SYSTEMATIC NOTES ON UROPHORA (DIPTERA, TEPHRITIDAE) SPECIES ASSOCIATED WITH CENTAUREA SOLSTITIALIS (ASTERACEAE, CARDUEAE) AND OTHER PALAEARCTIC WEEDS ADVENTIVE IN NORTH AMERICA

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Abstract. – The choice of Centaurea solstitialis plants of differing origin by Urophora jaculata and U. sirunaseva is described and the distribution of the flies is mapped. A key is provided to separate U. jaculata and U. sirunaseva from other species of current interest to North American weed biocontrol projects, namely U. cardui, U. jaceana, U. quadrifaciata, U. solstitialis and U. stylata. The identity of each species was verified by comparison with type specimens. A lectotype is designated for U. jaculata Rondani.

Three species of Urophora Robineau-Desvoidy (Diptera: Tephritidae) are associated with Centaurea solstitialis L. (yellow starthistle, YST or St. Barnaby's thistle) in the Palaearctic region, namely U. jaculata Rondani, U. sirunaseva (Hering) and U. quadrifasciata (Meigen). Yellow starthistle (Centaurea solstitialis) is widespread in the Mediterranean area (Dostal, 1976; Wagenitz, 1975), southern European USSR (Bessarabia, Black Sea coast, parts of the Dnieper and Don valleys, Crimea, Armenia and Caucasus) (Cherepanov, 1963), Iraq and Iran (Wagenitz, 1980). Yellow starthistle is adventive in western and central Europe, North and South America, South Africa, Australia, and New Zealand (Dostal, 1976; Maddox, 1981; Maddox et al., 1985; Maddox and Mayfield, 1985). In western United States yellow starthistle is a noxious weed that infests over 3 million hectares of land, especially rangeland. There is considerable interest in using phytophagous arthropods from the Palaearctic region for its biological control (Maddox and Mayfield, 1985; Maddox et al., 1985). Moore (1972) lists a further 28 species of *Centaurea* (*sensu lato*) that occur in North America, only two of which are native; the remaining species are all adventive weeds of Palaearctic origin.

A seedhead fly from Italy, named as "U. sirunaseva," was the first biological control agent found safe to introduce into western U.S. for yellow starthistle control (Zwölfer, 1969; Sobhian and Zwölfer, 1985), but introductions of this fly into California in 1969, 1976 and 1977 did not lead to its establishment (Maddox, 1981; Julien, 1982; Sobhian and Zwölfer, 1985). This failure to establish on Californian populations of yellow starthistle was attributed to host-plant incompatibility, because "the fly would ovi-

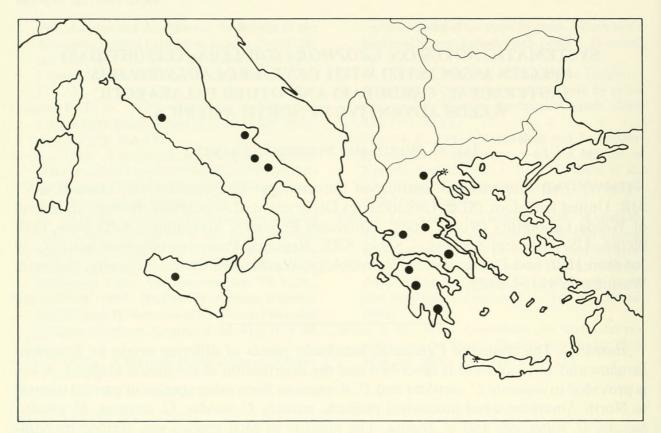


Fig. 1. Locations of populations of *Centaurea solstitialis* in Italy and Greece that supplied specimens of *U. jaculata* and *U. sirunaseva*. Spots indicate sites for *U. jaculata*; stars, *U. sirunaseva* (old records for Moldavian SSR and Turkey are not included). Due to the close proximity of some *U. jaculata* sites, some spots represent more than one site.

posit on the young buds, and the eggs would hatch, but the larvae would not develop" (D. M. Maddox, pers. comm. in Ehler and Andres, 1983). In 1981, however, a population of flies, also reported as *U. sirunaseva*, was discovered at Thermi, near Thessaloniki, Greece, that will attack yellow starthistle of U.S. origin (Sobhian and Zwölfer, 1985).

