XXXII SIREX WOODWASP

(*Sirex noctilio* Fabricius) (Hymenoptera: Siricidae)

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DESCRIPTION OF PEST

Taxonomy

Sirex noctilio (Fig. 1) from "Germania" was first described in 1793 by Fabricius. Synonyms were published in 1871 (*Sirex melanocerus* Thomson) and 1909 (*Paururus atlantidis* Ghiji) (Schiff et al., 2012). The genus *Sirex* has been revised for the Western Hemisphere where 14 species are known (one invasive and 13 native) from North America, Mesoamerica (an area from central Mexico to Guatemala), and the Greater Antilles, and more species are expected to exist. A total of 28 species are known from the Northern Hemisphere (Schiff et al., 2012).

Figure 1 Adult *Sirex noctilio* female ovipositing into the side of the cardboard barrel containing the pine bolt from which it emerged. E. Erin Morris.

Distribution

Sirex noctilio is native to Eurasia and northern Africa and has been known from New Zealand since 1900 (Miller and Clark, 1935). It is assumed to have been introduced into New Zealand in timber from Europe (Talbot, 1977). From New Zealand, *S. noctilio* continued to spread in the Southern Hemisphere, being first discovered in Tasmania in 1952, mainland Australia in 1961, Uruguay in 1980, Argentina in 1985, Brazil in 1988, South Africa in 1994, and Chile in 2001 (Hurley et al., 2007; Beèche et al., 2012). In 2004, *S. noctilio* was collected for the first time as an invasive species in the North Hemisphere, in New York State (Hoebeke et al., 2005), and in 2005 it was found in Ontario, Canada (de Groot et al., 2006). By 2012, the distribution of *S. noctilio* in North America included New York, Pennsylvania, Vermont, Michigan, Ohio, Connecticut, and New Jersey (NAPIS, 2012). The introduction of *S. noctilio* to North America likely occurred before 2004, based on the extent of the infestation when first detected. The North American invasion is the first instance of a *S. noctilio* introduction into a region with native pines, supporting native species of siricids (including species of *Sirex*) and their parasitoids.

Damage

Type *Sirex* species are generally considered pests of secondary importance in their native areas (Furniss and Carolin, 1977; Madden, 1988; Spradbery and Kirk, 1978), where they attack trees that are already stressed. *Sirex noctilio* differs because it is aggressive when invasive, attacking and killing seemingly healthy trees. *Sirex noctilio* females lay eggs within trees, at the same time depositing cells of a white rot fungus, *Amylostereum areolatum* (Chaillet ex Fr.) Boidin, and phytotoxic mucous. When mucous is injected, it initially causes tissue desiccation, collapse of phloem cells, and changes in plant respiration. Collectively these symptoms reduce the tree's resistance to the fungus (Coutts, 1969a; Fong and Crowden, 1973). The fungus subsequently dries out the sapwood by restricting sap flow to the crown (Coutts, 1969b; Kile and Turnbull, 1974). Together, the fungus and mucous kill the tree. *Sirex noctilio* prefers pines

(*Pinus* spp.), although other conifers, including *Auricaria* spp., are sometimes attacked (Madden, 1988; Ryan and Hurley, 2012).

Extent Although *S. noctilio* was first reported in New Zealand in 1904, it was not documented as a serious pest in New Zealand until approximately 1926 (Cameron, 2012). By 1946–51, up to one third of the 120,000 hectares of Monterey pine trees (*Pinus radiata* D. Don) on the North Island in New Zealand had been killed by the pest (Gilmour, 1965). Today, throughout much the Southern Hemisphere where *S. noctilio* has been introduced, this species is a major pest of pines, causing extensive damage and monetary loss in pine plantations. In the 1980s, a total of 1.8 million Monterey pine trees in southeastern Australia were killed due to a particularly dramatic outbreak population of *S. noctilio* (Haugen and Underdown, 1990). Outbreaks of *S. noctilio* are particularly associated with stands of pines that are stressed by overstocking and/or drought (Talbot, 1977; Cameron, 2012).

Biology of the Pest

The white rot fungus that *Sirex* females inject into coniferous trees during oviposition is required for development of their larvae. Therefore, the life cycle of *S. noctilio* must be explained in conjunction with that of its mutualistic fungus. Larvae benefit because the fungus rots and dries the wood and thus provides the environmental conditions, enzymes, and nutrients needed for larval growth (Madden and Coutts, 1979). Larvae of *S. noctilio* carry the fungus with them in their hypopleural organs, while adult females of *S. noctilio* carry fungal cells in a pair of intersegmental organs called mycangia, at the base of the ovipositor. In addition, females also have a reservoir containing phytotoxic mucous in their abdomens, and they inject this mucous into trees when they deposit eggs or fungus.

Sirex noctilio usually has one generation per year, but in colder climates one generation may require two to three years (Ryan and Hurley, 2012). Adult *S. noctilio* are highly variable in size, ranging from 9–35 mm in length (Hoebeke et al., 2005). Adults emerge from early summer to early autumn and then mate. Adult females are pro-ovigenic and each contains from 30–450 eggs upon adult eclosion, with the number of eggs depending on the size of the female (Madden, 1974). Females use their sawtooth ovipositors to drill into trees. Often, initial single drills by females are exploratory while females search for trees with acceptable osmotic pressure levels in the phloem sap. Once a female has accepted a tree, she creates an external hole in the bark and drills 1–4 holes, at different angles, up to 12 mm into the sapwood (Coutts and Dolezal, 1969). If there is only a single drilling event, fungal arthrospores and mucous are deposited, but when there are multiple drilling events in a tree, eggs and mucous are deposited in each insertion, except the last drill when fungus plus mucous are inserted. In an attacked tree, the fungus quickly begins to grow in the wood, and once eggs hatch, early instar larvae feed on the fungus (Madden and Coutts, 1979). There is some uncertainty if later instars of *S. noctilio* feed directly on the fungus or on the fungal-invaded wood, but later instars of the related *Sirex cyaneus* F. are reported as eating their symbiotic fungus (*Amylostereum chailletii* [Pers.] Boidin) to acquire the enzymes for digestion of wood (Martin, 1987), and *S. noctilio* may be similar in this regard. *Sirex noctilio* is considered to be more aggressive towards trees in comparison with other species of *Sirex* from Europe and North Africa, as it is the only European siricid tested that causes phytotoxicity in trees (Spradbery, 1973). Also, the mucous gland and reservoir of *S. noctilio* are larger than those of other siricids from Europe (Spradbery, 1977). A comparable evaluation of the mucous glands of native North American *Sirex* species has not been conducted, although North American *Sirex* generally do not kill vigorous trees (Morgan, 1968).

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

Thirteen species of *Sirex* are native to North America, Mesoamerica (an area from central Mexico to Guatemala), or the Greater Antilles, and among these, three *Sirex* species are native to the northeastern and north central United States, where *S. noctilio* now occurs. These eastern North American *Sirex* species show preferences for different tree genera: *Sirex nigricornis* F. (now including *S. edwardsii* Brullé [Goulet, 2012]) is predominantly reared from pine (*Pinus*). *Sirex nitidus* (T. W. Harris) is predominantly reared from spruce (*Picea*), and *S. cyaneus* is predominantly reared from fir (*Abies*). Although there is some flexibility in host use by each of these *Sirex* species, there is a greater chance

that *S. noctilio* will develop in the same trees as the native *S. nigricornis*, as both of these species prefer pines. In addition, five siricid species in the genus *Urocerus* are also native to North America and there is one invasive *Urocerus*. Because most species of *Urocerus* have broad host ranges that include some pines, there is also the chance that these insects could bore in the same trees as *S. noctilio*.

