European Parasitoids of the Pine False Webworm (*Acantholyda erythrocephala* (L.)) and Their Potential for Biological Control in North America

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ABSTRACT The pine false webworm (*Acantholyda erythrocephala*) is a pine defoliator of Palearctic origin introduced into North America early in the 20th century. A literature search and field surveys showed that the parasitoid complex of the pine false webworm is much richer in Europe than in North America. The potential for introducing European parasitoids into North America is evaluated here. The most promising biological control agent is the tachinid *Myxexoristops hertingi*, a larval parasitoid that lays microtype eggs on pine needles. The release of *M. hertingi* is proposed. Other larval parasitoids, particularly the ichneumonid *Xenoschesis* sp. and the egg parasitoid, *Trichogramma* sp., also show some potential but further studies are required before considering them for release into North America.

THE PINE FALSE webworm (PFW) (*Acantholyda erythrocephala* (L.)) (Hym.: Pamphiliidae) is a Palearctic insect, distributed from Japan to Britain and from Lapland to Italy. It was first observed in the United States in 1925 (Wells 1926) and in Canada in 1961 (Eidt and McPhee 1963). It reached pest status in the late 1970s when heavy damage was observed in young red pine (*Pinus resinosa*) plantations in Ontario (Syme 1981). In 1993, the first outbreaks occurred in mature red pine stands. In New York State, the first severe defoliation was noticed in the early 1980s; since then, the PFW has become a persistent and increasing problem in white pine (*Pinus strobus*) plantations in the Adirondack Mountains (Asaro and Allen 1999, Allen 2000). Although most defoliation reports have come from Ontario and New York, the PFW is in several states in the northeastern United States, Quebec, Alberta, and Newfoundland (Howse 2000). In addition to white and red pine, nearly all pine species are occasionally attacked. Persistent outbreaks, as observed in North America, cause severe growth loss (Allen 2000). Tree mortality often occurs after 5 to 7 years of heavy defoliation due to secondary pests such as bark beetles. Even low populations of the PFW can be particularly destructive in Christmas tree plantations, reducing the market value of the trees.

In contrast, the PFW is considered a minor pest in its area of origin. Outbreaks are rare and usually of short duration (2 to 3 years). Notable exceptions include an 8-year outbreak in the 1960s in eastern Austria (Schmutzenhofer 1974) and populations in southern Poland that remained at semi-outbreak levels for a decade in the 1980-1990's (M. Kenis, unpublished). In the late 1990s, unusually heavy outbreaks started in northwestern Italy in 40-year-old white pine plantations situated far from the natural distribution of pine species. As in North America, *A. erythrocephala* is found on most pine species, with the exception of Mediterranean species. The heaviest outbreaks were observed in plantations of *P. strobus*, *P. sylvestris*, and *P. nigra*. In addition, defoliation is often observed on isolated *P. mugho* and *P. cembra* in gardens, particularly in the Southern Alps (Hellrigl 1996).

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The biology and ecology of *A. erythrocephala* has been studied by several authors (e.g. Schwerdtfeger 1941, 1944; Schmutzenhofer 1974; Lyons 1994, 1995, 1996; Asaro and Allen 1999). Its life history can be summarized at follows. Adults emerge from the soil in spring, from March (Italy) to May (Canada). Mating and oviposition start soon after emergence. Eggs are laid in rows of one to ten on 1-year-old pine needles. Hatching occurs 3 to 4 weeks later and newly hatched larvae start feeding at the base of the needles, then construct silken webs within which they feed. On average, a larva destroys about 50 needles of *P. sylvestris*, most of them being only partly consumed. Males go through five instars and females go through six instars. From May to July, mature larvae (eonymphs) drop to the soil and build a pupal cell below the humus layer, usually at depths of 3 to 12 cm. After a summer diapause, most eonymphs transform to pronymphs, but some go into prolonged diapause for 2 to 3 years. The rate of prolonged diapause varies among years and with latitude. Pronymphs pupate in spring and adults emerge a few weeks later.