After one of us (IMW) compared flies from *C. solstitialis* from seven sites in Italy and eight sites in Greece with the type specimens of *U. jaculata* and *U. sirunaseva*, it was discovered that the flies from Italy and much of Greece were *U. jaculata*; only the flies from Thermi were the true *U. sirunaseva* (Fig. 1). This confirms the suggestion by Steyskal (1979) that the Italian flies released in California were *U. jaculata*, not *U. sirunaseva*, and dispels the notion of some weed biocontrol workers (see Maddox et al.,

1985; Sobhian and Zwölfer, 1985) that they were dealing with different biotypes or strains of "*U. sirunaseva*" in Italy and northern Greece.

The third species of Urophora associated with yellow starthistle is morphologically indistinguishable from U. quadrifasciata (Meigen), a species associated with the Centaurea subgenera Jacea (Miller) Hayek, Acrolophus (Cass.) Dobrocz. and Phalolepis (Cass.) Dobrocz. Urophora quadrifasciata was released in Canada where it is now established on C. (Acrolophus) biebersteinii DC. (= C. maculosa: auctt. N. America, nec Lam.) and C. (A.) diffusa Lam. (Harris and Myers, 1984), and this fly has now spread into Montana (Story, 1985b). Yellow starthistle in North America is not a known host for U. quadrifasciata, suggesting that the Mediterranean population on experimental plantings of Palaearctic and Nearctic yellow

starthistle in Italy may be a distinct hostrace or a separate biological species of Urophora. There are other Mediterranean populations that very closely resemble U. quadrifasciata; these possibly distinct species differ in their aculeus shape and length, and in the colour of their first flagellomere, and many of the host-plant records for U. quadrifasciata may therefore refer to undescribed species.

Data on the suitability of differing populations of yellow starthistle as breeding hosts for *U. jaculata*, *U. sirunaseva*, and *U. quadrifasciata* are presented here. This information was generated by garden plot experiments in Italy and Greece set up to measure overall levels of insect herbivory on various thistle species. A key is also presented which separates *U. jaculata*, *U. sirunaseva* and *U. quadrifasciata* from five other *Urophora* species that have been, or are likely to be, introduced to North America for biological weed control. Notes on the systematics, biology and distribution of these eight species are also presented.

GARDEN PLOT EXPERIMENTS

Methods.-Garden plots with different populations of yellow starthistle and up to three related thistle species were established in the grounds of the USDA Biological Control of Weeds Laboratory, Rome, Italy in 1983, 1984 and 1985, and on the Agricultural Research Farm, University of Thessaloniki, Greece in 1985. The first Rome garden was established on March 25, 1983 when 24 greenhouse-grown rosettes, representing six populations of yellow starthistle (source of seed was Brindisi, Italy; southern Spain; Walla Walla and Yakima, Washington; Concord and Tehama County, California), were transplanted into six rows in a plot 12×12 m. Representatives of the six populations (treatments) were arranged in a 6×6 Latin square with 1 m between plants. The plot was surrounded by several hundred plants of the local yellow starthistle population.

The 1984 and 1985 Rome garden plots occupied the same plot space $(12 \times 12 \text{ m})$, which was about 50 m east of the 1983 plot position. In both years greenhouse-grown rosettes were transplanted into the plots between April 3-5. In 1984, representatives of seven yellow starthistle populations (Rome; southern Spain; Walla Walla and Yakima, Washington; Lapwai, Idaho; Sacramento and Contra Costa Counties, California) and one cultivar of Carthamus tinctorius L. were arranged in an 8×8 Latin square with 1.5-2.0 m separating the plants. The 1985 plot contained representatives of five populations of yellow starthistle (Rome; southern Spain; Thermi; Lapwai; Sacramento) and one cultivar of C. tinctorius in each of four rows, using a randomized complete block design for a total of 24 plants. Row and plant spacing was 1.5 m. Urophora colonizing the 1984 and 1985 gardens came mostly from the nearby (50 m) planting of several hundred plants of the local yellow starthistle population, as no yellow starthistle could be found in the vicinity (0.5-1 km) of the laboratory.