Native Natural Enemies Affecting the Pest

In 1951, the native New Zealand parasitoid *Guiglia schauinslandi* (Ashmead) (Hymenop.: Orussidae) was found attacking *S. noctilio* larvae (Rawlings, 1957). In 1967, the native Tasmanian ichneumonid *Certonotus tasmaniensis* Turner was found parasitizing about 12% of *S. noctilio* larvae (Hocking, 1967). However, as would be predicted by the enemy release hypothesis, after introduction, populations of *S. noctilio* in the Southern Hemisphere reached outbreak levels without adequate levels of attack by these local natural enemies before classical biological control programs were carried out.

The situation is different in North America, because *S. noctilio* was introduced to a region with native siricids that prefer pine. Therefore, a natural enemy community already exists that may attack this invasive sawfly. Thus far, there is circumstantial evidence that native North American parasitoids are parasitizing *S. noctilio*. Long et al. (2009) studied parasitoids emerging from Scots pines (*Pinus sylvestris* L.) in New York State co-infested by *S. noctilio* and the native *S. nigricornis* (*S. edwardsii* is mentioned, but this species has now been synonymized with *S. nigricornis* [Goulet, 2012]). In this study, the ibaliid *Ibalia leucospoides ensiger* Norton caused 20.5% parasitism of the mixed species of siricids, while the ichneumonids *Megarhyssa nortoni* (Cresson) and *Rhyssa lineolata* (Kirby) each caused <1.0% parasitism. Because *S. noctilio* was much more abundant than *S. nigricornis* (94.3% of siricids emerging from wood were *S. noctilio*), the authors speculated that the majority of parasitoids from this study most probably had attacked *S. noctilio*. Ryan et al. (2012) reported similar levels of parasitism by *Ibalia leucospoides* (Hochenwarth) in pines infested by *S. noctilio* and *S. nigricornis* in Ontario, Canada. In New York State, Standley et al. (2012) reported that, in pines predominantly infested by *S. noctilio*, the cleptoparasite *Pseudorhyssa nigricornis* (Ratzeburg) attacked 26% of rhyssine parasitoids found.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

It is thought that *S. noctilio* was initially introduced to the Southern Hemisphere from Europe, although the exact origin of the introduction is not known. *Sirex noctilio* was subsequently moved among pine-growing countries in the Southern Hemisphere, country to country. The exact origin of *S. noctilio* introduced to North America is still uncertain, although one study suggests that the introduction came from Europe and not from the infestations in the Southern Hemisphere (Nielsen et al., 2009).

Areas Surveyed for Natural Enemies

Beginning in 1928, parasitoids of *S. noctilio* were collected in Europe with the goal of releasing them in New Zealand for permanent establishment. However, after *S. noctilio* was detected in Tasmania and mainland Australia, a much larger program of foreign exploration (1963–1970) was undertaken, funded by the Australian National Sirex Fund (Spradbery and Kirk, 1978). Approximately 400, 1 m long pieces of *Sirex*-infested wood were collected during fall and winter from 19 European countries, Turkey, and parts of North Africa. Wood was debarked and shipped to the United Kingdom, where it was placed in cages to rear out Hymenopteran parasitoids and parasitic nematodes from various *Sirex* species (Fig. 2). In addition, collections

Figure 2 Cages containing *Sirex*-infested logs collected during foreign exploration and used for rearing natural enemies at Silwood Park, Ascot, United Kingdom between 1963-1970. P. Spradbery.

were made by collaborating organizations and scientists in Canada (Vancouver and New Brunswick), the United States (California, Nevada, Arizona, New Mexico and the southeast), and Asia (India, Pakistan, and Japan) (Taylor, 1976; Bedding and Akhurst, 1978; Cameron, 2012). During foreign exploration, areas with Mediterranean climates were emphasized, when possible. Host collections were not restricted to *S. noctilio*, but included other conifer-feeding woodwasps (Murphy, 1998; Cameron, 2012), perhaps under the assumption that parasitoids of concealed hosts are frequently idiobionts, which often are not limited to single species (Quicke, 1997).

Natural Enemies Found during Foreign Exploration

Parasitoids Between 1928 and 1968, one species of stephanid, four species or subspecies of ibaliids and 13 species or subspecies of ichneumonids (all Hymenoptera) were found in the United States, Canada, Europe, or Asia and were sent to New Zealand or Australia (Table 1). One species, *R. lineolata*, a North American ichneumonid, was found in New Zealand without having been purposefully introduced there (Nuttall, 1974). Among these collections, Spradbery and Kirk (1978) reported that during their foreign exploration of Europe, Turkey, and North America, seven species of hymenopteran parasitoids were found (Table 2). It was discovered that one of these parasitoids, *P. nigricornis* (Ratzeburg) (previously reported as *P. maculocoxis* and *P. sternata*), was a cleptoparasite (Spradbery, 1969), and therefore work with this species was not continued. The six remaining parasitoid species reported by Spradbery and Kirk (1978) were collected in association with many species of siricids (Table 2).

Initially, right after *S. noctilio* was found in Australia in 1960, parasitoid shipments resulting from foreign exploration were compromised by low survival of parasitoids, but survival during transit later improved as the program continued (Cameron, 2012). Parasitoids released later in Southern Hemisphere countries other than New Zealand and Australia (including Tasmania) were redistributions from Southern Hemisphere areas infested earlier.

Table 1 Parasitoids found during foreign exploration and sent to New Zealand or Australia (Taylor, 1976; Nuttall, 1989; Hurley, 2007).

Species	Locations found
Family Stephanidae	
Schlettererius cinctipes (Cresson)	USA
Family Ibaliidae	
Ibalia leucospoides leucospoides (Hochenwarth)	Europe
Ibalia leucospoides ensiger Norton	USA
Ibalia rufipes rufipes Cresson	USA
Ibalia drewseni Borries	Europe
Family Ichneumonidae	
Megarhyssa nortoni nortoni (Cresson)	USA
Megarhyssa nortoni quebecensis (Provancher)	Canada
Megarhyssa praecellens (Tosquinet)	Japan
Megarhyssa emarginatoria (Thunberg)	Europe
Rhyssa persuasoria persuasoria (L.)	Europe
Rhyssa persuasoria himalayensis Wilkinson	India, Pakistan
Rhyssa amoena Gravenhorst	Europe
Rhyssa alaskensis Ashmead	USA
Rhyssa crevieri (Provancher)	Canada
Rhyssa hoferi Rohwer	USA
Rhyssa lineolata (Kirby)[*]	Canada
Odontocolon geniculatus (Kreichbaumer)	Europe

[*]This species was discovered in New Zealand without being purposefully introduced (Nuttall, 1974).

Table 2 Records of siricid hosts and their hymenopteran parasitoids reared from infested wood collected during foreign exploration of Eurasia and North Africa, 1963–1970 (from Spradbery and Kirk, 1978).

Host	Parasitoid Species					
	Rhyssa persuasoria (L.)	*Rhyssa amoena* (Gravenhorst)	*Megarhyssa emarginatoria* (Thunberg)	*Ibalia leucospoides leucospoides* (Hochenwarth)	*Ibalia rufipes drewseni* Borries	*Odontocolon geniculatum* (Kriechbaumer)
Sirex noctilio F.	+	-	-	+	+	+
Sirex torvus M. Harris*	+	+	+	+	+	+
Sirex juvencus (L.)	+	+	+	+	+	+
Urocerus gigas (L.)	+	+	+	+	+	+
Urocerus augur (Klug)	+	+	+	+	+	+
Urocerus sah (Mocsáry)	+	-	-	+	+	-
Urocerus fantoma (F.)	+	-	-	-	-	-
Xeris spectrum (L.)	+	+	+	+	+	

*Presented as *S. cyaneus* by Spradbery and Kirk (1978) but this European species has recently been designated as *S. torvus* (Schiff et al., 2012).

