Robineau-Desvoidy, lectotype designated); *U.jaceana* (Hering) (=*E.conyzae* Hering); *U.maura* (Frauenfeld) (=*E.texta* Hering); *U.mauritanica* Macquart (=*U.lejura* Rondani, Trypeta macrura Loew); *U.solstitialis* (Linnaeus) (=*E.son-derupi* Hering, *U.veruata* Rondani); *U.stylata* (Fabricius) (=*E.pia* Hering, *U.vulcanica* Rondani); *U.terebrans* (Loew) (=*E.approximata* Hering, *Teriolepidis* Loew, *Emanni* Hendel). The possibility that *U.quadrifas-ciata* 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
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 Palearctic origin that have become noxious weeds in North America (Juhen, 1987). The species which have been successfully established are U. affinis and U. quadraphasata for Centaurea cf. maculosa and C. diffusa, U. cardui for Cirsium arvense, and U. stylosa for Cirsium vulgare; two additional species are currently being considered as potential biocontrol agents, namely U. urusaseva 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 USSR and other Palearctic 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 Palearctic 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 Platyptomatidae 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 Aiimoneura which was described by Czerny (in Czerny & Strobl, 1909) for the Spanish species, U. stroblu. Czerny Between 1909 and 1963 the earlier name of Euribia was used by authors such as Hendel (1927) and Hennig (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 Palearctic 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 USSR, 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 Palearctic 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 Hennig (1933, 1935, 1937, 1938a, b, 1956, 1961). The only modern work on the genus was compiled by Steyskal (1979) who presented separate keys for the Palearctic 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. urusaseva 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. Hennig (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. Aepholomae*: 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 surstyl (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 angusti-fascia and both of the Echinops associated species (Figs 19-22). However, other species are very variable and have a sternite shape between these 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 McAlpme (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 cross-bands. 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) WI♀ = Wing length of female (millimeters) AL/WL = Aculeus length divided by wing length.

**Im mature 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 Margantis, 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 Dirbekova & Dirbek (1980) who recognized three groups, namely 'stigma', 'cardui' and 'solstitiais', 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 stroblu 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, V. stigma; 16, U. maura, showing part of basiphallus (bph.), plus detail of basal part of glans. Scale lines=0.1 mm.
introduced species in North America and Australia. Species in Taiwan, throughout the Palaearctic region, with a single species. Members of this group are found

range of gall (Lalonde & Shorthouse, 1982) on a narrow gall which is not within the capitulum of its host-

Myers, 1984). The only species known to form a lignified, gall from the ovary wall (Harris &

Conversely, be confused with the true multilocular galls. Multiply within a single flower head and they can 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 (Zwolfer, 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* (Vernoniaceae) (A. Freidberg, pers. comm.); an exception is the Afrotropical *U.pan-tomelaena* 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.
Western Palaearctic species of Urophora

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1. Labelled 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

- Labelled 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.] ......................................................... strobilii

- 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). Spermaphyllum scutellaris (Figs 25). [Central Europe, south-western U.S.S.R.] ........................................... mauro

- Femora black, at least in most of basal half. Not associated with Inula. Aculeus apex not pointed, with preapical steps (Figs 46, 54). Spermaphyllum scutellaris (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 (Figs 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.] ........................................... spatulata

6. Subapical crossband absent (Fig. 65). Orif present, separated from vein C (costa) by a hyaline area. ............................................................. 7

- Subapical 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 Matthiola 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 Calthrops. Wing usually with a rudimentary sub basal crossband. Preapical and apical crossbands usually separate. [Central Europe, east to Afghaniastan; introduced to western North America.] ........................................... affinis

- Aculeus without secondary steps (Fig. 45). Associated with some Citrus, Carduus and Galactites species. Wing usually without any trace of a subapical 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 CuA, 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 stern gill 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.] ...................................... cardai

- 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.aungstifascia which are darkened to black apically), and narrowly pointed (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 concave, meeting vein C about halfway between the r-m and dm-cu crossveins. [Northern Israel, Lebanon, western Syria] ........................................... syriaica