Very little is known about the population dynamics of the PFW in Europe, but natural enemies, particularly parasitoids and pathogens, have been commonly observed and have sometimes been associated with the collapse of outbreaks (e.g. Schwerdtfeger 1941, Rumphorst and Goossen 1960, Jahn 1967, Schmutzenhofer 1974). In North America, however, natural enemies are rare and of low incidence (Lyons 1995, Asaro and Allen 1999). Considering the differences between Europe and North America in terms of both natural enemy impact and outbreak frequency and duration, a biological control program was set up with the aim of introducing European natural enemies into North America. This paper presents information on PFW parasitism in North America and Europe as well as data on the main parasitoid species and an evaluation of their potential as biological control agents. More precise data on parasitoid collection and rearing will be presented elsewhere (Kenis and Kloosterman, in preparation).

Parasitoid Complex of *A. erythrocephala* in North America

The parasitoid complex of the PFW in North America is shown in Table 1. Egg parasitoids are nearly absent. The polyphagous species *Trichogramma minutum* Riley has occasionally been reared from PFW eggs in Ontario (Lyons 1995, Bourchier et al. 2000). Strains of *T. minutum* and *T. platneri* Nagarkatti have been used for inundative releases against the sawfly with some success (Bourchier et al. 2000).

Table 1. Parasitoids of *Acantholyda erythrocephala* in Canada and the USA

	Canada	USA
Egg Parasitoid		
Trichogramma minutum Riley (Trichogrammatidae)	X	
Larval Parasitoids		
Ctenopelma erythrocephalae Barron (Ichneumonidae)		X
Homaspis interruptus (Provancher) (Ichneumonidae)		X
Olesicampe sp. (Ichneumonidae)	X	
Sinophorus megalodontis Sanborne (Ichneumonidae)	X	

Sources: Canada: Bourchier et al. 2000; Lyons 1995, 1999
USA: Asaro and Allen 1999; Barron 1981

Four ichnemonid larval parasitoids were observed on the PFW in Canada and the USA. *Sinophorus megalodontis* Sanborne and *Olesicampe* sp. were reared from eonymphs in Ontario (Lyons 1995, 1999; Bourchier et al. 2000) and *Homaspis interruptus* (Provancher) was found parasitizing the PFW in New York (Asaro and Allen 1999). In addition, *Ctenopelma erythrocephalae* Barron was observed ovipositing in eggs of the PFW in New Jersey (Barron 1981). All these species are apparently of Nearctic origin and none of them seem to have an important impact on sawfly populations, probably because they are poorly adapted to their novel host. Larval parasitism has not exceeded 10%, even after 15 years of continuous outbreaks. *H. interruptus* is also known from another *Acantholyda* sp. and a *Cephalcia* sp. (Barron 1990), whereas the regular hosts of the three other parasitoid species are not known.

Parasitoid Complex of *A. erythrocephala* and Congeneric Species in Europe

Table 2 presents the parasitoid species found in the literature or during our own surveys in Poland, Italy, and Switzerland. The parasitoid complexes of the two congeneric species *A. posticalis* Matsumura (= *nemoralis* Thomson) and *A. hieroglyphica* (Christ) are added since they could represent alternative hosts for parasitoid collections should *A. erythrocephala* populations not be available in Europe. Comparing the parasitoid complexes of closely related hosts might also give important information on parasitoid specificity. Although the literature data on parasitoids of *Acantholyda* spp. were checked for the most obvious mistakes, the list presented in Table 2 has to be considered with caution because it probably contains taxonomic errors, such as different names referring to the same species or a single name referring to two species.

As expected, the parasitoid complex of the PFW is much richer in Europe than in North America. At least four to five egg parasitoids and 8 to 10 larval parasitoids attack *A. erythrocephala* in Europe. *A. posticalis* has a parasitoid complex that is similarly rich, with several species overlapping. Only three species were reared from *A. hieroglyphica*, probably because few studies focused on this species.