Predators During foreign exploration conducted by Spradbery and Kirk in Europe from 1963–1971, wood was collected in which woodpecker predation of *S. noctilio* larvae was evident (Spradbery, 1990). It was hypothesized that the great spotted woodpecker (*Dendrocopos major* [L.]) and black woodpecker (*Dryocopus martius* [L.]) were responsible for the majority of this predation.

Nematodes The nematode *Deladenus siricidicola* Bedding (= *Beddingia siricidicola* [Bedding]) was first found parasitizing *S. noctilio* in New Zealand in 1962 (Zondag, 1962), where it was thought to have been transported when *S. noctilio* itself invaded New Zealand. After *S. noctilio* was found in Australia in 1960, a worldwide search for parasitoids of siricid woodwasps in their native ranges in the Northern Hemisphere occurred (1963–1970), and in addition to parasitoids, this effort detected several hundred strains of seven species of *Deladenus* nematodes parasitizing various siricids (Bedding and Akhurst, 1978) (Table 3). Only two species of fungal symbionts were found to be associated with the collected siricids: the basidiomycete white rot fungi *A. areolatum* and *A. chailletii*. These nematode species had both mycophagous and parasitic phases and, consequently, cultures of the mycophagous phases were established in the laboratory. Strains of the nematodes were grown using potato dextrose agar cultures of the species of *Amylostereum* with which the siricid hosts were associated.

Several factors were used to evaluate the nematode species and strains collected by Spradbery and Kirk (1978) as potential biological control agents of *S. noctilio* in Australia. First, the candidate nematode had to be able to parasitize *S. noctilio*. Second, the nematode should not parasitize the hymenopteran parasitoids of *S. noctilio*. Third, the nematode had to be able to survive when feeding on *A. areolatum,* the symbiotic fungus carried by *S. noctilio*. Of all the nematode species found, most were able to survive only on one species of fungi, either *A. areolatum* or *A. chailletii*. Only one nematode, *Deladenus wilsoni* Bedding, was able to survive on both species of fungi (Bedding and Akhurst, 1978). The only nematodes that were able to feed on *A. areolatum* were *D. siricidicola* and *D. wilsoni*, but the latter species was rejected as a biological control agent because it also parasitized some of the parasitoids of *S. noctilio* (Bedding and Akhurst, 1978).

Once *D. siricidicola* was selected for use in biological control, different strains of this species were evaluated further for their suitability for use in a control program. Some strains of *D. siricidicola* that were eliminated from consideration were able to parasitize *S. noctilio* but failed to enter the eggs of the host and therefore were non-sterilizing (Bedding, 1972). Of the remaining strains of

Table 3 Records of insect and tree hosts of *Deladenus* nematodes collected during worldwide foreign exploration (from Bedding and Akhurst, 1978).[*],[**]

Deladenus species	*Amylostereum* species	Insect hosts[**]	Tree hosts	Collection locations
Deladenus canii Bedding	*Amylostereum chailletii* (Pers.) Boidin	*Sirex cyaneus* F.	*Abies* *Picea*	Europe North America
Deladenus imperialis Bedding	*A. chailletii*	*Sirex imperialis* Kirby	*Abies*	Pakistan
Deladenus nevexii Bedding	*A. chailletii*	*S. cyaneus* *Sirex longicauda* Middlekauff *Urocerus californicus* Norton *Urocerus albicornis* (F.) *Xeris spectrum* (L.) *Xeris morrisoni* (Cresson)	*Abies*	Europe North America Japan
Deladenus proximus Bedding	*A. chailletii*	*Sirex nigricornis* F.	*Pinus*	North America
Deladenus rudyii Bedding	*A. chailletii*	*Sirex juvencus* (L.) *S. cyaneus* *Urocerus gigas* L. *Urocerus augur* (Klug) *Urocerus japonicas* (Smith) *Urocerus antennatus* Marlatt *X. spectrum*	*Abies* *Chamaecyparis* *Cryptomeria* *Picea*	Europe North America Japan
Deladenus siricidicola Bedding	*Amylostereum areolatum* (Chaillet ex Fr.) Boidin	*Sirex noctilio* F. *S. juvencus* *Sirex nitobei* Matsumura *S. cyaneus* *X. spectrum*	*Larix* *Picea* *Pinus*	Europe North America Australia New Zealand Japan
Deladenus wilsoni Bedding	*A. chailletii, A. areolatum*	*S. juvencus* *S. cyaneus* *U. gigas* Multiple Rhyssines[***]	*Abies* *Cedrus* *Larix* *Picea* *Pinus*	Europe Turkey North America Japan India Morocco

[*]For each nematode species, entries for fungal associates (*Amylostereum*), insect hosts, tree hosts and collection locations demonstrate the diversity seen in foreign exploration collections; some more detailed data on associations at different locations can be found in Bedding and Akhurst (1978).

[**]Names for insect hosts in some cases are being revised or have recently been revised (Schiff et al., 2012; H. Goulet personal communication). Names presented in this table are those used by Bedding and Akhurst (1978).

[***]A list of 12 species of rhyssine ichneumonids is presented in Bedding and Akhurst (1978; Table 3).

D. siricidicola, the one ultimately chosen was from Sopron, Hungary, originating from a single specimen of *Sirex juvencus* (L.). In addition to its ability to parasitize and sterilize *S. noctilio* and grow on *A. areolatum*, the Sopron strain caused nearly 100% parasitism of emerging *S. noctilio*. Also, emerging adults of *S. noctilio* infected by this strain of the nematode were larger than adults parasitized by other strains of *D. siricidicola*. The large size of parasitized *S. noctilio* was important because larger individuals were able to fly farther and lay more eggs, thus helping to disseminate the nematode (Bedding, 2009).

Host Range Test Results

Southern Hemisphere Pines are not native to the Southern Hemisphere; therefore, there was no native community of pine-associated insects to use for host-range testing. However, tests were conducted to make sure that natural enemies to be released did not harm each other. Different species and strains of *Deladenus* were tested to evaluate their effect on parasitic Hymenoptera that also were being introduced. *Deladenus siricidicola*, the nematode that was chosen for release, did not parasitize any of these siricid-attacking parasitoids, but *D. wilsoni*, another candidate nematode, was rejected because it did (Bedding and Akhurst, 1978). In Europe, the wood-boring melandryid beetle *Serropalpus barbatus* (Schaller) is known to be parasitized by *D. siricidicola* (as well as by *D. wilsoni*), but this beetle does not occur in the Southern Hemisphere.

Northern Hemisphere In North America, the Kamona strain of *D. siricidicola* (Fig. 3) (so named because it was collected in the Kamona forest in Tasmania, the site where the original Sopron strain from Europe was released) was injected into pines naturally infested with *S. noctilio* and related insects in the field. Injected pines were subsequently taken to a rearing facility and insects reared out, preventing field release of *D. siricidicola*. Nontarget species in the nematode-injected trees were evaluated to see whether any had been parasitized by the Kamona strain of the nematode. These studies are ongoing and results have yet to be published.

Figure 3 Adult mycophagous *Deladenus siricidicola* Kamona strain female with eggs. E. Erin Morris.

Releases Made

Southern Hemisphere: Parasitoids Hurley et al. (2007) provide an excellent summary of the extensive literature on *Sirex* parasitoids released in the Southern Hemisphere. A total of 10 species or subspecies of parasitic Hymenoptera were variously released in Tasmania, mainland Australia, or New Zealand from 1962 to 1973. However, the large rearing program employed resulted in some mixing of parasitoid strains such that it is possible that some of the *I. leucospoides* released in New Zealand were actually hybrids between *I. l. ensiger* and *Ibalia leucospoides leucospoides* (Hochenwarth), and the *Rhyssa persuasoria* (L.) released were hybrids between *Rhyssa persuasoria persuasoria* (L.) and *Rhyssa persuasoria himalayensis* Wilkinson (Nuttall, 1989).