- 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 at about halfway 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
15 Subbasal crossband reaching hind margin of wing. Subbasal and discal crossbands joined between veins C and R5-6, between C and Rj, or between Rj and R5-6 (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

- Separation of discal and preapical crossbands along vein R4+5. Cell c black, R4+5 about 2.5 times as great as breadth of preapical crossband on R4+5. Cell c hyaline in at least basal third. Subbasal and discal crossbands only joined between veins C and Rj. Associated with Cyanus. Aculeus apex pointed (Fig. 40). [First flagellomere black, Turkey to Afghanistan.] ............................................... angustifascia

- Separation of discal and preapical crossbands along vein R4+5, less than breadth of the preapical crossband on R4+5. Cell c entirely black. Subbasal and discal crossbands joined between C and R5. Not associated with Cyanus. Aculeus apex truncate (Figs. 30-35) .............................................................. 15

- Subbasal crossband reaching hind margin of wing. Associated with Pilostemon. [Aculeus, Fig. 30. First flagellomere black, Crete.] .......................... neuenschwaneri

- 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

- 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 redescriptions 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 and secondary 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.sulphurea 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 Cyamus. [France, Italy, Sweden, Turkey and south-western U.S.S.R.] ......................... aprica

18 Associated with Carthusus. Aculeus pointed and with primary steps only; apex pointed (Fig. 42). [Mediterranean area.] ...................... mauritanica

- Not associated with Carthusus. 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 Cirsium or Cuspidatus. 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). [As associated with Cirsium eriostachyes. 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 (Cynamus) depressa. Aculeus without secondary steps (Fig. 51). [Tur] .. inedt. species near cuspidata
Western Palearctic species of Urophora

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.]

- 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. .

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. [North ern, western and central Europe; accidental established in eastern North America.]

- 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. .

Aculeus apex pointed; without preapical steps (Figs 38, 39). Separation of discal and preapical crossbands along vein R4+5 about equal to breadth of preapical crossband along Rn-5. [Italy, Greece.] .............................................................. jaculata

- Aculeus apex truncate; with distinct primary and secondary secondary steps (Fig. 52). Separation of discal and preapical crossbands along vein R4+5 about twice breadth of preapical crossband along Rn-5 (except in specimens found in Crete, some areas of Turkey and Israel). [North-eastern Greece, Turkey, south-western U.S.S.R. north ern Israel.] .................................................. sirunaseva

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.

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 Palearctic 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); Museum d'Histoire Naturelle, Lille, France (MHNL); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museo Zoológico dell'Università degli Studi di Firenze, Florence, Italy (MZf); Naturhistorisches Museum, Vienna, Austria (NMV); 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); Termeszettudományi 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).
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 glans 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 glans 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)


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

- 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; Zwolfer, 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 denseomentum 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 Ri and Ai; 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
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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 'Frfdl 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♂, Germany, Upper Rhine, Bamlach (BMNH). *C.maculosa*: 9♀, Austria, three eastern localities (BMNH); 1♀, Czechoslovakia, Moravia, near Nickelberg, 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, Gelandorf (BMNH). *C.tertilis*: 1♀, U.S.S.R., Ukrainian S.S.R., Crimea (ACR). *C.virgata*, 1♀, Turkey, Nigde, SW of Bor (USNM).


**Urophora affinis calcitratae** 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 denseomentum 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] and A', rarely between C and Ai; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands 1-3 times as broad along vein Rs-A; breadth of preapical crossbands on vein Rs-A; discal and apical crossbands separate. Terminalia: aculeus apex, Figs 58, 59. WL 3.3-3.4 mm; AL = 1.9-2.4 mm; AL/WL = 0.45-0.65.

**Diagnosis.** *U.affinis calcitratae* 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 Calcitrata* 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.

