

# Host Range of *Aphantorhaphopsis samarensis* (Diptera: Tachinidae), a Larval Parasite of the Gypsy Moth (Lepidoptera: Lymantriidae)

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**ABSTRACT** *Aphantorhaphopsis samarensis* (Villeneuve), a European tachinid, has been released in North America for classical biological control of the gypsy moth, *Lymantria dispar* (L.). This study examined the host range of *A. samarensis*. We used three approaches: (1) field collection and rearing of potential alternate or alternative hosts at European sites where *A. samarensis* was known to occur, (2) choice tests offering females of *A. samarensis* both gypsy moth and native North American species of Lepidoptera, and (3) host suitability tests in which we artificially inoculated European nontarget species with mature eggs of *A. samarensis* dissected from gravid females. In the field studies, we collected a total of 851 caterpillars, belonging to at least 54 species other than gypsy moth in 11 families, over several years, but none yielded *A. samarensis*, with the possible exception of a single larva of *Lymantria monacha* (L.) and the rusty tussock moth, *Orgyia antiqua* (L.), which yielded puparia resembling those of *A. samarensis*. In laboratory tests, we offered females of *A. samarensis* 11 native species of North American Lepidoptera in five families, but only the lymantriid *Orgyia leucostigma* (J. E. Smith), was successfully parasitized. In host suitability studies, we inoculated 10 species of Lepidoptera in eight families with mature eggs of *A. samarensis*, but parasitism was successful only in *L. dispar*. We conclude that *A. samarensis* has a high degree of host specificity.

**KEY WORDS** *Aphantorhaphopsis samarensis*, biological control, host range, host specificity, host suitability

*Aphantorhaphopsis* (= *Ceranthia*) *samarensis* (Villeneuve), a small tachinid fly of European origin, is a promising natural enemy for classical biological control of gypsy moth, *Lymantria dispar* (L.), in North America (Mills and Nealis 1992, Nealis and Quednau 1996). Most of our information on this parasite's potential for biological control comes from the collaborative work between the Centers for Applied Bioscience International (CABI) and the Canadian Forest Service (Mills and Nealis 1992, Quednau 1993, Nealis and Quednau 1996, Kenis and López-Vaamonde 1998). To determine the factors that control gypsy moth populations in non-outbreak situations, Mills and Nealis (1992) exposed gypsy moth larvae in areas in Europe where local gypsy moth populations were at low densities, recollected the hosts, and returned them to the laboratory to rear out the parasitoids. In these situations, *A. samarensis* was the most important parasitoid, with levels of parasit-

ization of *L. dispar* frequently >30%, whereas it is only occasionally encountered during outbreaks (Fuester et al. 1983, Maier 1990). This suggests that *A. samarensis* is a low host-density specialist that has good host-finding ability and responds quickly and effectively to local increases in the gypsy moth populations (Mills and Nealis 1992). In the field, most *A. samarensis* enter diapause (Mills and Nealis 1992), so it is essentially univoltine, and there is no alternate host required. Moreover, *A. samarensis* parasitizes mainly intermediate instars of gypsy moth (Quednau 1993), stages that usually sustain low rates of parasitism in North America (Ticehurst 1984), but it sometimes attacks and develops in late instars (Maier 1990).

Despite its promising attributes as a biological control agent, little was known about the potential host range of *A. samarensis*. In fact, no biological information was presented by Herting (1960) and Mesnil (1963) in their landmark publications on European Tachinidae. It is believed to be host specific (Mills and Nealis 1992), and our review of the literature revealed only two known hosts, both lymantriids: *L. dispar* (Fuester et al. 1983, Maier 1990, Mills and Nealis 1992, Kenis and López-Vaamonde 1998) and *Orgyia recens* (Hübner) (Mihalyi 1986). This fly was not listed among the parasitoid complexes of several European lymantriids that have been studied extensively: *Lymantria monacha* (L.) (Komarek 1937, Fahringer 1941, Thompson 1944–1950, Thompson and Simmonds 1964–1965, Herting 1976, Mills and Schoenberg 1985);