Subsequently, parasitoids, including putative hybrids, were accidentally or purposefully introduced into South America and South Africa (Hurley et al., 2007; Cameron, 2012). In South America, *I. leucospoides* was found in Uruguay in 1984, and it is thought to have been introduced when *S. noctilio* or the siricid *Urocerus gigas* L. were introduced. This parasitoid spread, either on its own or with human assistance, throughout the various parts of America infested with *S. noctilio*. *Ibalia l. leucospoides*

arrived in Chile along with *U. gigas* and readily switched to *S. noctilio* (Cameron, 2012). *Rhyssa persuasoria* and *M. nortoni* were also released in various South American countries, including Brazil (1996 and 1997, respectively), where *S. noctilio* was established (Hurley et al., 2007). In South Africa, *I. l. leucospoides* and *M. nortoni* were released in the Western Cape region, while only *I. l. leucospoides* was released in the KwaZulu-Natal and the Eastern Cape region (Hurley et al., 2007).

Southern Hemisphere: Nematodes After Zondag's discovery that *S. noctilio* populations on the North Island of New Zealand were parasitized with *D. siricidicola,* these nematodes were introduced on the South Island of New Zealand in 1969 (Zondag, 1979). By 1971, a strain of *D. siricidicola* called the Sopron strain (after its collection origin in Sopron, Hungary) had been selected for biological control and the Sopron strain was released throughout the Australian *Sirex* infestations. Also, the Sopron strain was released in Brazil in 1989 (Hurley et al., 2007). However, during an outbreak of *S. noctilio* in the Green Triangle in southeastern Australia in 1987–1990, it was discovered that the Sopron strain had declined in virulence (Bedding, 1993). Due to continuous rearing (over 20 years) of the nematode as the mycophagous form in laboratory cultures, this strain could no longer be induced to produce the infective form (Haugen and Underdown, 1993). To remedy this problem, in 1991 virulent nematodes were collected at one of the sites, Kamona forest, Tasmania, where the Sopron strain had originally been released. These nematodes were used to re-establish laboratory colonies capable of parasitic as well as mycophagous growth. This re-isolated strain was named the Kamona strain (Fig. 3), and it continues to be used in biological control programs across the Southern Hemisphere (Bedding, 2009). Precautions are now taken in laboratory rearing procedures to ensure that the Kamona strain does not lose the ability to readily switch to the parasitic form. The Kamona strain was introduced into Uruguay (1987), Argentina (1989), Brazil and South Africa (1995), and Chile (2006) (Hajek et al., 2005; Beèche et al., 2011).

Northern Hemisphere No natural enemies of *S. noctilio* have been released to date in North America (see Recommendations section below).

EVALUATION OF PROJECT OUTCOMES

Establishment of Agents and Effect on Pest

Southern Hemisphere parasitoid impact In New Zealand, the first country where parasitoids were introduced, *R. p. persuasoria*, *I. l. leucospoides*, *I. l. ensiger,* and *Megarhyssa nortoni nortoni* (Cresson) were recovered after release. Subsequently, parasitism by *I. l. leucospoides* and *Rhyssa* spp. was reported at 70% or more in some areas (Nuttall, 1989).

In Tasmania, where parasitoids were introduced next, the same species became established, as well as the stephanid *Schletererius cinctipes* (Cresson) (Taylor, 1978). *Megarhyssa nortoni* and *R. persuasoria* were reported as the most abundant parasitoids and were considered responsible for reducing *S. noctilio* populations significantly from 1965 to 1974. In Tasmania, parasitism of *S. noctilio* by *I. l. leucospoides* was found to be density-independent, while parasitism by *R. p. persuasoria* and *M. n. nortoni* showed delayed-density dependency (Taylor, 1978).

In Australia, where parasitoids were next released, three species of *Rhyssa* (*R. p. persuasoria*, *Rhyssa hoferi* Rohwer, and *R. lineolata*), two species of *Ibalia* (*I. l. leucospoides* and *I. l. ensiger*), *S. cinctipes,* and *M. n. nortoni* were recovered after release. In Victoria and New South Wales, *Ibalia* species were the most abundant parasitoids, causing up to 40% parasitism (Hurley et al., 2007).

In South America*, I. leucospoides* now occurs throughout areas infested by *S. noctilio* (Hurley et al., 2007). Percent parasitism in Brazil reached 39% but averaged 25%, and in the Patagonian region of Argentina, parasitism by *I. leucospoides* was 20–40%. *Rhyssa persuasoria* and *M. n. nortoni* have been mass-reared and released in Brazil but have not become established.

In South Africa, *I. l. leucospoides* was introduced but established only in some areas. *Megarhyssa n. nortoni* was released but has not yet been recovered following its release.

In summary, both establishment and degree of impact of different parasitoid species released in the Southern Hemisphere have varied widely among regions and parasitoid species. In some instances the numbers of parasitoids released or the numbers of individuals used to establish colonies were very small; this could have caused genetic bottlenecks that may explain lack of establishment in some cases and variable impacts in others (Hurley et al., 2007; Cameron, 2012).

Southern Hemisphere nematode impact The strain of *D. siricidicola* discovered on the North Island of New Zealand was the first strain of this nematode to be released (on the South Island). By 1975, >75% of the *S. noctilio* recovered from un-inoculated trees at some places in the South Island were found to be parasitized by *D. siricidicola.*

Subsequent to the releases from the North to South Island of New Zealand, efforts shifted to releasing the Sopron strain of *D. siricidicola* from Hungary. Releases of the Sopron strain in Australia resulted in almost 100% parasitism (Bedding and Akhurst, 1974). Releases in Tasmania in 1970 resulted in the presence of Sopron strain in 92% of *S. noctilio*-infested trees.

A third nematode isolate (the Kamona strain) was used for releases after it was discovered in 1987–1990 that the Sopron strain had lost virulence. The Kamona strain was released in Australia, South America, and South Africa. High levels of parasitism (>70%) by this strain of *D. siricidicola* were subsequently reported in Brazil (Iede et al., 2012), while in Argentina, parasitism by *D. siricidicola* was 58% in 2002, but increased to nearly 100% by 2007 (Klasmer and Botto, 2012). In the Cape Region of South Africa, 23% parasitism by the Kamona strain was reported after introduction, but two years later parasitism had increased to 96.1% (Tribe and Cilié, 2004). In the summer-rainfall region of South Africa, the Kamona strain of *D. siricidicola* initially parasitized <10% of *S. noctilio* (Hurley et al., 2007) although five years later, parasitism by the Kamona strain had risen to 50% in the bottom sections of trees at some sites (Hurley et al., 2012). Studies investigating why *D. siricidicola* success in South Africa has been low in some areas demonstrated that low moisture levels in the drier tops of trees are associated with poor nematode establishment (Hurley et al., 2008). In addition, competition between *A. areolatum* and sap staining fungi within trees may have limited the growth of *A. areolatum* and therefore the growth of the nematode, especially under conditions of lower water potential (Hurley et al., 2012).

Nontarget Effects

No nontarget effects from releases of natural enemies have been reported for the Southern Hemisphere.

Recovery of Affected Tree Species or Ecosystems

In the Southern Hemisphere, no native plant communities were affected by the *S. noctilio* invasion and it is too soon to discern the effect of this species on the native pine forests of North America. In pine plantations in the Southern Hemisphere, the introduction of the parasitic nematode and species of parasitic Hymenoptera have proven to be important components of an integrated control program against *S. noctilio*, when used in concert with silvicultural practices that promote forest health. It does not seem possible to identify whether nematodes or parasitoids or silviculture are the most important agent/practice. In these Southern Hemisphere areas, land managers must maintain diligence. Classical biological control introductions do not remain established at high enough levels forever. At sites with low densities of *S. noctilio*, the introduced nematode does not persist for more than a decade (Carnegie and Bashford, 2012); therefore, if increasing *S. noctilio* populations are detected in such areas, the nematode must be reintroduced, using an inoculative strategy. For this purpose, Ecogrow Environment (Queanbeyan, NSW, Australia) mass produces and sells the Kamona strain of *D. siricidicola.*

Broad Assessment of Factors Affecting Success or Failure

The factors affecting the success of biological control of *S. noctilio* in the Southern Hemisphere are discussed by Slippers et al. (2012). As in many classical biological control programs, differences in phenology between areas can make movement of natural enemies difficult, an extreme case being the inversion of seasons that must be overcome when biological control agents are moved between the northern and southern hemispheres. For example, when parasitoids are emerging in the Southern Hemisphere, *S. noctilio* in the field in Europe and North America is in the larval stage in the middle of the winter.