The Thermi, Greece garden $(12 \times 12 \text{ m})$ contained representatives of three populations of yellow starthistle (Thermi; Lapwai; Sacramento), *Cirsium creticum* (Lam.) D'Urv., *Cynara scolymus* L., and *Carthamus tinctorius* in each of six rows, using a randomized complete block. The 18 yellow starthistle rosettes were transplanted into the garden on March 11, 1985. Row and plant spacing was 1.0–1.5 m. There were a few wild plants of yellow starthistle near the plot (within 5 m) and a group of about 40 plants about 10 m away.

The ground around and between the Rome garden plots was periodically hoed or machine-tilled to remove weeds. Weeding by hand or with a hoe was done to thin-out aggressive weeds in the Thermi garden. Occasional rain was the only source of water for the yellow starthistle plants in all of our garden-plots.

Sampling was done by harvesting capitula

Table 1. Number of adults of *Urophora quadrifasciata* and *U. jaculata* that emerged from capitula of yellow starthistle of differing origin grown together in experimental garden plots, Rome, Italy 1983–85.

Source of Seed for the YST Plants	Number of Flies per Year					
	U. quadrifasciata			U. jaculata		
	1983	1984	1985	1983	1984	1985
Europe	301	1	aiss	- she	100	na R
Central and						
southern Italy	7	2	38	1	3	6
Southern Spain	0	0	2	0	0	0
Northern Greece	-	-	2	-	-	0
United States						
Washington State	9	1	-	0	0	_
Idaho State	_	2	17	_	0	0
California State	0	4	2	0	0	0

- Plants not grown.

in the flower head and seed formation stages (see Maddox, 1981, for description of stages) on each yellow starthistle plant at 3-10 day intervals. Samples were returned to the laboratory where Urophora were reared and pinned for identification. All capitula (n = 46,694) were dissected; the presence or absence of Urophora galls in the various population groups in the Rome garden was recorded, but only total numbers were recorded from Thermi. Although there was some temporal variation in bud formation and flowering among yellow starthistle populations in all of the plots, such was not the case between plants of the local strain inside and outside of the plots (Clement, unpublished data).

Results. — The number of adults of *U. jaculata* and *U. quadrifasciata* that emerged from the capitula of several different population groups of yellow starthistle in the Rome garden plots is shown in Table 1. Flowerhead receptacle galls of *U. jaculata* were found only in Italian yellow starthistle plants, from which 10 flies emerged. When this small data base is considered along with the statement by Ehler and Andres (1983) that the Italian fly released in California was

unable to develop on yellow starthistle in California, our conclusion is that U. jaculata (called "U. sirunaseva" by Ehler and Andres, 1983) is restricted to its own local populations of yellow starthistle in southern Europe. Table 1 also shows that yellow starthistle of several origins is a suitable host for a population of flies that are morphologically indistinguishable from U. quadrifasciata (emerged mid July to mid August, 1983–1985). Although it is possible that U. quadrifasciata is a species complex (see earlier in this paper), what is important for biological weed control is that North American yellow starthistle is a suitable host-plant for some populations of the fly presently known as U. quadrifasciata.

