

Tachinid (Diptera) parasitoids of *Hyphantria cunea* (Lepidoptera: Arctiidae) in its native North America and in Europe and Asia – a literature review

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The polyphagous pest fall webworm, *Hyphantria cunea* (Drury), from North America has invaded at least 20 European, 2 Eurasian (Russia and Turkey) and 10 Asian countries since 1940. At least 54 species of tachinids (Diptera: Tachinidae) from 3 subfamilies, 10 tribes and 30 genera parasitise it. Forty six (85%) of the species are from the subfamily Exoristinae, and 17, 12 and 10 species are from 3 of its tribes, Goniini, Eryciini and Exoristini, respectively. Twenty eight of the 54 species are from 7 of the 30 genera: *Exorista* Meigen (7), *Panzeria* Robineau-Desvoidy (4), *Blondelia* Robineau-Desvoidy (4), *Carcelia* Robineau-Desvoidy (4), *Hyphantrophaga* Townsend (3), *Lespesia* Robineau-Desvoidy (3) and *Zenillia* Robineau-Desvoidy (3). The majority of the 30 genera either deposit microtype eggs that are consumed by the host or oviposit on the host.

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1. Introduction

Human activity has expanded the natural range of a great number of plant pests. Across the globe, those exotic pests, including the fall webworm *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), have collectively inflicted massive economic and social costs in their new environments. According to Warren and Tadic (1967), the development of rapid transport systems that can quickly move passengers, equipment and merchandise around the world undoubtedly contributed to the spread of this extremely polyphagous, foliar-feeding pest that is native to Can-

ada, Mexico and the United States of America (USA).

This review documents parasitism of *H. cunea* by tachinids (Diptera: Tachinidae) across its original and expanded ranges from 1891 to 2011. The areas covered include its emergence as a pest; original distribution and expansion of range; and a short overview of tachinid ecology, taxonomy and distribution, as well as tabulation and referencing of parasitoid species, including the names from the original references, ovipositional strategies and parasitism percentages. It also covers the distribution of parasitoids, classical biological control attempts, host-parasitoid

ecology in new environments and prospects for future interaction between *H. cunea* and tachinids.

The authors have reported on the ichneumonid, chalcidoid and tachinid parasitoids of *H. cunea* in the Carsamba-Terme district of the Samsun region of Turkey where it is an important pest in hazelnut plantations (Sullivan *et al.* 2010, 2011, 2012), and considered that it would be useful to investigate its tachinid parasitoids across its full tricontinental range. To the authors' knowledge, the only earlier attempt was by Warren and Tadic (1967), as a part of their review of all parasitoids of this pest.

2. Review and discussion

In an enlightening account of the history of the fall webworm in the USA and Canada, Baird (1917) reported that the first record was from specimens collected near New York in about 1770. It was described by Drury (1773) as *Phalanea cunea* Drury. Baird (1917) further reported that it had been recorded as a "very destructive pest" for the first time in 1797 in the southern American state of Georgia.

The fall webworm first arrived in Europe via Hungary in 1940 and rapidly expanded its range into Austria, Bulgaria, the former Czechoslovakia, Poland, Romania, the former Soviet Union and the former Yugoslavia (Nonveiller 1951, Warren & Tadic 1970, Szalay-Marzós 1972). According to Kiritani and Morimoto (2004) it was first seen in Japan in 1945 and Niimura (1949) reported it from Tokyo in 1948. In 1958, it appeared in Seoul, South Korea, and spread rapidly, causing serious damage (Woo 1961). It was first seen in the European part of Turkey in 1975 and rapidly spread to its Black Sea coast in Asia (İren 1977). In 1979, it was first reported in China where it has attacked most cultivated plants in infested areas, particularly ornamentals, planted forests and fruit trees (Yang *et al.* 2008). Warren and Tadic (1970) reported that across its range it feeds on more than 630 plant species and is among the most polyphagous insects. In addition to its polyphagy, the polyvoltinism and ecological flexibility of *H. cunea* are major barriers to its control (Varjas & Sehna 1973).