In addition, agents used in the Southern Hemisphere may not be climatically adapted to colder continental climates of the invaded area in North America because the original foreign exploration from 1963–1970 emphasized the collection of parasitoids from areas with milder climates similar to the invaded areas of Australia (Cameron, 2012).

One factor that strongly affected the success of this project in Australia was the loss of infectivity of the nematode *D. siricidicola* in mass rearing, when growing only the mycophagous phase for many generations. Currently, methods have been developed to maintain the virulence of nematode strains under mass rearing conditions (see Recommendations below).

BIOLOGY AND ECOLOGY OF KEY NATURAL ENEMIES

The Nematode *Deladenus siricidicola*

Deladenus siricidicola has two very different life stages, including a free-living form and a parasitic form. The free-living form of feeds on the symbiotic fungus used by *S. noctilio*, while the parasitic form invades larvae of both female and male *S. noctilio*, leading to sterilization of adult females (Bedding, 2009). Individual nematodes from the two life cycles of *D. siricidicola* differ in morphology as well as biology. Mycophagous and parasitic nematodes differ so much in morphology that initially, it was thought that *D. siricidicola* from the different life cycles belonged to two different nematode families. The fungal-feeding forms are larger in size, with spermatozoa 10–12 um in diameter, and are usually oviparous. The parasitic forms are smaller, with spermatozoa 1–2 um in diameter, and ovoviviparous (Bedding, 1972). The fungal-feeding form of *D. siricidicola* lives in pine trees and undergoes 20–30 generations per year, during which the nematodes eat the growing hyphal tips of *A. areolatum* (Bedding, 2009). Mycophagous nematodes spread through the tracheids of the wood as they follow the growth of the fungus. However, the presence of *S. noctilio* larvae in the vicinity of the nematode, induces transformation to the parasitic stage via environmental cues. Mycophagous male and female nematode larvae respond to elevated CO_2 levels and lower pH and develop into parasitic adults. Parasitic adults mate and then from 1–100 adult females invade a single *S. noctilio* larva. Once inside the host, the female nematodes shed their outer cuticles so they can absorb food directly from the host blood via microvilli that cover their bodies. Females grow rapidly, increasing up to a 1000 fold in volume within a few weeks, although their reproductive system is not triggered to develop eggs until the pupation of the host. Nematode eggs hatch into juveniles that then migrate to the reproductive organs of the host. In female hosts, juvenile nematodes travel into the ovaries, where virulent forms (including the biological control strain) penetrate the developing host eggs before the chorions harden. When adult females of *S. noctilio* emerge from trees as adults, they mate and lay eggs filled with juvenile nematodes in new trees. The nematodes within infected host eggs are injected into the tree by the woodwasp, along with the fungus *A. areolatum*. At this point in their life cycle, the juvenile nematodes develop into the mycophagous form (Bedding, 2009). Male *S. noctilio* hosts are a dead end for *D. siricidicola*, as the nematodes invade the testes after sperm has already been transferred to the vesiculae seminales, and the nematodes are not transferred to females during copulation. One generation of the mycophagous form of *D. siricidicola* is thought take about two weeks, while one generation of the parasitic form requires 1–3 years (Bedding, 1972).

Parasitoids (*Ibalia*, *Rhyssa,* and *Megarhyssa*)

There are two main groups of parasitic Hymenoptera that attack *S. noctilio*: Ibaliidae and Ichneumonidae. Species of *Ibalia* (Family Ibaliidae) oviposit in first or second instar larvae, close to the bark. Oviposition occurs either during summer, after *S. noctilio* eggs hatch, or in spring if hatching of host eggs has been delayed (i.e., in cases where *S. noctilio* oviposited into trees late in the season).

Species of *Rhyssa* (Fig. 4) and *Megarhyssa* (Ichneumonidae) parasitize *S. noctillio* by using their very long ovipositors to lay eggs on older instar host larvae deep within the wood. These ichneumonids are idiobionts: adults paralyze larval hosts with venom and then larvae feed as ectoparasitoids outside of the host.

Figure 4 Adult *Rhyssa lineolata* female ovipositing in a pine tree. Jessica Nix Greenberg.

Several *S. noctilio* parasitoids (e.g., the *Ibalia* species, *R. persuasoria,* and *M. nortoni*) are attracted to the symbiotic fungus carried by *S. noctilio* (Madden, 1968; Spradbery, 1970, 1974), which helps them find trees and areas on trees where *S. noctilio* larvae are located within the sapwood.

EVALUATION OF THE POTENTIAL FOR CLASSICAL BIOLOGICAL CONTROL OF *SIREX* IN NORTH AMERICA

After *S. noctilio* was found in North America, a pest risk analysis was conducted, both to estimate the potential damage that *S. noctilio* could cause in the United States and to make control recommendations. *Sirex noctilio* was rated as "high risk" with regard to numerous factors. Control strategies recommended by the risk analysis included restricted movement of infested trees and logs, population monitoring, good silvicultural practices in managed stands or plantations to raise tree resistance, and the release of biological control agents, primarily *D. siricidicola* (Borchert et al., 2007).

Parasitic Hymenoptera

During exploration for natural enemies to release in the Southern Hemisphere, collections were made in California, the southwestern and southeastern United States, British Columbia, and New Brunswick, but collections were not made from the areas of eastern North America where the *S. noctilio* invasion was located in 2012. Regardless, most widespread hymenopteran parasitoids of native siricids attacking conifers in North America (Coyle and Gandhi, 2012) were released or accidentally introduced in the Southern Hemisphere (Taylor, 1976; Hurley et al., 2007; Krombein and Hurd, 1978). Unfortunately, the full ranges of specific host associations for most of the *Sirex*-associated parasitoids in North America are unknown, in large part because the larval stages that are attacked live within wood and the host larvae often have not been determined. While many of the parasitoid species introduced against *S. noctilio* in the Southern Hemisphere already occur in North America and attack native siricids, some of the siricid parasitoids that were found in Europe and released in the Southern Hemisphere do not occur in North America. However, since most siricid parasitoids have broad host ranges, European siricid parasitoids are probably unsuitable for introduction to North America, because they likely would parasitize other siricid species. At this time, release of parasitic Hymenoptera against *S. noctilio* in North America is not being considered and extensive host range testing would be necessary before this would be possible.

Parasitic Nematodes

In contrast to parasitoids, the nematode *D. siricidicola* has been considered for introduction to North American against *S. noctilio* populations, although there are numerous aspects that must be considered before proceeding. However, there are several key differences between applicability of *D. siricidicola* in the Southern Hemisphere (where this nematode has been released in many countries) and North America:

(1) Exotic plantations vs. complex natural forest communities Pines are not native to the Southern Hemisphere, but have been introduced and are grown on plantations. In North America, there are many native *Pinus* species both in natural forests and plantations, as well as native species of *Sirex* woodwasps that carry their own species and strains of *Amylostereum* as well as of *Deladenus*. Consequently, the rich diversity that exists within the North American *Pinus-Sirex-Amylostereum* complex plus associates may complicate a biological control program involving *D. siricidicola*.