Egg Parasitism. Several gregarious *Trichogramma* species are reported from the PFW and other *Acantholyda* spp. in Europe. Schwerdtfeger (1944) mentions high parasitism by *T. evanescens* Westwood on *A. erythrocephala* in Germany in the 1940s and Burzynski (1961) reports *T. embryophagum* (Hartig) as a parasitoid of *A. erythrocephala* in Poland. Both species are also known to attack *A. posticalis* (Herting 1977). Recently, an undescribed *Trichogramma* sp. of the group *fasciatum* was found attacking outbreak populations of *A. posticalis* and low-density populations of *A. erythrocephala* in the Valle d'Aosta, northeastern Italy. This species is univoltine, overwinters in host eggs, and is more specific than the majority of its congeneric species. Screening tests were made on four Lepidopteran species frequently used as rearing hosts for *Trichogramma* spp. (Bourchier et al. 2000). The *Trichogramma* sp. refused to oviposit in *Anagastes kuehniella* (Zeller), *Actebia fennica* (Tauscher), and *Choristoneura fumiferana* (Clemens), whereas oviposition was observed on *Lambdina fiscellaria* (Guenée) but no development occurred. In additional tests (Kenis and Kloosterman, unpublished), females rejected eggs of two diprionid pine sawflies, *Diprion pini* L. and *Gilpinia frutetorum* F. The species most closely related to the undescribed *Trichogramma* sp., both ecologically and morphologically, is *T. cephalciae* Hochmut & Martinek, a parasitoid mainly associated with *Cephalcia* spp., another pamphiliid genus

Table 2. Parasitoids of *Acantholyda erythrocephala, A. posticalis,* and *A. hieroglyphica* in Europe; data is from the literature (L) and own surveys (S)

	A. erythr.	*A. postic.*	*A. hierogl.*
Egg Parasitoids			
Trichogramma sp. (Trichogrammatidae)	S	L,S	
Trichogramma cephalciae Hochmut & Martinek (Trichogr.)		L	
Trichogramma embryophagum (Hartig) (Trichogrammatidae)	L	L	
Trichogramma evanescens Westwood (Trichogrammatidae)	L	L	
Trichogramma semblidis (Aurivillius) (Trichogrammatidae)	S	S	
Aprostocetus sp. (Eulophidae)		S	
Neochrysocharis formosa (Westwood) (Eulophidae)	L,S	L,S	
Mesopolobus subfumatus (Ratzeburg) (Eulophidae)		L,S	
Larval Parasitoids			
Ctenopelma lucifer (Gravenhorst) (Ichneumonidae)		L	
Ctenopelma nigrum Holmgren (Ichneumonidae)	L	L	
Holocremnus heterogaster Thomson (Ichneumonidae)	L		
Homaspis rufinus (Gravenhorst) (Ichneumonidae)	L	L	
Notopygus sp. (Ichneumonidae)	S	S	
Olesicampe monticola (Hedwig) (Ichneumonidae)	L		
Netelia oscellaris (Thomson) (Ichneumonidae)	L		
Sinophorus sp. (Ichneumonidae)	S		
Sinophorus crassifemur (Thomson) (Ichneumonidae)	L	L	
Xenoschesis sp. (Ichneumonidae)	S		
Xenoschesis fulvipes (Gravenhorst) (Ichneumonidae)	L	L	L
Euexorista obumbrata (Pandellé) (Tachinidae)		L	
Exorista larvarum (L.) (Tachinidae)		L	
Myxexoristops bonsdorffi (Zetterstedt) (Tachinidae)		L,S	
Myxexoristops hertingi Mesnil (Tachinidae)	L,S		
Nemorilla maculosa (Meigen) (Tachinidae)			L
Pseudopachystylum gonioides (Zetterstedt) (Tachinidae)	L	L	
Undetermined Tachinidae			L