Hyphantria cunea has now been reported from at least 20 countries in western, southern and eastern Europe, including France (d'Aguilar & Riom 1979, Moussion & Gravaud 1987), Greece (Mouloudis *et al.* 1980), Italy (Montermini & Oliva 1984, Deseo *et al.* 1986); 2 in Eurasia, Turkey (İren 1977) and Russia (Sharov & Izhevskiy 1987); and 10 in Asia, including China (Shi 1981), Azerbaijan (Nurieva 2002), Mongolia and Uzbekistan (Grichanov & Ovsyannikova 2003), Iran (Rezaei *et al.* 2003), Kazakhstan and Kyrgyzstan (Anonymous 2005) and Georgia (Japoshvili *et al.* 2006).

The family Tachinidae, commonly referred to as tachinids, is one of the most diverse dipteran families, with approximately 10,000 described species worldwide (Irwin *et al.* 2003, O'Hara 2009), about 1,550 species in the Palaearctic region (Herting & Dely-Draskovits 1993) and close to 880 species in Europe (Tschorsnig *et al.* 2005). The tachinids are found in nearly all terrestrial environments across the world, including deserts, forests, grasslands, mountains and tundra (Crosskey 1976). Stireman and Singer (2003a, b) and Stireman *et al.* (2006) reported on many aspects of tachinid research, including phylogeny, geographic diversity and ecology. The great breadth of host use across 11 orders (principally 6 orders) by the family is accompanied by broad host ranges in some tachinid species (Stireman *et al.* 2006). Obligate endoparasitism of arthropods is common to all tachinids (Pape 1992), and their predominant role as parasitoids of the larval stage of Lepidoptera and other major groups of herbivorous insects ensures they play a major role in limiting herbivore populations and in structuring natural and managed communities (Stireman *et al.* 2006).

Warren and Tadic (1967) reported 27 tachinid species from *H. cunea*, with 16, 11 and 3 species from North America, Europe and Asia, respectively, including a small degree of overlap. The current review includes their species and those of many other authors. All species names were updated, according to Arnaud (1978), Herting (1984), Wood (1987), Tschorsnig and Herting (1994), Tschorsnig and Richter (1998), O'Hara (2002, 2009, 2010), Kara and Tschorsnig (2003), Tschorsnig *et al.* (2005), Shima (2006), and Cerretti and Tschorsnig (2010).

Across its entire natural and expanded range, 54 species of tachinids from 30 genera, 10 tribes and 3 subfamilies have been reported from the fall webworm (Table 1). These totals assume at least 2 species of *Winthemia* Robineau-Desvoidy in North America (Arnaud 1978) and 2 unidentified *Exorista* species in South Korea (Kim et al. 1968a). Twenty three, 20 and 17 tachinid species are reported from North America, Asia and Europe, respectively, with a minor overlap of species. In its expanded range of Europe and Asia, the fall webworm hosts a minimum of 32 species. This means there are now more species attacking it in its expanded range than in its native range.

Overall, the number of reported species has increased from 27 (Warren & Tadic 1967) to 54, and genera from 12 (Warren & Tadic 1967) to 30 (Table 1). Forty six (85%) of the 54 species are from the Subfamily Exoristinae and 17, 12 and 10 species are from its tribes Goniini, Eryciini and Exoristini, respectively. Collectively, the 39 species from these three tribes account for 72% of the listed species.

Sheehan (1994) and Stireman and Singer (2003a) reported that host species having abundant, gregarious and host plant generalist caterpillars are attacked by considerably more tachinid species than host species with rare, specialist and solitary caterpillars. Stireman and Singer (2003a) further reported that more tachinid species attack hairy caterpillars than smooth ones. In addition, Jeffries and Lawton (1984) found a positive relationship between tachinid diversity and both gregariousness and shelter building. Since the larvae of *H. cunea* are abundant, gregarious, hairy, host plant generalist and shelter building, they fulfill five criteria for vulnerability to attack (Jeffries & Lawton 1984, Sheehan 1994, Stireman & Singer 2003a). The 54 species listed for *H. cunea* in this review attest to that vulnerability.