Urophora sirunaseva was the only Urophora species that attacked the three population groups of yellow starthistle in the Thermi, Greece garden plot. The percentage of galls in the capitula of the control (Greek) and Idaho plants that were harvested between June 22 and July 4 averaged ($\bar{x} \pm$ SE), $5.63 \pm 1.70\%$ (n = 6 plants) and $2.92 \pm 0.95\%$ (n = 6), respectively. These average values are not significantly different (F = 1.72, P > 0.05, data arcsine transformed). During the same time period, only two out of five California plants were attacked by U. sirunaseva, with 5.10% (n = 98 capitula) and 25.0% (n = 12) of the flowerheads of these plants containing galls. Overwintering larvae in galls were found in four capitula, which were collected between July 25 and August 1 on two Idaho plants and one Greek plant. The number of adults that emerged in the laboratory from July 1-17, per population group of yellow starthistle, were as follows: 17, Greek control; 13, Idaho; 5, California.

Sobhian and Zwölfer (1985) stated that the percentage of attack of yellow starthistle heads by *U. sirunaseva* in northern Greece varied in different yellow starthistle population groups, but they presented no data to support this claim. From our data we cannot conclude that *U. sirunaseva* showed a preference for any one population of yellow starthistle.

SEPARATION OF SPECIES

Eighty-six nominal species of Urophora are listed in the recent Catalogue of Palaearctic Diptera (Foote, 1984), of which 65 species and one subspecies are regarded as good species group taxa. Most of these species are separated by Steyskal (1979), but his paper is largely a compilation of scattered published data rather than a revision. In particular, Steyskal notes that the section of his key including U. algira (Macquart), U. jaculata, U. jaceana (Hering), U. sirunaseva and U. solstitialis (Linnaeus) is tentative; Steyskal (1979) also presented a separate key to the North American species of Urophora.

Steyskal (1979) noted that a full revision of Urophora is needed, using characters of the male and female terminalia dissected from reared specimens. One of us (IMW) has started to gather data for a revision of Palaearctic Urophora species and about 50 species have so far been examined, including 10 that may be new to science. It has been found that the form of the male terminalia is of value for diagnosing the species groups associated with Anthemideae, Cardueae and Inuleae, but they are not of practical value for separating species associated with Cardueae. Conversely, the shape of the female's aculeus tip, used in combination with other characters, does provide a reliable method of identification. As the aculeus characters have not previously been described for most species, the aculeus shape and other diagnostic features of the species of current interest to North American weed biocontrol projects are described. For convenience of use, these data are arranged as a key which includes enough diagnostic information to separate these species from all of the Palaearctic species so far studied; sufficient characters are also given to safeguard

against the possibility of any of the native North American species being confused with the introduced Palaearctic species. The terminology used in the following diagnoses and key follows White (1987a) and is based on that of McAlpine (1981) plus the wing crossband terms of Steyskal (1979).

Diagnostic characters of the subfamily Myopitinae.—Cell cup closed by a convex vein CuA_2 , so that there is no cup extension; head with 1 pair of orbital setae; dorsocentral setae present.

Diagnostic characters of *Urophora* Robineau-Desvoidy, as defined by Steyskal (1979).—Proboscis elongate, with narrow reflexed labella; lower facial margin not protruding; fold of proboscis and palpi not extending beyond lower facial margin; vein M ending at or close to wing tip.

Diagnostic characters of the Urophora species group associated with Cardueae. – Colour predominantly black; scutellum yellow; legs and usually antennae mostly orange; labellum about 1.5 times as long as 1st flagellomere; palpi (of species included here) orange; wings (of species included here) banded (Fig. 2); wing base yellow or hyaline (except in species associated with Echinops); male distiphallus reduced to a narrow membraneous sack, with no sclerotized areas; female spermathecae not sclerotized.

KEY TO FEMALES OF SELECTED SPECIES OF UROPHORA

Abbreviations: AL = aculeus length; WL = female wing length.