Sources: *A. erythrocephala*: Kenis and Kloosterman (unpublished surveys in Poland, Italy and Switzerland); Burzynski 1961; Eichhorn 1988 (review); Hellrigl 1996; Herting 1964, 1977 (review); Jahn 1967; Joakimov 1921; Pschorn-Walcher 1982 (review); Rumphorst and Goossen 1960; Schmutzenhofer 1974; Schwerdtfeger 1941, 1944; Thompson 1944 (review)
A. posticalis: Kenis and Kloosterman (unpublished surveys in Italy); Casale and Campò 1977; Eichhorn 1988 (review); Herting 1977 (review); Hochmut and Martinek 1963; Pschorn-Walcher 1982 (review); Thompson 1944 (review)
A. hieroglyphica: Herting 1977 (review); Pschorn-Walcher (1982 (review)

that feeds mainly on spruce. *T. cephalciae* has also been occasionally reared from *A. posticalis* (Hochmut and Martinek 1963). This species is partly univoltine and apparently specific to Pamphiliidae, but is morphologically distinguishable from undescribed *Trichogramma* sp. (Pintureau, Stefanescu, and Kenis, in preparation). Another species, the multivoltine, polyphagous *T. semblidis* (Aurivillius) was reared occasionally from the same populations of *A. posticalis* and *A. erythrocephala* in Italy (Kenis and Kloosterman, in preparation).

Burzynski (1961) and Kenis and Kloosterman (in preparation) reared the solitary eulophid *Neochrysocharis formosa* Westwood (=*Achrysocharella ovulorum* Ratzeburg) from *A. erythrocephala* in Poland. *N. formosa* is a polyphagous parasitoid also known from *A. posticalis* (Casale and Sampò 1977; Herting 1977; Kenis and Kloosterman, in preparation) and pine diprionid sawflies (e.g. Pschorn-Walcher and Eichhorn 1973).

Larval Parasitism – Ichneumonidae. Several ichneumonid species are reported from *A. erythrocephala* and congeneric species (Table 2), but usually only one or two species are mentioned per host population. The ichneumonids most commonly associated with *A. erythrocephala* belong to the genera *Xenoschesis* and *Sinophorus*. In previous studies, they were usually identified as *X. fulvipes* (Gravenhorst) and *S. crassifemur* (Thomson) (e.g. Schwerdtfeger 1944, Schmutzenhofer 1974), two species better known as parasitoids of *Cephalcia* spp. However, a closer examination of *Xenoschesis* sp. from Poland and Italy and *Sinophorus* sp. from Poland (Kenis and Kloosterman, in preparation) revealed morphological differences when compared with specimens reared from *Cephalcia* spp. Since the phenology of *Cephalcia* spp. is at least one month later than that of *A. erythrocephala* and *A. posticalis*, it is likely that the two host genera support different, closely related parasitoids. A similar taxonomic problem arises with *Ctenopelma lucifer* (Gravenhorst), the main parasitoid found in *A. posticalis* outbreaks in the Valle d'Aosta, Italy (Casale and Sampò 1977). Recent observations in the same area suggest that it is not *C. lucifer*, but *Notopygus* sp., a species also reared from *A. erythrocephala* in Poland (Kenis and Kloosterman, in preparation).

Two other ichneumonid species worth mentioning are *Olesicampe monticola* (Hedwig), a parasitoid usually associated with *Cephalcia* spp. that was found parasitizing 44% of the larvae of an isolated population of *A. erythrocephala* in South Tyrol, Italy (Hellrigl 1996), and *Holocremnus heterogaster* Thomson, the dominant parasitoid during an *A. erythrocephala* outbreak from 1915 to 1917 in Bulgaria (Joakimov 1921).

Ichneumonid parasitoids of *Acantholyda* spp. attack eggs or larvae and kill their host in the pupal cell, either before or after the winter. In most cases, ichneumonids are able to follow their host into prolonged diapause (Kenis and Kloosterman, unpublished). Eggs and young larvae are frequently encapsulated in the host haemolymph.