Hyphantria cunea is parasitised by multiple species within some genera. The most prominent examples are *Exorista* Meigen (7), *Panzeria* Robineau-Desvoidy (4), *Blondelia* Robineau-Desvoidy (4), *Carcelia* Robineau-Desvoidy (4), *Hyphantrophaga* Townsend (3), *Lespesia* Robineau-Desvoidy (3) and *Zenillia* Robineau-Desvoidy (3) (Table 1). Twenty eight (52%) of the 54 listed species are from these 7 genera (Table 1).

The almost ubiquitous *Compsilura concinnata* (Meigen) is common to Europe, Asia and North America (introduced), and *Bessa parallela* (Meigen), *Exorista larvarum* (Linnaeus), *Pales pavidata* (Meigen) and *Zenillia libatrix* (Panzer) are common to Europe and Asia. *Compsilura concinnata*, *E. larvarum* and *P. pavidata*, which all have a broad host range (Arnaud 1978, Boettner et al. 2000, Strazanac et al. 2001), have been reported from at least 13, 9 and 8 countries, respectively. In contrast, there are single reports of 16 species listed in Table 1.

Tachinids have 2 major ovipositional strategies – direct and indirect. The overall total of 6 strategies includes direct oviposition (4 strategies) that is external or internal and further subdivided by ovarvipary and ovipary, and also indirect oviposition (2 strategies) featuring ovarvipary or the deposition of microtype eggs that are ingested during feeding (Stireman et al. 2006).

The tachinids reported from *H. cunea* in its original range in North America, which is in the Nearctic region, employ 5 of the 6 ovipositional strategies, with the exception being direct internal (unincubated egg) oviposition. Of the 11 North American genera, 6 oviposit indirectly, 3 genera are from the Tribe Goniini (microtype eggs) and 3 are from the Tachininae. Stireman, J. O. (pers. comm., 2012) reported that Tachininae are generally ovarviparous (e.g. *Panzeria*) and deposit eggs on substrates frequented by their hosts; the eggs hatch and the larvae wait for passing hosts.

In the expanded range of *H. cunea* in Europe and Asia, which are in the Palaearctic region, representatives from the same 5 subdivisions parasitise *H. cunea*. This review reports 21 genera from those 2 continents, including 10 genera (48%) from the tribe Goniini, and 5 genera (24%) from the tribe Eryciini, which is characterized by direct external oviposition of incubated eggs.

Tachinid species, complexes and rates of parasitism vary widely from site to site, study to study and nation to nation. Nagy et al. (1953) reported from Hungary that up to 62% of larvae were parasitised by *Exorista* (as *Tachina*) *larvarum*. In contrast, Jermy (1957) reported 10 tachinids from Hungary but cautioned that their life cycles are not synchronised with that of *H. cunea* and that they were unlikely to decisively control outbreaks. From France, d'Aguilar and

Table 1. Tachinid (Diptera: Tachinidae) parasitoids of *Hyphantria cunea* (Lepidoptera: Arctiidae) in Asia (A), Europe (E) and North America (NA) listed according to subfamily, tribe, species (alphabetical order) and references (chronological order).