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.
Urophora angustifascia (Hering) (Figs 19,40)

Euribia angustifascia Hering, 1956: 83. Euribia phaeocera (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 1-1.5 times length of first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar tomentum which obscures the underlying cuticle; first flagellomere. Thorax: scutum with a dense tomentum which obscures the underlying cuticle; postpronotal lobe largely yellow; basal scutellar tomentum which obscures the underlying cuticle; first flagellomere.

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: ♀, ♂, Turkey, Adana, Karatas (BMNH); ♀, Afghanistan, Badakschan (BMNH).

Urophora aprica (Fallen) (Figs 48,49)

Tephritis aprica Fallen, 1820: 7.

♀ Urophora brunicornis Robineau-Des/yoid, 1830: 772. Urophora centaureae (Fabricius, 1794); Robineau-Des./oyoid, 1830: 772 [misidentification].

Urophora scutellata Rondani, 1970: 15, 21. Urophora aprica (Fallen); 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
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\(^\text{\textgreater}\) 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\(\text{\textgreater}\) female =2.6-3.8 mm; AL=1.2-2.2 mm; AL/WL=0.40-0.57.

**Biology.** This species has been reared from *Centuarea* (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 Fallen species, Hering (1938b) actually described *U.approximata* as a new species for what he thought was the 'aprica' of Fallen 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. bruni-cornis* 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**


**Other type data**


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


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; \(\text{\textlarger}\) terminalia, Figs 1, 2,12. \(\text{\textlarger}\) sternites 4 and 5, Fig. 21. WL\(\text{\textlarger}\) =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. *calcitraperae*; 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 Palaearctic 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 syn-types 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). No host data: 1 ♀, Yugoslavia, Macedonia, Lake Ochrid, (BMNH).

*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; post-pronotal 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 A3; 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* (Zwolfer, 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)


**Redescription.** Head: first flagellomere orange; palpi yellow, darkening to orange
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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 A^ 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 R 4+5 as breadth of preapical crossband on vein R.4+5; preapical and apical crossbands usually joined between C and R 3-3, 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 syn-type 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: (MHNHP). 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.col-lina: l♂, 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.stroblii; 64, U.stigma. Scale line for aculeus=0.5 mm; scale line for aculeus tip=0.1 mm.
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 R.2+3. Terminalia: aculeus apex, Fig. 51. WL♀=4.7-4.9 mm; AL=3.4-3.8 mm; XL/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♀ (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 infuscate, usually more deeply orange anterior to vein R+t+s than rest of wing. Terminalia: aculeus apex, Fig. 46. WL♀=4.6-5.0 mm; AL=3.4-3.8 mm; XL/WL=0.70-0.80.

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

Material examined


Urophora hispanica Strobl (Figs 23, 36, 37)

Urophora (affinis ?ssp.) hispanica Strobl, 1906: 358. Urophora affinis (Frauenfeld, 1857); Zwolfer, 1965:141 [misidentification], Urophora sp. nr affinis (Frauenfeld, 1857); Zwolfer, 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
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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: 1♀, 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.
Urophora jaceana (Hering) (Figs 60, 61, 66)

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

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 A,, 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 R_{4+5} as breadth of preapical crossband on vein R_{4+5}; preapical and apical crossbands usually joined between C and R.2+3, or C and R.4+5, but sometimes separate. Ter-minalia: aculus apex, Figs 60, 61. WL = 3.2-4.6 mm; AL/WL=0.50-0.70.

Biology. U. jaceana attacks the capitula of 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 aculus 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 conyzae, 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♀, 1♀, England, seven localities (BMNH). C.phrygia, 1♀, Austria, Eisenstadt (SMNS). C.spinabadia: 8♀, France, Pyrenees Oriental, Collioure, Tour Madelec (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 & Straitspey, Gran town (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...
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orange. Wing: base hyaline to yellow; subbasal crossband extending between veins C and A; 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 R as breadth of preapical crossband on vein R; preapical and apical crossbands joined between C and R. Termi-nalia: 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 (MZF). Other material, Centaurea ? napifolia: 2 ♀, Italy, Catanzaro (not reared) (SMNS). C.solstitialis: 4 ♀, 2 ♀, Italy, five localities from Rome to Sicily (BMNH).