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browntail moth, *Euproctis chryssorhea* (L.) (Burgess and Crossman 1929, Sisojević et al. 1976); satin moth, *Leucoma salicis* (L.) (Pawłowicz 1936, Piscià et al. 1978, Drea and Fuester 1979); rusty tussock moth, *Orgyia antiqua* (L.) (Wellenstein and Fabritius 1973, Drea and Fuester 1979, Mills and Schoenberg 1985); and pale tussock moth, *Calliteara pudibunda* (L.) (Herting 1960, Wellenstein 1978). However, some tachinids have very broad host ranges, and there is increasing concern about nontarget effects in biological control programs. For example, *Compsilura concinnata* (Meigen), one of the first parasitoids introduced from Europe for biological control of gypsy moth (Howard and Fiske 1911), has been reared from 200 species and 20 families of Lepidoptera (Clausen 1956), and Boettner et al. (2000) suggested that reported declines in populations of native saturniids in New England might have been caused by the introduction of the fly. Although *A. samarensis* has been released in Canada (Mills and Nealis 1992, Nealis and Quednau 1996), and biological control workers wanted to release it in the United States, we felt that additional information on the host range of *A. samarensis* should be acquired before making releases. In this article, we present the results of field observations and laboratory screening tests on host specificity.

### Materials and Methods

**CABI Field Studies in Europe.** Field collections of possible alternate hosts were made by CABI scientists (M.K. and C.L.-V.) at sites in Europe where *A. samarensis* was abundant. Collections of macrolepidopteran larvae were made at Delémont (Jura), Switzerland, in 1993 and Plancher-Bas (site 1) (Haute-Saône), France in 1994 and 1999, simultaneously with exposures of gypsy moth larvae. Exposure and recollection of gypsy moth larvae were done as described in Mills and Nealis (1992). Cohorts of second-instar gypsy moth larvae were exposed on small oak, *Quercus robur* (L.), and hornbeam, *Carpinus betulus* (L.), trees during 3 wk. Collections of possible alternate hosts were made the same days as the recollection of gypsy moth larvae, i.e., 8 June–9 July 1993 in Switzerland, as well as on 24 June–1 July 1994, and on 12–16 June 1999 in France. Caterpillars were collected by beating trees and shrubs and sweeping grass in the surroundings of the trees on which gypsy moth larvae were exposed. They were then reared singly in plastic vials (54 by 27 mm) and fed with fresh foliage of the plant or tree species on which they were found until pupation or formation of parasitoid puparia and cocoon. Tachinid puparia resembling those of *A. samarensis* were kept at 22°C and 90% RH until emergence.

In spring 1995, a large gypsy moth outbreak occurred at Haguenau (site 1) (Bas-Rhin, France) with substantial parasitism by *A. samarensis* (M.K., unpublished data). Therefore, it was expected that high numbers of the tachinid would emerge in 1996 from overwintering puparia and attack the residual gypsy moth population as well as potential alternative hosts. Macrolepidopteran larvae were collected at the out-

break site (13–28 June 1996) and reared in the laboratory as described above, except that larvae of the same species were reared in maximum groups of 20 in 1.3-liter plastic cylinders.

**USDA Field Studies in Europe.** Independent collections and rearings were made by the USDA-Agricultural Research Service-European Biological Control Laboratory (F.H.) at other sites where *A. samarensis* was known to occur, but slightly different methods were used. At Val-Suzon (Côte d'Or), France, we collected 32, 17, and 5 fifth instars of *L. monacha* under burlap bands on *Q. robur* on 23 June, 30 June, and 13 July 1995, respectively. During 1995, 1996, and 1999, we made collections of other possible alternate hosts by examining the foliage and picking caterpillars, individually. On 26 July 1995, at Haguenau (site 2), France, we collected five fourth instars of *O. antiqua* on leaves of *Q. robur*. During 1996, at Plancher-Bas (site 2), France, we collected 20 third instars of *O. antiqua* on leaves of *Q. robur*. During 1999, collections of potential alternate or alternative hosts were made at both sites. They were reared individually in aerated round plastic containers (100 by 85 mm) and fed fresh oak leaves.