(2) Climatic tolerances and fungal requirements of nematodes We do not know if the Kamona strain of *D. siricidicola* would survive the winters of northeastern North America (see Williams et al., 2012). However, the Kamona strain of *D. siricidicola* will grow on a diversity of *A. areolatum* strains (Hurley et al., 2012; Morris et al., 2012); and as long as this fungal species is present in a tree, the nematodes should survive in the mycophagous forms until *S. noctilio* larvae are present.

(3) Compatibility of Kamona D. siricidicola *with North America S. noctilio population* Another factor that could affect the use of *D. siricidicola* for biological control in North America is the possibility that the Kamona strain of *D. siricidicola* is incompatible with the strain of *S. noctilio* present in North America. Bedding (1972) found that parasitism by *D. siricidicola* differed in strains of *S. noctilio* from different geographic regions; the timing of

host and nematode development must be well matched in order for the juvenile nematodes to migrate into the host eggs before the egg chorions have formed. This was demonstrated when *D. siricidicola* juveniles were unable to enter eggs of a Belgian strain of *S. noctilio*, but were able to enter eggs of Australian *S. noctilio* (recall that no one knows the exact Northern Hemisphere origin of *S. noctilio* in the Southern Hemisphere) (Bedding, 1972). Only when eggs are sterilized is the nematode an effective biological control agent. At least some of the *S. noctilio* populations present in North America are thought to differ from *S. noctilio* in the Southern Hemisphere (Nielsen et al., 2009; Bergeron et al., 2011). Studies are being conducted to investigate the relationship between the strain of *S. noctilio* present in North America and the Kamona strain of *D. siricidicola*.

(4) Interactions with native North America species of **Deladenus** The presence of other nematodes parasitizing native *Sirex* species further complicates decisions regarding use of the Kamona strain of *D. siricidicola* for biological control of *S. noctilio* in North America. Bedding and Akhurst (1974) found several nematodes, i.e., *D. wilsoni*, *Deladenus nevexii* Bedding, *Deladenus proximus* Bedding, and *Deladenus canii* Bedding, parasitizing native *Sirex* species in North America. *Deladenus siricidicola*, *D. wilsoni*, and *D. proximus* all occur in pines, leading to potential co-infestation of trees with both the invasive *S. noctilio* and the native *S. nigricornis* or potentially other *Sirex* species. Studies are investigating the extent to which native nematodes might parasitize *S. noctilio* and the extent that the Kamona strain of *D. siricidicola* might parasitize native *Sirex*.

(5) Potential nontarget effects of Kamona nematode on native siricid Perhaps of greatest importance, it is presently not known whether the Kamona strain of *D. siricidicola* will parasitize and sterilize the native *Sirex* species, when they co-occur in the same trees as *S. noctilio*, or to what extent this might happen.

(6) *Potential for hybridization of sterilizing and non-sterilizing strains of* **D. siricidol** To complicate matters further, in 2007 and 200, a strain of *D. siricidicola* was found parasitizing *S. noctilio* in Ontario, Canada, pine forests. This was the first record of *D. siricidicola* in North America (Yu et al., 2009). Upon examination of the parasitized Canadian *S. noctilio* females, it was found that the juvenile nematodes were inside of the host egg sheath,

but not inside host eggs and therefore were not sterilizing the hosts. It is considered most likely that this nematode arrived with *S. noctilio* when *S. noctilio* invaded. A recent study has documented the occurrence of the non-sterilizing strain of *D. siricidicola* within one individual of *S. nigricornis* (E. E. Morris unpublished data). However, parasitism of *S. nigricornis* by non-sterilizing *D. siricidicola* was only found in one out of fourteen parasitized *S. nigricornis* individuals, and all the others were parasitized by a native species of *Deladenus*. Conversely, two *S. noctilio* out of 19 included in this study were found to be parasitized by a native *Deladenus* usually found in *S. nigricornis*. The 'non-sterilizing' North American strain of *D. siricidicola* could pose a threat to a biological control program involving nematodes. Akhurst (1975) conducted a study in which different species and strains of *Deladenus* were crossed; it was found that while crosses between different *Deladenus* species only rarely produced viable eggs, crosses between strains of the same species of *Deladenus* always resulted in normal numbers of viable offspring. Based on this study, it seems possible that the non-sterilizing strain of *D. siricidicola* could hybridize with the Kamona strain, which might reduce parasitic sterilization of *S. noctilio* (Williams et al., 2012).

(7) Effects of native species and strains of the fungus **Amylosterem** The presence of native species and strains of *Amylostereum* (Williams et al., 2012) is another factor that could influence the success of the *D. siricidicola* as a biological control agent against *S. noctilio* in North America. While native *Amylostereum* taxa might negatively affect activity and persistence of the Kamona strain of *D. siricidicola* (i.e., if the Kamona strain nematode will not feed or reproduce well on native *Amylostereum*), the opposite situation also could occur. Morris et al. (2012) found that the Kamona strain of the nematode *D. siricidicola* produced significantly different numbers of offspring when feeding on different strains of *A. areolatum*, with the highest number of nematodes being produced on a strain of *A. areolatum* native to North America. In the past, most North American *Sirex* species were believed to carry *A. chailletii* as their symbiotic fungus (Gilbertson, 1984), a fungus that *D. siricidicola* will not consume (Bedding and Akhurst, 1978). However, recent data demonstrate that at least some of the native *Sirex* in the eastern United States at times carry *A. areolatum* and not *A. chailletii* (Nielsen et al., 2009; R. Kepler and A. E. H., unpublished data). The native *S. nigricornis* is one of the species that carries both *A. areolatum* and *A. chailletii* and that

species frequently develops in the same pines as *S. noctilio* (Long et al., 2009; Nielsen et al., 2009; Ryan et al., 2012; A.E.H. unpublished data). While there is potential for both *A. areolatum* and *A. chailletii* to co-occur within the same tree, these fungal species are vegetatively incompatible and will not grow in the same exact locations in a tree. Over time, *D. siricidicola* could spread throughout parts of a tree colonized by *A. areolatum*, but areas colonized by *A. chailletii* would not support the nematode. This could prevent the spread of nematodes throughout the tree and thus limit the ability of the nematode to locate and parasitize *S. noctilio* within trees.

(8) Effects of other native fungi Additionally, if they are able to out-compete *A. areolatum*, other fungi commonly found in pine wood might negatively influence *D. siricidicola* reproduction, . Ryan et al. (2011) found that *A. areolatum* strains that occur in Canada were poor competitors in the presence of two "blue-stain" fungi vectored by bark beetles, and Hurley et al. (2012) showed that *A. areolatum* strains present in the Southern Hemisphere were sometimes outcompeted by sap-staining fungi.

To begin answering some of the questions about release of the Kamona strain of *D. siricidicola* in North America, these nematodes were injected into *S. noctilio*-infested trees during four field seasons, and subsequently, the inhabitants of these trees were reared in cages (Williams and Mastro, 2011). In particular, these studies have been conducted to determine (1) if inoculation methods developed in Australia would work well in the United States, (2) if the Kamona strain of the nematode could establish in American pine species, and (3) if the nematode could survive the winter temperatures of the northeastern United States. Also, these studies hoped to measure the effects of parasitization by the non-sterilizing strain versus the Kamona strain of *D. siricidicola* in different pine species and the effects that different strains of *A. areolatum* might have on these nematodes.