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

Urophora aprica (Fallen, 1820); auct. 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 A; 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 R as breadth of preapical crossband on vein R; preapical and apical crossbands joined between C and R. Termi-nalia: aculeus apex, Figs 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).


Non-type material, C. Iscabiosa: 1♀ (not dissected), Austria, Hornstein Chalk Quarry (not reared) (BMNH); 1♀, U.S.S.R., Moldavian S.S.R., Kishinev (IBPP). No host data; 1♀, Austria, Modling (Franz) (private coll. H. Franz).

Urophora mauritanica Macquart (Fig. 42)

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 fore-femur. Wing: base hyaline to yellow; subbasal crossband extending between veins C and Aj; 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 R 4+5 as breadth of preapical crossband on vein R 4+5, but up to 4 times in some areas of North Africa; preapical and apical crossbands separate, or joined, often as far as vein R 4+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-l .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 MNHN 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: ♀, no label data (UMO). Syntypes, T.macrura, GREECE: ♀ (not dissected but aculeus tip exposed), ♂ (not dissected) (Kiesewetter) (ZMHB). Syntypes, U.lejura, ITALY: ♀, 4♂ (not dissected), Apennine mountains near Parma (as 'Apenninis montuosus ditionis par-mensis') no label data (MZF). 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, Osetsavo (BMNH); 2♀, Libya, Tripolitania, Horns (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 nieuenschwanderi Freidberg (Fig. 30)

Urophora nieuenschwander 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 R 4+5; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands less than half as broad along vein
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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 \( \varphi = 3.5-3.6 \) 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 *Staehelina 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, \( \varphi \) (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 \( \varphi \) (one labelled allotype, none dissected), 2 \( \delta \), Crete (TAU). Other material, *P.chamaepeuce*: 1 \( \delta \), 2 \( \varphi \), 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 dzieduszyckiipontica* Hering, 1937:244. *Urophora dzieduszycki 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\(^{\varphi}\) 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; \( \varphi \) terminalia, Figs 5, 14; \( \delta \) sternites 4 and 5, Fig. 20. WL \( \varphi = 2.6-3.0 \) 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. dzieduszycki*, 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.dzieduszycki* 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 \( \delta \)) and 0.8 (1 \( \varphi \)) 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 \( \varphi \), 1 \( \delta \)) 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 \( \varphi \)). 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 \( \varphi \) (not dissected), 1 \( \delta \) (not dissected), Russian SFSSR, near Volgograd, Sarepta (Becker 36581) (BMNH, \( \varphi \) ZMHB); specimens labelled as types, but not listed in original description, 2 \( \varphi \) (one in BMNH dissected), Sarepta (Becker 33610 and 42081) (BMNH, ZMHB). Other material, *Echinops ritro*: 1 \( \varphi \), 1 \( \delta \) (neither dissected), France, Vaucluse, Chateau neuf du Pape (LTUB). *Echinops* sp.: 2 \( \varphi \), 2 \( \delta \), France, Aveyron, Peyreleau (BMNH); 1 \( \varphi \) (not dissected), Turkey, Ban-dirma (BMNH).
Urophora quadrifasciata (Meigen)

Trypeta quadrifasciata Meigen, 1826: 331.  
Urophora dejeanii Robineau-Desvoidy, 1830- 772. Urophora quadrifasciata (Meigen, 1826); Stey- skal, 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.)] ............................ qudrifasciata 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 greater than 2.0 mm (Fig. 32). Associated with knapweeds (mostly 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.).  
— Aculeus usually more than 2.0 mm long (1.8—3.0 mm); sample means less than 2.0 mm (Fig. 31). 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.).  
— Aculeus usually less than 2.0 mm long (AL= 1.3-2.1 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.).  