Collections of gypsy moth caterpillars were made to rear out *A. samarensis*, and rates of parasitism were determined. During 1995, the last year of the gypsy moth outbreak at Haguenau (site 2), larvae from the natural population were collected by examining the foliage and picking caterpillars, individually. During 1996, 1997, and 1999 (first to fourth year of the latency phase) cohorts of laboratory reared gypsy moths in the second–fifth stadia were exposed for periods of 15 d at Haguenau (site 2), 29 May–2 July 1996; at Plancher-Bas (site 2), 30 May–4 July 1996; at Haguenau (site 2), 29 April–22 July 1997; at Plancher-Bas (site 2), 12–21 May 1997 (site 2); and for periods of 10 d at Haguenau (site 2), 6 May–29 July 1999; and at Plancher-Bas (site 2), 5 May–28 July 1999. They were reared individually in 118-ml cups with paper lids on artificial diet (high wheat germ formula, Bell et al. 1981).

**Laboratory Tests on Host Specificity.** The gestation period of mated females of *A. samarensis* ranges from 7 to 8 d at 22°C to 17 d at 15:10°C (at a photoperiod of 12:12 [L:D] h) (Quednau and Lamontagne 1998); but because of variations in the time of day when mating occurs and the metabolism of individual females, not all females in a cohort necessarily begin ovulation on the same day. Therefore, a choice test format was used, because false negatives could occur if a female that was not yet gravid were exposed to a nontarget species. Host specificity tests were conducted in the quarantine facility at the ARS Beneficial Insect Introduction Research Unit at Newark, DE, in a rearing room at 25°C, 50–60% RH, and a photoperiod of 14:10 (L:D) h. Screened cages (46 by 33 by 40 cm) with sliding Plexiglas doors were used as test arenas. Flies were provided with sponges soaked in distilled water for moisture, and sugar cubes and jelly (Quednau and Lamontagne 1998) for food. Host exposures consisted of 15 gypsy moth larvae (second or early third instars) on a bouquet of red oak, *Quercus rubra*

(L.), and with 15 larvae of a nontarget species of similar size on a bouquet of its preferred host plant. Exposures were 48 h in duration, and cages were gently atomized with distilled water at least twice a day. When exposures were completed, caterpillars were reared out to determine if parasitization had occurred. Small ventilated plastic cages with false bottoms similar to those described by Loan and Holdaway (1961) were used, so that any maggots of *A. samarensis* emerging could drop to the bottom and not be chewed up by any unparasitized caterpillars. Larvae of gypsy moth were fed artificial diet (Bell et al. 1981); those of nontarget species were fed small bouquets of their host plant (or artificial diet if from a laboratory culture). Hosts were reared to the pupal stage or until death, and categorized as parasitized, unparasitized (healthy), diseased, desiccated, or dying of unknown causes. Hosts dying before reaching the pupal stage were dissected to see if parasitization had occurred. Trials in which neither *L. dispar* nor the nontarget species were parasitized were considered inconclusive and excluded from our tabulations.

**Laboratory Tests on Host Suitability.** *Aphantorhaphopsis samarensis* lays mature eggs that immediately hatch when placed on a host larva (Quednau 1993). Tests on host suitability were done by artificially inoculating larvae of gypsy moth and selected nontarget species with mature eggs of *A. samarensis* that had been dissected from uteri of gravid females at least ten days old. Inoculations were done by endorming a host larva with CO<sub>2</sub>, and placing a freshly hatched maggot on the back of the larva with a moistened brush. Maggots were kept damp with Ringer's solution while searching for an entry site. Once a site was chosen, entry through the integument took 10–30 s. Larvae of gypsy moth and *Mamestra brassicae* (L.) came from a laboratory rearing in Delémont, Switzerland; whereas the other species were obtained at Delémont by catching females using a light trap and rearing their progeny until the second or third instar. Larvae were reared on their natural host plant until *A. samarensis* emergence or host pupation. One month after oviposition, the larvae that were still alive or had not pupated were dissected.