CONCLUSIONS

Pines are economically important forest trees around the world. In the Southern Hemisphere where pines have been introduced, invasive *S. noctilio* populations have jeopardized this resource. As is true of projects using classical biological control, this invasive woodwasp is not considered a pest where it is native. In the Southern Hemisphere, introduction of a parasitic nematode and several species of parasitic Hymenoptera have been extremely important agents of biological control of *S. noctilio*, especially when combined with sound silvicultural practices (Slippers et al., 2012). It does not seem possible to identify whether nematodes, parasitoids, or silviculture practices were the most important factor, as is often typical of integrated pest-management programs. The recent introduction of *S. noctilio* to North America is the first time that this aggressive pine-killing woodwasp has been introduced to an area where pines, woodwasps, and their associates are native. At of 2012, *S. noctilio* only occurs in parts of northeastern North America, where pines are not the most abundant trees, and biological control has only been investigated in the laboratory. It is thought that the importance of *S. noctilio* as a pest in North America and the extent to which nematodes might be used for control will be determined within the next few decades, as this invasive spreads further south, where pines are major tree species and are extensively grown in plantations.

REFERENCES

Akhurst, R. J. 1975. Cross-breeding to facilitate the identification of *Deladenus* spp., nematode parasites of woodwasps. *Nematologica* 21: 267–272.

Bedding, R. A. 1972. Biology of *Deladenus siricidicola* (Neotylenchidae) an entomophagous-mycetophagous nematode parasitic in siricid woodwasps. *Nematologica* 18: 482–493.

Bedding, R. A. 1993. Biological control of *Sirex noctilio* using the nematode *Deladenus siricidicola*, pp. 11–20. *In* Bedding, R., R. Akhurst, and H. Kaya (eds.). *Nematodes and the Biological Control of Insect Pests*. CSIRO, East Melbourne, Australia.

Bedding, R. A. 2009. Controlling the pine-killing woodwasp, *Sirex noctilio,* with nematodes, pp. 213–235. *In* Hajek, A. E., T. R. Glare, and M. O'Callaghan (eds.). *Use of Microbes for Control of Invasive Arthropods.* Springer, Dordrecht, The Netherlands.

Bedding, R. A. and R. J. Akhurst. 1974. Five new species of *Deladenus* (Neotylenchidae), entomophagous-mycetophagous nematodes parasitic in siricid woodwasps. *Nematologica* 20: 204–225.

Bedding, R. A. and R. J. Akhurst. 1978. Geographical distribution and host preferences of *Deladenus* species (Nematoda: Neotylenchidae) parasitic in siricid woodwasps and associated hymenopterous parasitoids. *Nematologica* 24: 286–294.

Beèche, M., D. Lanfranco, M. Zapata, and C. Ruiz. 2012. Surveillance and control of the *Sirex* woodwasp: The Chilean experience, pp. 299–245. *In* Slippers, B., P. de Groot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest.* Springer, Dordrecht, The Netherlands.

Bergeron, M. J., I. Leal, B. Foord, G. Ross, C. Davis, B. Slippers, P. de Groot, and R. Hamelin. 2011. Putative origin of clonal lineages of *Amylostereum areolatum*, the fungal symbiont associated with *Sirex noctilio* retrieved from *Pinus sylvestris*, in eastern Canada. *Fungal Biology* 115: 750–758.

Borchert, D., G. Fowler, and L. Jackson. 2007. Organism pest risk analysis: risks to the conterminous United States associated with the woodwasp, *Sirex noctilio* Fabricius, and the symbiotic fungus, *Amylostereum areolatum* (Fries: Fries) Boidin. USDA-APHIS-PPQ-CPHST-PERAL. Rev.1. http://www.aphis.usda.gov/plant_health/ea/downloads/sirex-ea.pdf. Accessed 29 June 2012.

Cameron, E. A. 2012. Parasitoids in the management of *Sirex noctilio*: Looking back and looking ahead, pp. 103–117. *In* Slippers, B., P. deGroot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest.* Springer, Dordrecht, The Netherlands.

Carnegie, A. J. and R. Bashford. 2012. Sirex woodwasp in Australia: Current management strategies, research and emerging issues, pp. 175–201. *In* Slippers, B., P. deGroot, and M. J. Wingfield. (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest.* Springer, Dordrecht, The Netherlands.

Coutts, M. P. 1969a. The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. II. Effects of *S. noctilio* mucus. *Australian Journal of Biological Science* 22: 1153–1161.

Coutts, M. P. 1969b. The mechanism of pathogenicity of *Sirex noctilio* on *Pinus radiata*. I. Effects of the symbiotic fungus *Amylostereum* sp. (Thelophoraceae). *Australian Journal of Biological Science* 22: 915–924.

Coutts, M. P. and J. E. Dolezal. 1969. Emplacement of fungal spores by the woodwasp *Sirex noctilio* during oviposition. *Forest Science* 15: 412–416.

Coyle, D. R. and K. J. K. Gandhi. 2012. The ecology, behavior, and biological control potential of hymenopteran parasitoids of woodwasps (Hymenoptera: Siricidae) in North America. *Environmental Entomology* 41: 731–749.

de Groot P., K. L. Nystrom, and T. A. Scarr. 2006. Discovery of *Sirex noctilio* (Hymenoptera: Siricidae) in Ontario, Canada. *Great Lakes Entomologist* 39: 49–53.

Fong, L. K. and R. K. Crowden. 1973. Physiological effects of mucus from the wood wasp, *Sirex noctilio* F., on the foliage of *Pinus radiata* D. Don. *Australian Journal of Biological Sciences* 26: 365–378.

Furniss, R. L. and V. M. Carolin. 1977. *Western Forest Insects.* Miscellaneous Publication No. 1339, USDA Forest Service, Washington, D.C.

Gilbertson, R. L. 1984. Insects and wood-rotting basidiomycetes, pp. 130–165. *In* Wheeler, Q. and M. Blackwell (eds.). *Fungus-Insect Relationships: Perspectives in Ecology and Evolution.* Columbia University Press, New York, USA.

Gilmour, J. W. 1965. The life cycle of the fungal symbiont of *Sirex noctilio*. *New Zealand Journal of Forestry* 10: 80–89.

Goulet, H. 2012. *Sirex* systematics: Problems and solutions, pp. 1–14. *In* Slippers, B., P. deGroot, M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest.* Springer, Dordrecht, The Netherlands.

Hajek, A. E., M. L. McManus, and I. Delalibera Júnior. 2005. *Catalogue of Introductions of Pathogens and Nematodes for Classical Biological Control of Insects and Mites* (see p. 38). FHTET-2005-05, USDA Forest Service, Morgantown, West Virginia, USA.

Haugen, D. A. and M. G. Underdown. 1990. *Sirex noctilio* control program in response to the 1987 Green Triangle outbreak. *Australian Forestry* 53: 33–40.

Haugen, D. A. and M. G. Underdown. 1993. Reduced parasitism of *S. noctilio* in radiata pines inoculated with the nematode *Beddingia siricidicola* during 1974–1989. *Australian Forestry* 56: 45–48.

Hocking, H. 1967. A native ichneumonid, *Certonotus tasmaniensis* Turn. parasitizing *Sirex noctilio* F. (Siricidae) in Tasmania. *Journal of the Australian Entomological Society* 6: 57–60.

Hoebeke, E. R. D. A. Haugen, and R. A. Haack. 2005. *Sirex noctilio*: Discovery of a Palearctic siricid woodwasp in New York. *Newsletter of the Michigan Entomological Society* 50: 24–25.

Hurley, B. P., B. Slippers, and M. J. Wingfield. 2007. A comparison of control results for the alien invasive woodwasp, *Sirex noctilio*, in the southern hemisphere. *Agricultural and Forest Entomology* 9: 159–171.

Hurley, B. P., B. Slippers, P. K. Croft, H. J. Hatting, M. van der Linde, A. R. Morris, C. Dyer, and M. J. Wingfield. 2008. Factors influencing parasitism of *Sirex noctilio* (Hymenoptera: Siricidae) by the nematode *Deladenus siricidicola* (Nematoda: Neotylenchidae) in summer rainfall areas of South Africa. *Biological Control* 45: 450–459.