Subfamily, Tribe Species References*, **, ***	Continent
Dexiinae, Voriini	
<i>Thelaira nigripes</i> (Fabricius)	E
Sharov & Izhevskiy 1987, Sisojevic & Cepelák 1987	
Exoristinae, Blondeliini	
<i>Blondelia eufitchiae</i> (Townsend)	NA
Swain 1937 as <i>Masicera eufitchiae</i> Town., Warren & Tadic 1967, Arnaud 1978, O'Hara 2009	
<i>Blondelia hyphantriae</i> (Tohill)	NA
Tohill 1922 as <i>Lydella hyphantriae</i> Toth., Schaffner & Griswold 1934 as <i>Anetia hyphantriae</i> Tohill, Swain 1937 as <i>A. hyphantriae</i> , Swain 1937 as <i>L. hyphantriae</i> , Thompson 1946 as <i>L. hyphantriae</i> , Warren & Tadic 1967, Arnaud 1978, O'Hara 2009	
<i>Blondelia nigripes</i> (Fallen)	E
Györfi 1954 as <i>Lydella nigripes</i> Fallen	
<i>Blondelia obconica</i> (Walker)	NA
Aldrich 1931 as <i>Tachina obconica</i> Walk.	
<i>Compsilura concinnata</i> (Meigen)	A, E, NA
Tohill 1922, Schaffner & Griswold 1934, Swain 1937, Thompson 1946, Böhm & Pschorn-Walcher 1952, Schimitschek 1952, Bogavac 1953, Jermy 1953, Nagy <i>et al.</i> 1953, Sisojevic 1953, Dyadechko 1954, Györfi 1954, Jermy 1957, Szalay-Marzso 1957, Bogavac 1958, Sikura 1959, Capek 1961, Cepelák 1963, Schimitschek 1964, Tadic & Kosac 1967, Warren & Tadic 1967, Tadic 1975, Morris 1976, Arnaud 1978, Riom & Menassieu 1978, d'Aguilar & Riom 1979, Trenchev 1980, Baş 1982, Tóth 1985, Allegro 1987, Sharov & Izhevskiy 1987, Ziegler 1987, Tóth 1988, Tuncer 1992, Nurieva 2002, Kan <i>et al.</i> 2003, Watanabe 2005, Yang <i>et al.</i> 2008, Cerretti & Tschorsnig 2010, Sullivan <i>et al.</i> 2012	
Exoristinae, Eryciini	
<i>Bactromyia aurulenta</i> (Meigen)	A
Shima 2006	
<i>Carcelia bombylans</i> Robineau-Desvoidy	E
Bogavac 1958, Nanni 1991, Cerretti & Tschorsnig 2010	
<i>Carcelia gnava</i> Meigen	A
Kim <i>et al.</i> 1968a	
<i>Carcelia protuberans</i> (Aldrich and Webber)	NA
Schaffner & Griswold 1934 as <i>Zenillia protuberans</i> Aldrich & Webber, Swain 1937 as <i>Z. protuberans</i> , Thompson 1946, Warren & Tadic 1967, Arnaud 1978, O'Hara 2009	
<i>Carcelia sumatrana</i> (Townsend)	A
Shima 2006	
<i>Drino inconspicua</i> (Meigen)	E
Bogavac 1953 (misspelled as <i>Drina inconspicua</i>), Jermy 1957 as <i>Sturmia inconspicua</i> (Meigen), Bogavac 1958	
<i>Drino inconspicuoides</i> (Baranov)	A
Watanabe 2005	
<i>Lespesia aletiae</i> (Riley)	NA
Webber 1930 as <i>Achaetoneura aletiae</i> (Riley), Schaffner & Griswold 1934 as <i>A. aletiae</i> , Swain 1937 as <i>A. aletiae</i> , Thompson 1946 as <i>A. aletiae</i> , Warren & Tadic 1967, Arnaud 1978, Stireman & Singer 2003b, O'Hara 2009	
<i>Lespesia archippivora</i> (Riley)	NA
Stireman & Singer 2003b	
<i>Lespesia frenchii</i> (Williston)	NA
Webber 1930 as <i>Achaetoneura frenchii</i> (Will.), Schaffner & Griswold 1934 as <i>A. frenchii</i> , Swain 1937 as <i>A. frenchii</i> , Thompson 1946 as <i>A. frenchii</i> , Tadic 1963 as <i>A. frenchii</i> , Warren & Tadic 1967, Arnaud 1978, Stireman & Singer 2003b, O'Hara 2009	
<i>Nilea hortulana</i> (Meigen)	A
Takano 1956, Hasegawa 1966, Shima 2006	
<i>Senometopia prima</i> (Baranov)	A
Shima 2006	