## Results

**Field Studies in Europe.** *CABI Collections.* In 1993 (Switzerland), 1994, and 1999 (Plancher-Bas, site 1), field exposures of gypsy moth larvae provided 25 *A. samarensis* out of 2,665 host larvae, 354 out of 956 larvae, and 293 out of 1,596 larvae, respectively. At the same time, 205 caterpillars representing 27 other species in nine macrolepidopteran families were collected. A single puparium morphologically identical to that of *A. samarensis* was reared from a larva of *L. monacha* collected at Plancher-Bas in 1994, but the identity of the species could not be determined with certainty, because no adult emerged (Table 1). No other hosts yielded puparia resembling *A. samarensis*. In 1996, macrolepidopteran larvae were collected at Haguenau (site 1), at sites where gypsy moth and *A.*

*samarensis* had been observed in high numbers the previous year. Surprisingly, not a single gypsy moth larva was found. A total of 454 caterpillars, belonging to 13 species in seven families, were collected, but no *A. samarensis* was reared from these larvae.

*USDA Collections.* During 1995, no *A. samarensis* was obtained from 54 larvae of *L. monacha* collected at Val-Suzon, and three *A. samarensis* emerged from one out of 1,433 gypsy moth larvae collected at the same site. In 1995, nine puparia morphologically resembling those of *A. samarensis* were reared from one of five larvae of *O. antiqua*, collected at Haguenau (site 2), but the identity of the species could not be determined with certainty, because no adult emerged (Table 1). During the same year, *L. dispar* was abundant at Haguenau, but *A. samarensis* was rather scarce, and only 0.97 and 1.0% of the larvae collected there on 14 June and 30 June, respectively, were parasitized. At Plancher-Bas (site 2) during 1996, six out of 112 recaptured gypsy moth larvae were parasitized by *A. samarensis*, but no *A. samarensis* was obtained from 20 larvae of *O. antiqua* collected there. During 1996, no *A. samarensis* was obtained from the 234 gypsy moth larvae recaptured at Haguenau (site 2). However, substantial numbers of *A. samarensis* were recovered the following year at both sites. During 1997, at Haguenau (site 2), 289 *A. samarensis* were obtained from 2,474 recaptured gypsy moth larvae. No *A. samarensis* was obtained from the gypsy moth larvae exposed before 27 May 1997. The peak of abundance of *A. samarensis* (emerged from 37% of recaptured hosts) occurred in larvae exposed 27 May through 10 June 1997. During 1997, at Plancher-bas (site 2), 223 *A. samarensis* were obtained from 651 recaptured gypsy moth larvae. The peak of abundance of *A. samarensis* (emerged from 65% of recaptured hosts) occurred in larvae exposed 9–23 June 1997. These results indicate that the abundance of *A. samarensis* at these sites might vary from year to year, but that the habitat is very favorable for this tachinid, and parasitization of gypsy moth can be quite high.

During 1999, at Haguenau (site 2), 208 *A. samarensis* were obtained from 2,297 recaptured gypsy moth larvae. No *A. samarensis* was obtained from the hosts exposed before 27 May 1999. The mean peak of abundance of *A. samarensis* (emerged from 25.7% of recaptured hosts) occurred in larvae exposed 27 June–8 July 1999. In one of two plots at Haguenau, the parasitism peaked at 37.4% on 26 June 1999. Collections of other Lepidoptera at Haguenau comprised 32 specimens in 20 species (including 15 undetermined geometrids and noctuids) in five families, but none was parasitized by *A. samarensis*. During the same year at Plancher-Bas (site 2), 176 *A. samarensis* were obtained from 2,367 recaptured gypsy moth larvae. There was no particular mean peak of emergence at this site. Mean parasitism by *A. samarensis* in both plots varied from 8.1% to 12.1% in the five recollections made 5 June–17 July 1999. However, in one of the two plots at this site, parasitism peaked at 29% on 7 July 1999. Collections of other Lepidoptera at this site comprised 81 specimens in 23 species (18 undeter-