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3

- Wing with subbasal and discal crossbands fused from C to, or almost to, R₄₊₅. Femora black, except apically. (Preapical and apical crossbands fused from C to, or almost to, R₄₊₅.)
- Wing often without a subbasal crossband; if subbasal crossband present, it is separated from the discal crossband by a yellow area. Femora orange, sometimes striped with black
- 2. Discal and preapical crossbands fused from midway between M and CuA_1 , to hind margin of wing. 1st flagellomere orange, with black apex. Large; WL = 4.9–5.3 mm. Aculeus trun-

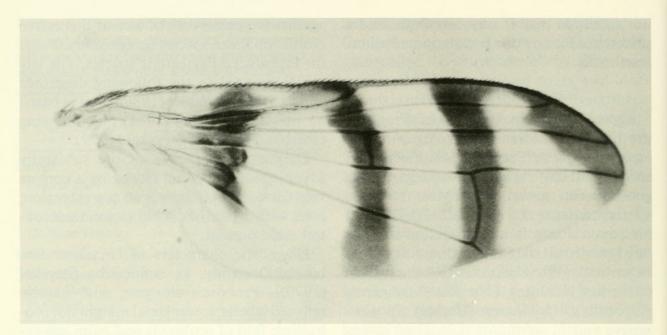


Fig. 2. Wing of *U. sirunaseva*. From wing base to wing apex the four crossbands are named as follows: subbasal, discal, preapical and apical.

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6

cate and with a single pair of subapical steps (Fig. 3). (AL = 1.7 mm) cardui (Linnaeus)

- 4. Aculeus with 2 distinct pairs of subapical steps (Figs. 6, 7). (Wing with a subbasal crossband.)
- Aculeus with 1 distinct pair of subapical steps (Figs. 8–10), often with a trace of a second pair of subapical steps (Figs. 9, 10)
- 5. Aculeus secondary steps (the pair nearest the apex) placed about three-quarters of the way between the primary steps and the apex (Fig. 6). (WL = 3.1-4.5 mm. AL = 2.6-3.4 mm)solstitialis (Linnaeus)
- Aculeus secondary steps placed about half way between the primary steps and the apex (Fig. 7). (Wing, Fig. 2. WL = 2.6-3.3 mm. AL = 1.4-2.0 mm) sirunaseva (Hering)
- 6. Aculeus without secondary steps and margin of aculeus straight between primary steps and apex (Fig. 8). (Wing without, or at most with

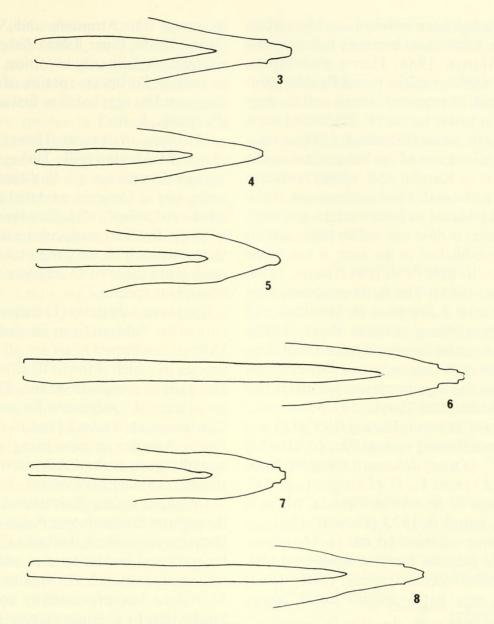
a trace, of a subbasal crossband. WL = 4.0-4.8 mm. AL = 2.9-3.5 mm)

- Aculeus with a trace of secondary steps (Figs.
- 9, 10)
- 7. Small; WL = 2.7-3.2 mm.; AL = 1.4-1.8 mm.Femora yellow. Subbasal crossband reduced, usually only from R₁ to A₁+CuA₂. Preapical crossband only one-third to half as broad as its proximal hyaline area. Preapical and apical crossbands separate. (Aculeus, Fig. 9)
- Large; WL = 3.5-4.3 mm.; AL = 2.0-2.6 mm. Fore and hind femora usually with some black markings. Subbasal crossband distinct, from C to A₁+CuA₂. Preapical crossband usually slightly broader than its proximal hyaline area. Preapical and apical crossbands usually joined, sometimes to beyond R₄₊₅. (Aculeus, Fig. 10)