Subfamily, Tribe Species References*, **, ***	Continent
Exoristinae, Exoristini	
<i>Bessa parallela</i> (Meigen) Sisojevic 1953 as <i>Bessa selecta</i> (Meigen), Jermy 1957 as <i>Ptychomyia selecta</i> Meigen, Hasegawa 1966 as <i>B. selecta</i> , Tadic & Kosac 1967 as <i>B. selecta</i> , Sharov & Izhevskiy 1987, Watanabe 2005, Shima 2006	A, E
<i>Chetogena claripennis</i> (Macquart) Schaffner & Griswold 1934 as <i>Phorocera claripennis</i> Macq., Swain 1937 as <i>P. claripennis</i> , Thompson 1946 as <i>P. claripennis</i> , Warren & Tadic 1967 as <i>Euphorocera claripennis</i> (Macq.), Arnaud 1978 as <i>E. claripennis</i> , O'Hara 2009	NA
<i>Chetogena scutellaris</i> (Wulp) Swain 1937 as <i>Phorocera floridensis</i> (Town.), Warren & Tadic 1967 as <i>Euphorocera floridensis</i> Town., Arnaud 1978, O'Hara 2009	NA
<i>Exorista fasciata</i> Fallen Shu & Yu 1985	A
<i>Exorista japonica</i> (Townsend) Kato <i>et al.</i> 1951 as <i>Eutachina japonica</i> Town., Warren & Tadic 1967 as <i>E. japonica</i> , Kim <i>et al.</i> 1968a as <i>E. japonica</i> , Poong <i>et al.</i> 1981 as <i>E. japonica</i> , Shi 1981, Shu & Yu 1985, Kan <i>et al.</i> 2003, Watanabe 2005, Yang <i>et al.</i> 2008	A
<i>Exorista larvarum</i> (Linnaeus) Böhm & Pschorn-Walcher 1952, Schimitschek 1952, Bogavac 1953, Jermy 1953, Nagy <i>et al.</i> 1953 as <i>Tachina larvarum</i> L., Sisojevic 1953, Györfi 1954 as <i>T. larvarum</i> , Jermy 1957 as <i>T. larvarum</i> , Szalay-Marzsó 1957, Bogavac 1958, Manolache <i>et al.</i> 1958, Sikura 1959, Schimitschek 1964, Tadic 1975, Tóth 1988, Baş 1982, Allegro 1987, Sharov & Izhevskiy 1987, Tuncer 1992, Nurieva 2002, Cerretti & Tschorsnig 2010	A, E
<i>Exorista segregata</i> (Rondani) Sisojevic 1953 as <i>Exorista fasciata moreti</i> (Robineau-Desvoidy), Györfi (1954) as <i>Parasetigena segregata</i> Rond., Jermy 1957	E
<i>Exorista xanthaspis</i> (Wiedemann) Bogavac 1953 as <i>Exorista fallax</i> Meigen, Nagy <i>et al.</i> 1953 as <i>Tachina fallax</i> Meigen, Sisojevic 1953 as <i>E. fallax</i> , Györfi 1954 as <i>T. fallax</i> , Jermy 1957, Bogavac 1958, Manolache <i>et al.</i> 1958, Trenchev 1980, Sharov & Izhevskiy 1987 as <i>E. fallax</i>	E
<i>Exorista</i> sp. (1) Kim <i>et al.</i> 1968a	A
<i>Exorista</i> sp. (2) Kim <i>et al.</i> 1968a	A
Exoristinae, Goniini	
<i>Cadurcia</i> sp. Tadic 1975	E
<i>Ceromasia auricaudata</i> (Townsend) Arnaud 1978, O'Hara 2009	NA
<i>Clemelis pullata</i> (Meigen) Railyan 1974	E
<i>Eurysthaea scutellaris</i> (Robineau-Desvoidy) Tadic 1975	E
<i>Gonia bimaculata</i> (Wiedemann) Bogavac 1953, Herting 1960	E
<i>Hyphantrophaga blanda</i> (Osten Sacken) Schaffner & Griswold 1934 as <i>Zenillia blanda</i> (Osten Sacken), Swain 1937 as <i>Z. blanda</i> , Thompson 1946 as <i>Z. blanda</i> , Warren & Tadic 1967 as <i>Eusisyropa blanda</i> (Osten Sacken), Morris 1976 as <i>E. blanda</i> , Arnaud 1978 as <i>E. blanda</i> , O'Hara 2009	NA
<i>Hyphantrophaga hyphantriae</i> (Townsend) Townsend 1891 as <i>Meigenia hyphantriae</i> Town., Townsend 1893 as <i>M. hyphantriae</i> , Coquillett 1897, Swain 1937, Warren & Tadic 1967, Arnaud 1978 as <i>Hyphantrophaga desmiae</i> (Sellers), Stireman & Singer 2003b, O'Hara 2009	NA
<i>Hyphantrophaga virilis</i> (Aldrich and Webber) Schaffner & Griswold 1934 as <i>Zenillia virilis</i> Aldrich & Webber, Swain 1937 as <i>Z. blanda virilis</i> Aldrich & Webber, Thompson 1946 as <i>Z. virilis</i> , Warren & Tadic 1967 as <i>Eusisyropa virilis</i> (Aldrich & Webber), Arnaud 1978 as <i>E. virilis</i> , O'Hara 2009	NA