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; genna about 0.25-0.3 times eye height; labelum 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. cbmm.). Sobhian & Zwolfer (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 & Zwolfer (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: l ♂ (not dissected), l ♀ (not dissected), (‘Mühlheim am Rhein’) no label data (MNHNP). Other material, Centaurea alba: 2 ♀, Italy, Rome (BMNH). C.arenaria: l ♂, 9 ♀, Romania, Hanu Conachi (BMNH). C. caryophyllus: 3 ♀, 1 ♂, Greece, Agios Prodromus (BMNH). C.diffusa: 2 ♀, Greece, Macedon 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); 55, Romania, Iasi Socola (BMNH). C.nigra: 12, England, Surrey, Riddlesdown (BMNH). C.sivasica: 2 ♀, Turkey, two localities (BMNH) [plants det. by G. Wagenitz]. C.solstitialis: l ♂, 6 ♀, Italy, Rome (BMNH); l ♀, 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, Nar-a-been West (BMNH).

Other type data


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 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. The known hosts of U. quadrifasciata algerica are starrthistles belonging to the Centaurea subgenera Seridia and Solstitialia.

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.congra. 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.l884 (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: 1 ♀, Italy, two Puglia localities (BMNH). No host data: 1 ♀, Algeria (BMNH).

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


Redescription. First flagellomere yellow in 60%, grey in 40% of specimens (n= 17); aculeus apex, Figs 33-35; WL ♀=2.4-3.8 mm; AL=1.9-3.0 mm; apex breadth at least 8 ×m (see key); AL/WL=0.60-0.80; 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.sjunorum* 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.hyaloolepis*: 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


**Urophora satunini** (Zaitzev)


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)


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 *A*; 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 *R*₄₋₅ as breadth of preapical cross-band on vein *R*₄₋₅, except in Crete and Israel where the separation is only about equal to the breadth of preapical crossband on vein *R*₄₋₅; preapical and apical crossbands separate, except in Crete and Israel where they are joined almost to *R*₄₋₅. 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♀, l♂, (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), l♀, 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]. *Cidaea:* l♂, 2♂, Greece, Crete (BMNH). *C. solstitialis:* 10♀, l♂, Greece, Kos and two north-eastern localities (BMNH); 2♀, Israel, Hermon Reserve, HarDov (BMNH); 35 ♀, Turkey, thirteen localities (USNM); l♂, U.S.S.R., Ukrainian S.S.R. near Odessa, Velikodolyn-skoe (ZMM).

**Urophora solstitialis** (Linnaeus)

(Figs 6,17, 53)


**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; preapical 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 Aj; 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 R_{4+5} as breadth of preapical crossband on vein R_{4+5}; preapical and apical crossbands separate, or sometimes joined, but rarely beyond R. 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 *Cardus* species, namely *C. canthoides*, *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 *Cardus* 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 *C. cespitata* 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 vulgar*; rather than from a species of *Cardus*; 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 *Cardus* associated and its identity is assumed from that information (White, 1987). Similarly, the types of *U. dauci*, *U. leuca-canthis* 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**


**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; label-lum 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 *c* yellow. 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)


*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] and A.; 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, sometimes to just below R]. Terminalia: aculeus apex, Fig. 45.

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 variety of Carduus species in Japan. In Cirsium vulgare its larvae induce a multilocular gall (Harris & Wilkinson, 1984) and its larvae emerge through the second instar (Redfern, 1968).

Comments. The type of U.stylata lacks an abdomen, so even if it is a female the identity can 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 sub-basal crossband. Similarly, U.vulcanica could only be identified by its wing pattern and no syntypes of U.cirsii or U.jacobeae 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.campestris Ito are very similar to U.stylata, and their status will be discussed in a later paper (Kor-neyev & 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 Umbardae 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 (MZF). Syntype, U.vulcanica, ITALY: 1♂, (not dissected), near Vesuvius ('prope Vesuvium'), no label data (MZF). Holotype, ♂ (not dissected), E.pia, FRANCE: Lot, Douelle, ix.1934 (Lhomme) (BMNH). Other material, Cardus 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). Ceriophorum: 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, Ab-bottabad (BMNH); 1♀, Japan, Honsyu, Akita, Yuzu (BMNH); 1♀, Romania, Muldau, Boto-sani (BMNH); 1♀, Turkey, Bursa, 10 km S Karacadabey (BMNH).