Larval Parasitism – Tachinidae. Only two tachinid species are reported from *A. erythrocephala* (Table 2). *Pseudopachystylum gonioides* (Zetterstedt), a species frequently reared from *A. posticalis* in Central Europe, has also been cited as a parasitoid of *A. erythrocephala* (Herting 1977). However, the most regularly encountered tachinid parasitoid of *A. erythrocephala* is *Myxexoristops hertingi* Mesnil. It is found throughout the entire European distribution of its host and has often been mentioned as the main parasitoid of the PFW; Rumphorst and Goossen (1960) suggested that the fly was the main cause of the collapse of an outbreak in Germany. *A. posticalis* and the closely related *Cephalcia* spp. are attacked by the congeneric species *M. bonsdorffi* (Zetterstedt) and *M. abietis* Herting, respectively (Herting 1964, Eichhorn 1988), suggesting high host specificity in this genus. *M. hertingi* was found in low density populations on isolated *Pinus cembra* in the Swiss and Italian Alps. Specimens were also reared from the closely related host *Acantholyda pumilionis* (Giraud) in the same areas (Kenis and Kloosterman, in preparation). However, these had a much more rapid development, with large larvae found in mature host larvae dropping to the soil, which suggests the possible existence of sibling species.

M. hertingi lays over 1,000 microtype eggs on pine needles that are ingested by sawfly larvae. Parasitoid development occurs when the eonymph is in the soil. The winter is passed as a mature maggot in the dead host skin. In spring, the maggot climbs to the soil surface to build a puparium. Adults emerge after about a month and mate soon after emergence. *M. hertingi* puparia are sometimes heavily attacked by hyperparasitoids such as a gregarious diaprid wasp *Trichopria* sp. that killed over 20% of the puparia in an outbreak in Italy in 1999 (Kenis and Kloosterman, in preparation).

In recent years, we have put much emphasis on the development of a rearing method for *M. hertingi*. Although possible, rearing *M. hertingi* in the laboratory proved to be very difficult for two reasons: (1) the low rate of mating success and (2) the poor development of tachinids after egg ingestion (Kenis and Kloosterman, in preparation).

Biological Control Potential

There is general agreement on the most important attributes of a good biological control agent to introduce against an exotic pest (e.g. Cock 1986). In particular, the natural enemy should (1) have an important impact on the host in the region of origin, (2) be host specific, (3) be well synchronized with the host, (4) have a high searching capacity, (5) be well adapted to a wide range of environmental conditions, and (6) occupy an empty ecological niche in the natural enemy community of the pest in the region of introduction. The tachinid *M. hertingi* combines all these attributes. Literature and field surveys showed that it is the most abundant and frequently encountered parasitoid of the PFW in Europe. Its broad distribution indicates that it has a wide climatic range and the observation of isolated PFW populations being attacked in the Alps suggest that the fly has a good search capacity. There is no tachinid or other late larval parasitoid reported from the PFW in North America. *M. hertingi* is a univoltine parasitoid and is well synchronized with its host. Finally, *M. hertingi* is apparently very specific and is probably restricted to one or two *Acantholyda* spp. Therefore, we recommend *M. hertingi* for introduction into North America.

The difficulty in rearing *M. hertingi* suggests that releases in North America may have to be made with field collected material. Since outbreaks in Europe are scarce, every opportunity should be taken to collect *M. hertingi* when sizeable populations are available. However, efforts should be made to improve laboratory mating techniques because establishment in North America would more likely be achieved by releasing mated females than unmated flies.

Ichneumonids, particularly the most common species *Xenoschesis* sp., may represent additional candidates. Ichneumonids have long been considered less specific than *M. hertingi* because the same species were reported from *Acantholyda* spp. and *Cephalcia* spp. However, recent observations showed that a complex of sister species was involved that was probably more specific than previously thought. Further studies, however, are needed on the taxonomy, specificity, biology, and ecology of the main species before considering them for introduction. In particular, the high rates of encapsulation often observed in Europe may hamper their establishment or efficiency in North America.

Finally, the undescribed *Trichogramma* sp. would merit further studies. In contrast to most other *Trichogramma* spp., it is univoltine and would not require an alternate host to become established in North America. Host specificity would need to be further evaluated but preliminary observations suggest that this species is more host specific than most of its congeneric species. However, its real impact and occurrence in Europe as well as its taxonomic status need to be further assessed.

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