Subfamily, Tribe Species References*, **, ***	Continent
<i>Isoturmia picta</i> (Baranov)	A
Kim <i>et al.</i> 1968a as <i>Sturmia picta</i> Baranoff, Poong <i>et al.</i> 1981 as <i>S. picta</i>	
<i>Kuwanimyia conspersa</i> (Townsend)	A
Shima 2006	
<i>Pales pavidata</i> (Meigen)	A, E
Niimura 1951, Bogavac 1953 as <i>Ctenophorocera pavidata</i> Meigen, Jermy 1953, Nagy <i>et al.</i> 1953, Sisojevic 1953 as <i>C. pavidata</i> , Bogavac 1958, Tadic & Kosac 1967, Warren & Tadic 1967, Szalay-Marzsó 1972, Baş 1982, Shu & Yu 1985 as <i>C. pavidata</i> , Sharov & Izhevskiy 1987 as <i>C. pavidata</i> , Tuncer 1992, Richter 1996, Camerini & Groppali 1999, Hubenov 2001, Watanabe 2005, Cerretti & Tschorsnig 2010	
<i>Patelloa leucaniae</i> (Coquillett)	NA
Thompson 1946 as <i>Phorocera leucaniae</i> Coq., Warren & Tadic 1967, Arnaud 1978, O'Hara 2009	
<i>Pseudogonia parisiaca</i> (Robineau-Desvoidy)	E
Anonymous 1997	
<i>Sturmia bella</i> (Meigen)	A
Kato <i>et al.</i> 1951, Hasegawa 1966	
<i>Zenillia dolosa</i> (Meigen)	A
Watanabe 2005, Shima 2006	
<i>Zenillia libatrix</i> (Panzer)	A, E
Niimura 1951, Jermy 1957, Hasegawa 1966, Warren & Tadic 1967, Allegro 1987, Shima 2006, Cerretti & Tschorsnig 2010	
<i>Zenillia</i> sp.	A
Kato <i>et al.</i> 1951, Shima 2006	
Exoristinae, Winthemiini	
<i>Winthemia</i> spp.	NA
Schaffner & Griswold 1934, Swain 1937, Arnaud 1978	
Tachininae, Ernestiini	
<i>Panzeria aldrichi</i> (Townsend)	NA
Swain 1937 as <i>Varichaeta aldrichi</i> Town., Thompson 1946 as <i>Ernestia aldrichi</i> Town., Warren & Tadic 1967 as <i>Mericia aldrichi</i> (Town.), Wood 1987, O'Hara 2009	
<i>Panzeria ampelus</i> (Walker)	NA
Coquillett 1897 as <i>Panzeria radicum</i> (Fabr.), Tothill 1922 as <i>Ernestia ampelus</i> (Walk.), Schaffner & Griswold 1934 as <i>E. ampelus</i> , Swain 1937 as <i>P. radicum</i> , Swain 1937 as <i>E. ampelus</i> , Swain 1937 as <i>Nemoraea nigricornis</i> Williston, Thompson 1946 as <i>E. ampelus</i> , Tadic 1963 as <i>Mericia ampelus</i> (Walk.), Warren & Tadic 1967 as <i>M. ampelus</i> , Nordin <i>et al.</i> 1972 as <i>M. ampelus</i> , Morris 1976 as <i>M. ampelus</i> , Arnaud 1978 as <i>M. ampelus</i> , O'Hara 2009	
<i>Panzeria arcuata</i> (Tothill)	NA
Arnaud 1978 as <i>Mericia arcuata</i> (Tothill), O'Hara 2009	
<i>Panzeria johnsoni</i> (Tothill)	NA
Swain 1937 as <i>Ernestia johnsoni</i> Tothill, Thompson 1946 as <i>E. johnsoni</i> , Warren & Tadic 1967 as <i>Mericia johnsoni</i> (Toth.), Arnaud 1978 as <i>M. johnsoni</i> , O'Hara 2009	
Tachininae, Nemoraeini	
<i>Nemoraea pellucida</i> (Meigen)	E
Riom & Menassieu 1978, d'Aguilar & Riom 1979, Moussion & Gravaud 1987, Tiberi & Bin 1987, Ziegler 1990, Tuncer 1992, Tschorsnig & Herting 1994, Marchesini <i>et al.</i> 1998, Cerretti & Tschorsnig 2010, Sullivan <i>et al.</i> 2012	
Tachininae, Polideini	
<i>Hystricia abrupta</i> (Wiedemann)	NA
Schaffner & Griswold 1934 as <i>Bombyliopsis abrupta</i> (Wied.), Swain 1937 as <i>B. abrupta</i> , Thompson 1946 as <i>B. abrupta</i> , Warren & Tadic 1967 as <i>B. abrupta</i> , Arnaud 1978 as <i>B. abrupta</i> , O'Hara 2002, 2009	
Tachininae, Tachinini	
<i>Archytas aterrimus</i> (Robineau-Desvoidy)	NA
Arnaud 1978, O'Hara 2009	