Other type data

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


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 A, or A 2; subbasal and discal crossbands joined between C and R 4+5; discal and preapical crossbands separate; hyaline area between preapical and discal crossbands up to 2 times as broad below vein R 4+5 as breadth of preapical crossband on vein R 4+5, but narrower than preapical crossband above R 4+5; preapical and apical crossbands joined from C to R 4+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.

**Material examined**

Holotype, ♀ (not dissected), E. syriaca, SYRIA: (NMHV). Holotype, ♂ (not dissected), E. erichischmidtii, SYRIA: 5 km from Tartus, 'Nahr el Houssaine' (BMNH). Other material, Echinops sp.: 1 ♀, Israel, Mount Meiron, Kefar Shammany (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)


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 A! or A 2; 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: 4.0-5.3 mm; AL=2.6-4.9 mm; AL/ WL=0.55-1.00.

Biology. U. terebrans has been reared from the capitula of Cirsium eriophorum, C. vulgaris and Onopordon, 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. Consequently, it is assumed that the types of U. mannii are simply aberrant specimens of U. terebrans.

Material examined

Syntypes, T. terebrans. [FRANCE/SPAIN?] ‘die Pyreneen’: 1 ♀ (aculeus tip broken) (Kiesenwetter) (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. mannii, AUSTRIA: no label data (NHMV). Paralectotype, E. mannii, 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, Hohenhain (not reared) (BMNH), Cirsium eriophorum: 2♀, France, Pyrenees, Forges d’Abel (BMNH); 2♀, Germany, Thuringen, Mulihhausen (reared from receptacle gall) (BMNH). C. vulgaris: 1♀, [unknown country], Pomaz (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). Onopordon 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 glans reduced to a long membranous tube with a distinct basal sclerite (Fig. 16).

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


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). Mihalyi (1960) also records it from *I.ensifolia*, and Richter (1970) lists *L.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: l♂ (not dissected), Vienna ('Mauer nachst Wien'), no label data (NHMV). Holotype, ♀, E.tecta, FRANCE: Lot, Douelle, ix.1934 (Lhomme) (BMNH). Other material, _Inula montana: l♀, France, Aveyron (not reared) (BMNH); l, Austria, Ost.-Hainleite (BMNH); l♀, France, Angouleme (BMNH)._
Urophora stigma (Loew) (Figs 10, 11, 15, 24, 26, 64)

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

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 Zwolfer (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. jacea 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. jacea have been found on a species of Acrolophus on the Mediterranean coast of France. Furthermore, flies which are the size of U. jacea, 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 sympathy, 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) spinabuda, are unlikely to be genetically typical U. jacea, 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. jacea 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 morpho-metrically 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 Cardus and Galactites.

Urophora solstitialis attacks Cardus 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 Zwolfer (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. Zwolfer). 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 *Mantisalca* (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. Dostal (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.