**Table 1.** Numbers of specimens of macrolepidoptera collected by CABI and USDA and recoveries of *Aphantorhaphopsis samarensis* in Europe, 1993–1999

Species	CABI	USDA	Total	No. parasitized by <i>A. samarensis</i>
	Pieridae			
<i>Gonepteryx rhamni</i> (L.)	0	1	1	0
	Nymphalidae			
<i>Vanessa atalanta</i> (L.)	22	0	22	0
<i>Inachis io</i> (L.)	75	0	75	0
<i>Aglais urticae</i> (L.)	4	0	4	0
<i>Araschnia levana</i> (L.)	12	0	12	0
<i>Clossiana selene</i> (Schifferrmüller)	2	0	2	0
<i>Melicta athalia</i> (Rottensburg)	0	5	5	0
	Drepanidae			
<i>Drepana binaria</i> (Hufnagel)	2	0	2	0
	Geometridae			
<i>Abraxis grossulariata</i> (L.)	1	0	1	0
<i>Semiothisa liturata</i> (Clerck)	2	0	2	0
<i>Ectropis crepuscularia</i> (Denis & Schifferrmüller)	13	0	13	0
<i>Ennomos quercinaria</i> (Hufnagel)	3	0	3	0
<i>Plagodis dolabria</i> (L.)	1	0	1	0
<i>Acaris viretata</i> (Hübner)	2	0	2	0
4 undetermined species	55	0	55	0
10 undetermined species	0	35	35	0
	Lasiocampidae			
<i>Malocosoma neustria</i> (L.)	5	3	8	0
	Saturniidae			
<i>Aglia tau</i> (L.)	2	0	2	0
<i>Saturnia pavonia</i> (L.)	1	0	1	0
	Thaumetopoeidae			
<i>Thaumetopoea processionea</i> (L.)	5	0	5	0
	Notodontidae			
<i>Phalera bucephala</i> (L.)	7	0	7	0
	Arctiidae			
<i>Tyria jakobaeae</i> (L.)	4	0	4	0
<i>Arctia caja</i> (L.)	1	1	2	0
	Lymantriidae			
<i>Elkneria pudibunda</i> (L.)	0	7	7	0
<i>Orgyia antiqua</i> (L.)	0	25	25	1?
<i>Orgyia recens</i> (L.)	0	7	7	0
<i>Lymantria monacha</i> (L.)	6	54	60	1?
<i>Euproctis chrysorrhea</i> (L.)	4	0	4	0
	Noctuidae			
<i>Colocasia coryli</i> (L.)	188	0	188	0
<i>Acronicta auricoma</i> Denis & Schifferrmüller	29	0	29	0
<i>Cryphia muralis</i> (Forster)	1	0	1	0
<i>Amphipyra pyramidea</i> (L.)	1	0	1	0
<i>Cucullia</i> sp.	1	0	1	0
<i>Moma alpium</i> Osbeck	0	2	2	0
<i>Mythimna albipuncta</i> Denis & Schifferrmüller	4	0	4	0
2 undetermined species	201	0	201	0
10 undetermined species	0	52	52	0
Total	659	192	851	2?

mined geometrids and noctuids) in five families, and again, none was parasitized by *A. samarensis*.