* Oliver (1964) reported 4 unnamed species from Louisiana, USA.

** Györfi (1954) reported *Exorista rustica* but it is a parasitoid of sawflies and is probably a misidentification.

*** Thompson (1946), Arnaud (1978), Shima (2006) and O'Hara (2009) are catalogues and their listings are usually based on the respective original records.

Riom (1979) reported approximately 30% parasitism in 1977–1978, with the rate of parasitism of the second generation being higher than in the first because of better synchronisation of the development. However, from the former Yugoslavia, Tadic and Kosac (1967) reported less than 1% parasitism by tachinids in 1967. Poong *et al.* (1981) reported parasitism ranging from 2.4% to 10.7% across sites in Korea and that *Exorista (Eutachina) japonica* (Town) was the most common tachinid. From China, Yang *et al.* (2008) reported parasitism rates of 4% to 15.7% for *E. japonica* and 2% for *C. concinnata*. From France, Moussion and Gravaud (1987) reported that *Nemoraea pellucida* (Meigen) and *C. concinnata* contributed 84% and 16% of tachinid parasitism, respectively, but didn't report the actual percentage of pupae parasitised. From the Samsun region of Turkey, Tuncer (1992) reported tachinid parasitism of 4.2% and 18% from overwintered pupae in 1990 and 1991, respectively. Sullivan *et al.* (2012) reported total parasitism by *N. pellucida* and *C. concinnata* of overwintered pupae of 1.9% in 2008 and 4.5% in 2009 in the Samsun region. They also reported that *N. pellucida* and *C. concinnata* contributed 95% and 5%, respectively, of total parasitism. Watanabe (2005) reported that the highest percentage parasitism due to a tachinid complex of 6 species in Tsukuba, Japan from 1995–1997 was 70–80% in third generation larvae in the wandering stage. That report suggests that larvae that leave the web can be highly vulnerable to tachinid attack.