.....jaceana (Hering)

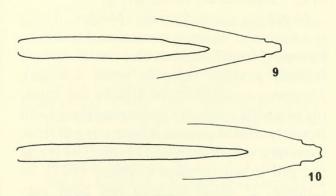
BIOLOGY AND DISTRIBUTION

Urophora affinis (Frauenfeld, 1857) is a native of central and southern Europe where it attacks *Centaurea* (Acrolophus) diffusa Lam., C. (A.) maculosa Lam., C. (A.) vallesiaca (DC.) Jordan and C. (Phalolepis) sterilis Steven. Middle Eastern populations on C. (Calcitrapa) iberica Trev. ex Sprengel are larger and may represent another species (WL = 3.3-4.2 mm; AL = 2.0-2.4 mm).



Figs. 3–8. Aculei of *Urophora* spp.: dorsoventral outline with detail of apex. 3, *U. cardui*; 4, *U. quadrifasciata*; 5, *U. jaculata*; 6, *U. solstitialis*; 7, *U. sirunaseva*; 8, *U. stylata*.

In the western U.S. and Canada U. affinis has been successfully established on C. (A.) diffusa and C. (A.) biebersteinii DC. (= C. maculosa: auctt. N. America) (Julien, 1982; Piper, 1985). Unfortunately, there are no Palaearctic records of any tephritids associated with C. biebersteinii, but this is probably a result both of its great rarity and the difficulty of distinguishing it from C. maculosa. Following the use of U. affinis in combination with U. quadrifasciata, seed production of Canadian C. biebersteinii and



Figs. 9–10. Aculei of *Urophora* sp.: dorsoventral outline with detail of apex. 9, *U. affinis*; 10, *U. jaceana*.

C. diffusa has been reduced, and in certain cases the total plant biomass has now declined (Harris, 1984; Harris and Myers, 1984). *Urophora affinis* forms lignified unilocular galls of receptacle tissue and the eggs hatch first instar larvae (P. Harris, in litt.).

Urophora cardui (Linnaeus, 1758) is a native of cooler areas of the Palaearctic region as far east as Kazakh SSR where it attacks *Cirsium arvense* (L.) Scop. Urophora cardui has been released in both western and eastern Canada; it died out in the west, and although established in the east, it has failed to reduce the area of its host (Harris, 1984; Peschken, 1984). The fly is established on *C. arvense* at a few sites in Montana and Washington (Story, 1985b; Piper, 1985). Urophora cardui forms a lignified multilocular stem gall (Lalonde and Shorthouse, 1982) and the eggs hatch second instar larvae (Peschken and Harris, 1975).

Urophora jaceana (Hering, 1935) is a native of western and central Europe where it attacks C. (Jacea) debeauxii Gren. & Godron, C. (J.) jacea L., C. (J.) nigra L. and C. (J.) phrygia L. In eastern Canada, where it was first found in 1923 (Shewell, 1961), it has become established on C. (J.) nigra. Urophora jaceana forms a lignified multilocular gall of receptacle tissue (Varley, 1947) and the eggs hatch second instar larvae (Varley, 1937).

Urophora jaculata Rondani, 1870 occurs in Italy and Greece (Fig. 1) where it forms lignified unilocular galls of receptacle tissue in *C.* (Solstitiaria) solstitialis L.

Urophora quadrifasciata (Meigen, 1826) is a native of western, central and southern Europe (Middle Eastern and north African records possiby refer to other species). Urophora quadrifasciata attacks the capitula of a wide range of Centaurea species and possibly related genera; it forms its gall from the ovary wall (Harris and Myers, 1984) and the gall is not lignified (Varley, 1937). In Canada, U. quadrifasciata has been successfully established on the same plants as U. affinis (see above) and it has extended its range into Montana and Washington (Story, 1985a; Piper, 1985). Urophora quadrifasciata is primarily bivoltine, unlike other central European species of known biology, and its eggs hatch as first instar larvae (P. Harris, in litt.).