<table>
<thead>
<tr>
<th>Host plant</th>
<th>Family Asteraceae (=Compositae)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inula L. (samphire)</strong></td>
<td>Subfamily Asteroideae</td>
</tr>
<tr>
<td>britannica L.</td>
<td>Tribe Inuleae</td>
</tr>
<tr>
<td>hirta L.</td>
<td><strong>maura</strong> [Frauenfeld, 1857,1863]</td>
</tr>
<tr>
<td>oculus-christi L.</td>
<td><strong>maura</strong> [Frauenfeld, 1857,1863]</td>
</tr>
<tr>
<td>ensifolia L.</td>
<td><strong>maura</strong> [Frauenfeld, 1857,1863]</td>
</tr>
<tr>
<td>montana L.</td>
<td>?<strong>maura</strong></td>
</tr>
<tr>
<td>salicina L.</td>
<td><strong>maura</strong> [not reared]</td>
</tr>
<tr>
<td><strong>Anthemis L. (chamomile)</strong></td>
<td><strong>stigma</strong> [Schlechtendal, 1891] <strong>stigma</strong> [Schlechtendal, 1891]</td>
</tr>
<tr>
<td>arvensis L. cotulah.</td>
<td><strong>stigma</strong></td>
</tr>
<tr>
<td>Achillea L. (yarrow)</td>
<td><strong>stigma</strong></td>
</tr>
<tr>
<td>millefolium L.</td>
<td><strong>stigma</strong></td>
</tr>
<tr>
<td>nobilis L.</td>
<td><strong>stigma</strong></td>
</tr>
<tr>
<td>Leucanthemum Miller (ox-eye daisy) vulgareham.</td>
<td><strong>stigma</strong> [Schlechtendal, 1891]</td>
</tr>
</tbody>
</table>
Tribe Cardueae (=Cynareae)
Subtribe Carduinae

*Cynara* L. (globe artichoke)

*cardunculus* L.  
*terebrans* [not reared]

*Cousinia* Cass.

*hermonis* Boiss.

*hermonis*

*Arctium* L. (burdock)

*lappa* L. *minus* Btzn.  
*? solstitialis* [Zwolfer, 1965; aberrant host ?]

*Galactites* Moench (some thistles) *tomentosa* Moench

*Onopordon* L. (some thistles) *sp.*  
*stylata* [Neuenschwander e/a/., 1983; aberrant host ?]

*Cirsium* Miller (some thistles) *arvense* Scop. *arvense*

*creticum* (Lam.) D'Urv.  
*cardui*

*eriochorum* (L.) Scop. *eriochorum erisithales* (Jacq.)

*Scop. helenoides* (L.) Hill  
*pannonicum* (L.fil.) Link

*phylocepalum* Boiss. & Bl.  
*vulgare* (Savi) Ten. *vulgare
vulgare*

*Ptilostemon* Cass.

*chamaepeuce* (L.) Less.  
*gnaphaloides* (Cyr.)

*Sojak*

*Carduus* L. (some thistles) *acanthoides*

*acanthoides crispus* L. *defloratus* L. *nigrescens*

*Vill. mutans* L. *personata* (L.) Jacq.

*pyrnocephalus* L.  
*neuenschwanderi* [not reared]

*Subtribe Centaureinae

*Serratula* L. (saw-wort)

*tinctoria* L. *tinctoria*  
*quadrifasciata quadrifasciata* [Zwolfer, 1965] *spoliata*

*Mantisalca* Cass. (some knapweeds) *salmantica* (L.) *Briq.* & *Cavillier*

*hispanica*
Western Palearctic species of Urophora

Centaurea L.

sg. Lopholoma (Cass.) Dobrocz (some knapweeds)
apesistris cuspidata [not reared]
Hegetschw. cuspidata
sadorinah. lopholomae
sadleriana Janka cuspidata
escabiosa L. ? lopholomae [not reared]
escabiosa scabiosa

Centaurea L. quardifasciata quadrifasciata [Zwolfer, 1965]
g. Acrolophus (Cass.) Dobrocz (some
arenaria Bieb. ex Willd.
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are
sg. *Phalolepis* (Cass.) Dobrocz. (some alba *L.*

sg. *Jacea* (Miller) Hayek (some knapweeds *jacea*L., *jacea nigra* *L.* nigra nigrescens Willd. phrygia *L.*

sg. *Cyanus* (Miller) Hayek (cornflowers) cyanus *L.* cyanus depressa *Bieb.*

*Carthamus* *L.* (some thistles)

lanatus *L.* temuis (Boiss. & Bl.) Bornm.

*Staehelina* *L.*

arborea Schreber

*Carlina* *L.* (carline thistle) vulgaris*L.*

terebrans [not reared]

*Echinops* *L.* (globe thistle) *ritro* *L.* sp.

*pontica* syriaca [Kugler & Freidberg, 1975]