A known parasitoid in one country can be present but not reported as a parasitoid in another country. For example, *Carcelia bombylans* Robineau-Desvoidy, *C. gnava* (Meigen), *E. larvarum*, *N. pellucida* and *Thelaira nigripes* (Fabricius) have been reported from Japan but were not listed among the 14 parasitoids of *H. cunea* there (Shima 2006). Those 14 species from Japan and 13 from Hungary (Györfi 1954, Jermy 1957, Szalay-Marzsó 1972) beg the question of whether those numbers reflect exceptional diversity of ecological conditions and/or thorough investigation, or whether there may be under-reporting in other countries. For example, only 3 species have been reported from China (Shi 1981, Shu & Yu 1985, Yang *et al.* 2008), 4 species from Turkey (Baş 1982, Çanakcioğlu & Selmi 1988,

Tuncer 1992, Kara & Tschorsnig 2003, Sullivan *et al.* 2012), 5 species from South Korea (Kim *et al.* 1968a) and 7 species from Italy (Cerretti & Tschorsnig 2010).

Approximately 100 tachinid species have been employed in biological control programs of crop and forest pests, and many of those programs have met with partial or complete success (Hedlund & Schroder 1981, Grenier 1988). In attempts at classical biological control of *H. cunea*, a number of species were introduced from North America to Europe and Asia. Tadic (1958) reported the introduction of *Panzeria* (as *Mericia*) *ampelus* (Walker) to the former Yugoslavia but noted serious problems with hibernation and the detection of European secondary hosts. Later, Bjegovic (1962) reported an unsuccessful attempt to introduce *Lespesia* (as *Achaetoneura*) *aletiae* (Riley) to the same country. Pupae were placed in an outdoor shelter at 0–10°C for overwintering, but all died. Kim *et al.* (1968b) reported an attempt to introduce *P.* (as *Mericia*) *ampelus* to South Korea. It failed because of the asynchronous life cycles of the host and parasitoid, and the lack of alternative hosts when the correct stage of *H. cunea* was not available. *Compsilura concinnata* was initially introduced into North America in 1906 to combat the exotic forest pest, the gypsy moth, *Lymantria dispar* Linnaeus (Koch & Hutchison 2011). *Exorista larvarum*, *Drino disparis* Sabrosky and *D. inconspicua* (Meigen) were also introduced for the control of the gypsy moth and they parasitised *H. cunea* in laboratory studies (Hedlund & Schroder 1981).

However, in the broader context of biological control, it would be remiss of the authors of this review not to mention that, according to Boettner *et al.* (2000), some introduced tachinids have had catastrophic effects on non-target species. *Compsilura concinnata* and *L. aletiae* have broad host ranges (Arnaud 1978, Stireman *et al.* 2006), and with the benefit of hindsight, they may well be seen as inappropriate choices for biological control programs.

Anecdotal evidence suggests that in the 70 years and 60 years since its accidental introduction into Europe and Asia, respectively, the initial impact of *H. cunea* has been tempered by management and ecological factors, including para-

sitism by indigenous tachinids. From Hungary, its original entry point to Europe, Ripka, G. (pers. comm., 2011) reported that *H. cunea* usually has a low level pest status in most of the country. Rarely, in certain dry and warm years, the infestation level is higher, generally in private gardens and on street trees. In the Black Sea region of Turkey, local ‘hotspots’ still occur in the Samsun Region, especially in hazelnut plantations, but the last major outbreak was in 1984–1985. From 2007–2012, there was a much less extensive outbreak in its Carsamba–Terme district. In 2011, 3 generations defoliated hundreds of hectares of hazelnut plantations and fruit trees, including mulberry, a preferred host, and in 2012, the first generation alone defoliated a larger but different area in the same district. According to Warren and Tadic (1967), the generally lower pest status of the fall webworm over time in its expanded range may be partly due to indigenous species coming to prefer it to their native hosts, resulting in a greater degree of life cycle synchronisation and increased specificity of attack.

3. Closing remarks

The fall webworm has proven to be a supremely adaptable pest across its natural range in North America and in its greatly expanded European and Asian ranges. Overall, it remains to be seen whether it has reached the limit of its range across the globe. Evidence to the contrary comes from New Zealand where it gained a toehold in the Auckland area in 2003 but it was quickly eradicated (Anonymous 2005). However, the Southern Hemisphere may yet be the scene for future encounters between this extraordinarily resilient pest and endemic tachinids.

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