Urophora sirunaseva (Hering, 1938) occurs in Moldavian SSR, Turkey and northeastern Greece on C. (Solstitiaria) solstitialis, and in Crete on a related plant which is believed to be C. (S.) idaea Boiss. & Heldr. It forms lignified unilocular galls of receptacle tissue which we were unable to distinguish from those of U. jaculata in the same host-plant species.

Urophora solstitialis (Linnaeus, 1758) occurs in the Palaearctic as far east as Kazakh SSR; its confirmed hosts are all *Carduus* L. species in which if forms lignified multilocular galls of receptacle tissue. The possibility of using *U. solstitialis* for the control of *Carduus acanthoides* L. and *C. nutans* L. in North America is now being investigated by colleagues at the CAB International Institute of Biological Control.

Urophora stylata (Fabricius, 1775) occurs throughout Europe (some Asian species may be synonyms) where it attacks Cirsium Miller species, Carduus species and Galactites tomentosa Moench. In British Columbia, U. stylata has substantially reduced seed production by Cirsium vulgare (Savi) Ten.; it was also released in Quebec, but it died out after the release site was mowed (Harris, 1984; Harris and Wilkinson, 1984). The fly has become established at all release sites in Washington state (Piper, 1985). Urophora stylata forms lignified multilocular galls of receptacle tissue (Harris and Wilkinson, 1984) and its eggs hatch second instar larvae (Redfern, 1968).

Watson and Harris (1984) list *U. maura* (Frauenfeld, 1857) and *U. kasachstanica* (Rikhter, 1964) as potential biocontrol agents of *Acroptilon repens* (L.) DC. in Canada. Unfortunately, the two species associated with *A. repens* were not available for study and they could not be included in the

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above key; this reference to U. maura is almost certainly based on a misidentification, as the true U. maura attacks Inula L. species (Inuleae). Moore (1972) lists several other Centaurea species that are attacked by Urophora species in Europe; these are not included in the above key because these Centaurea species are not serious weeds in North America and their associated tephritids are unlikely to be required as biological control agents. These other Centaurea species and their associated Urophora species are as follows: U. cf. quadrifasciata on C. (Calcitrapa) iberica Trev. ex Sprengel; undescribed Urophora sp. on C. (Mantisalca) salmantica L.; U. cuspidata (Meigen) on C. (Lopholoma) scabiosa L.

TYPES EXAMINED

Depositories of specimens referred to in this paper are as follows: BMNH, for British Museum (Natural History), London, England; LS, Linnaean Society, London, England; MNHP, Museum National d'Histoire Naturelle, Paris, France; MZF, Museo Zoologico dell'Università degli Studi di Firenze, Florence, Italy; NHMV, Naturhistorisches Museum, Vienna, Austria; ZMUC, Zoologisk Museum, Universitets Copenhagen, Copenhagen, Denmark. Type localities are listed by Foote (1984).

Trypeta affinis Frauenfeld, 1857.—Syntypic male bearing a handwritten label "Frfld 1856" plus 2 female and 2 male possible syntypes; 1 female dissected (NHMV).

Musca cardui Linnaeus, 1758.—Lectotype female, based on an illustration, designated by White (1987b); specimens presumed destroyed.

Euribia jaceana Hering, 1935.—Seven male and 8 female syntypes; 1 female dissected (BMNH).

Urophora jaculata Rondani, 1870. – Lectotype female here designated; dissected (MZF). Two other female specimens against the name "jaculata" in the Rondani collection (MZF) are another, possibly undescribed, species. *Trypeta quadrifasciata* Meigen, 1826.– Syntypic female examined, but not dissected (MNHP).

Euribia sirunaseva Hering, 1938.—Three male and 4 female syntypes; 1 female dissected (BMNH).

Musca solstitialis Linnaeus, 1758.—Possible male syntype examined by White (1987b) (LS).

Musca stylata Fabricius, 1775.—Presumed syntype, without an abdomen, examined (ZMUC).

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