**Field Collection Summary.** The distribution of individuals within species, over all samples of macrolepidoptera collected in our field study, typified the structure one expects to find in samples taken from natural communities. Excluding gypsy moth, most species were represented by only a few individuals, and only seven species by 25 or more specimens: two lymant-

riids, *L. monacha* and *O. antiqua*; three noctuids, *Acronicta auricoma* (Denis & Schifferrmüller), *Cryphia muralis* (Forster), and an undetermined species; one undetermined geometrid; and one nymphalid, *Inachis io* (L.) (Table 1). Over the 5 yr observations were made, a total of 851 lepidopteran larvae (other than *L. dispar*) belonging to at least 54 species in 11 families were collected and reared by CABI and USDA scientists, but no verifiable recoveries of *A. samarensis* re-





from other lymantriids, suggest that this fly could not be exerting high levels of parasitization on a wide range of lymantriids.

The results of our laboratory host specificity tests against North American species were consistent with our field studies and known host records from Europe. Only species in the lymantriid genera *Lymantria* and *Orgyia* were successfully parasitized by the fly, further evidence that *A. samarensis* has a narrow host range, probably confined to the Lymantriidae. It is noteworthy that *A. samarensis* is not known to attack *Euproctis* or *Leucoma* in Europe, and did not attack *Dasychira* in our lab tests. These three genera overwinter as caterpillars, whereas *Lymantria* and *Orgyia*, genera known to be attacked, overwinter in the egg stage. In Europe, attacks by *A. samarensis* on gypsy moth occur primarily on second- and third-instar hosts from late May to early July (Mills and Nealis 1992), so attacks on species that overwinter as caterpillars seem problematic. Based upon our studies, we conclude that, in the event of its establishment, attacks by *A. samarensis* on North American lymantriids other than gypsy moth could occur on *Orgyia* spp., but would be sporadic and low in frequency.

The negative results from rearings of other lepidopteran taxa collected (Table 1) are also of interest, because many of the genera sampled occur in North America. Considering first the superfamily Noctuoidea exclusive of Lymantriidae, the arctiids, *Arctia caja* (L.) and *Tyria jakobaeae* (L.), have subspecies in North America, and the noctuid genera *Acronicta*, *Amphipyra*, *Colocasia*, *Cryphia*, and *Cucullia* have vicariant North American species (Arnett 1985). This grouping comprised over half of the specimens collected ( $n = 492$ ). Similarly, about half of the remaining moth genera encountered (*Drepana*, *Ennomos*, *Plagodis*, *Semiothisa*, *Malacosoma*, and *Saturnia*) have vicariant representatives in North America and one of the geometrids, *Ectropis crepuscularia*, is holarctic (Arnett 1985). We collected seven butterfly species, two of which, *C. selene* (Schiffermüller) and *Vanessa atalanta* (L.), occur in North America, and a third genus, *Aglais*, has vicariant species there (Arnett 1985).

Although gravid females of *A. samarensis* at our study sites were foraging in their natural habitats, many host species were collected in small numbers, so we cannot conclude with 100% certainty that this tachinid never attacks those species recovered in small numbers. However, our data show that *A. samarensis* is not widely polyphagous; otherwise we should have made numerous recoveries scattered over the various taxa collected. The results obtained at Haguenau (site 1) in 1995–96, were noteworthy, because both gypsy moths and *A. samarensis* had been abundant there in 1995, suggesting that many adults of this tachinid would emerge there the following spring. In 1996, however, no gypsy moth larvae were found, yet not one of 454 caterpillars (13 species and seven families) of other Lepidoptera collected during and after the oviposition period of *A. samarensis* were parasitized by the fly. This suggests that *A. samarensis* does not attack

other species of lepidopterous larvae when its habitual hosts are at low densities. Moreover, the fact that no nontarget species artificially inoculated in Europe yielded living parasitoids suggests that *A. samarensis* has such stringent host suitability requirements, that most nontargets would be safe even if occasional attacks occurred accidentally. Therefore, we feel that if *A. samarensis* becomes established in North America, the probability of it attacking native Lepidoptera other than lymantriids approaches zero.

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