Hurley, B. P., H. J. Hatting, M. J. Wingfield, K. D. Klepzig, and B. Slippers. 2012. The influence of *Amylostereum areolatum* diversity and competitive interactions on the fitness of the *Sirex* parasitic nematode *Deladenus siricidicola*. *Biological Control* 61: 207–214.

Iede, E. T., S. R. C. Penteado, and W. R. Filho. 2012. The woodwasp *Sirex noctilio* in Brazil: Monitoring and control, pp. 217–228. *In* Slippers B., P. de Groot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, The Netherlands.

Kile, G. A. and C. R. A. Turnbull. 1974. Drying in the sapwood of radiata pine after inoculation with *Amylostereum areolatum* and *Sirex* mucus. *Australian Forestry Research* 6: 35–40.

Klasmer, P. and E. Botto. 2012. The ecology and biological control of the woodwasp *Sirex noctilio* in Patagonia, Argentina, pp. 203–215. *In* Slippers B., P. de Groot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, The Netherlands.

Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Burks. 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, D.C.

Long, S. J., D. W. Williams, and A. E. Hajek. 2009. *Sirex* species (Hymenoptera: Siricidae) and their parasitoids in *Pinus sylvestris* in eastern North America. *The Canadian Entomologist* 141: 153–157.

Madden, J. L. 1968. Behavioural responses of parasites to the symbiotic fungus associated with *Sirex noctilio* F. *Nature* 218: 189–190.

Madden, J. L. 1974. Oviposition behaviour of the woodwasp, *Sirex noctilio* F. *Australian Journal of Zoology* 22: 341–351.

Madden, J. L. 1988. *Sirex* in Australasia, pp. 407–429. *In* A. A. Berryman (ed.). *Dynamics of Forest Insect Populations*, Plenum Publishing Corp., New York.

Madden, J. L. and M. P. Coutts. 1979. The role of fungi in the biology and ecology of woodwasps (Hymenoptera: Siricidae), pp. 165–174. *In* Batra, L. R. (ed.). *Insect-Fungus Symbiosis*. Allanheld, Osmun & Co., Montclair, New Jersey, USA.

Martin, M. M. 1987. *Invertebrate-Microbial Interactions: Ingested Fungal Enzymes in Arthropod Biology*. Comstock Publishing Association, Ithaca, NewYork.

Miller, D. and A. F. Clark. 1935. *Sirex noctilio* (Hym.) and its parasite in New Zealand. *Bulletin of Entomological Research* 26: 149–154.

Morgan, F. D. 1968. Bionomics of Siricidae. *Annual Review of Entomology* 13: 239–256.

Morris, E. E., A. Jimenez, S. J. Long, D. W. Williams, and A. E. Hajek. 2012. Variability in growth of *Deladenus siricidicola* on strains of the white rot fungus *Amylostereum areolatum*. *BioControl* 57: 677–686.

Murphy, S. T. 1998. Indigenous siricid spp. parasitoid communities and principal biological control agents of *Sirex noctilio* in Australasia: A review, pp. 31–35. *In Proceedings of a Conference: Training in the Control of* Sirex noctilio *by the Use of Natural Enemies*. USDA Forest Service FHTET 98–13, Morgantown, West Virginia, USA.

NAPIS (National Agricultural Pest Information System). 2012. Survey status of *Sirex* woodwasp - *Sirex noctilio*. Purdue University. http://pest.ceris.purdue.edu/map.php?code=ISBBADA&year=alltime. Accessed: 09 December 2012.

Nielsen, C., D. W. Williams, and A. E. Hajek. 2009. Putative source of the invasive *Sirex noctilio* fungal symbiont, *Amylostereum areolatum*, in the eastern United States and its association with native siricid woodwasps. *Mycological Research* 113: 1242–1253.

Nuttall, M. J. 1974. *Rhyssa lineolata* (Hymenoptera: Ichneumonidae), as a parasite of *Sirex noctilio* in New Zealand. *New Zealand Journal of Forest Science* 4: 487–494.

Nuttall, M. J. 1989. *Sirex noctilio* F., sirex wood wasp (Hymenoptera: Siricidae), pp. 299–306. *In* Cameron, P. J., R. L. Hill, J. Bain, and W. P. Thomas (eds.). *A Review of Biological Control of Pests and Weeds in New Zealand, 1974–1987*. Technical Communication No. 10, Commonwealth Agricultural Bureaux International & DSIR, Wallingford, United Kingdom.

Quicke, D. L. J. 1997. *Parasitic Wasps*. Chapman & Hall, London, England

Rawlings, G. B. 1957. *Guiglia schauinslandi* (Ashmead) (Hym: Orussidae), a parasite of *Sirex noctilio* (Fabricius) in New Zealand. *The Entomologist* 90: 35–36.

Ryan, K., J.-M. Moncalvo, P. DeGroot, and S. M. Smith. 2011. Interactions between the fungal symbiont of *Sirex noctilio* (Hymenoptera: Siricidae) and two bark beetle-vectored fungi. *The Canadian Entomologist* 143, 224–235.

Ryan, K. and B. P. Hurley. 2012. Life history and biology of *Sirex noctilio*, pp. 15–30. *In* Slippers, B., P. deGroot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, The Netherlands.

Ryan, K., P. DeGroot, R. W. Nott, S. Drabble, I. Ochoa, C. Davis, S. M. Smith, and J. J. Turgeon. 2012. Natural enemies associated with *Sirex noctilio* (Hymenoptera: Siricidae) and *S. nigricornis* in Ontario, Canada. *Environmental Entomology* 41: 289–297.

Schiff, N., H. Goulet, D. R. Smith, C. Boudreault, A. D. Wilson, and B. E. Scheffler. 2012. Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere. *Canadian Journal of Arthropod Identification* 21 (July 2012): DOI 10.3752/cjai.2012.21

Slippers, B., P. de Groot, and M. J. Wingfield (eds.). 2012. *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, The Netherlands.

Spradbery, J. P. 1969. The biology of *Pseudorhyssa sternata* Merrill (Hym., Ichneumonidae), a cleptoparasite of Siricid woodwasps. *Bulletin of Entomological Research* 59: 291–297.

Spradbery, J. P. 1970. Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid woodwasps. *Animal Behaviour* 18: 103–114.

Spradbery, J. P. 1973. A comparative study of the phytotoxic effects of siricid woodwasps on conifers. *Annals of Applied Biology* 75: 309–320.

Spradbery, J. P. 1974. The responses of *Ibalia* species (Hymenoptera: Ibaliidae) to the fungal symbionts of siricid woodwasp hosts. *Journal of Entomology* 48: 217–222.

Spradbery, J. P. 1977. The oviposition biology of siricid woodwasps in Europe. *Ecological Entomology* 2: 225–230.

Spradbery J. P. 1990. Predation of larval siricid woodwasps (Hymenoptera: Siricidae) by woodpeckers in Europe. *The Entomologist* 109: 67–71.

Spradbery, J. P. and A. A. Kirk. 1978. Aspects of the ecology of siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research* 68: 341–359.

Standley, C. R., E. R. Hoebeke, D. Parry, D. C. Allen, and M.K. Fierke. 2012. Detection and identification of two new native hymenopteran parasitoids associated with the exotic *Sirex noctilio* in North America. *Proceedings of the Entomological Society of Washington,* 114 (2): 238-249.

Talbot, P. H. B. 1977. The *Sirex-Amylostereum-Pinus* association. *Annual Review of Phytopathology* 15: 41–54.

Taylor, K. L. 1976. The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. *Entomophaga* 21: 429–440.

Taylor, K. L. 1978. Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. *Oecologica* 32: 1–10.

Tribe, G. D. and J. J. Cilié. 2004. The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. *African Entomology* 12: 9–17.

Williams, D. W. and V. Mastro. 2011. Adapting nematode-based biological control systems to North American populations of *Sirex noctilio*. USDA, Forest Service, General Technical Report (GTR) NRS-P-75, see pp. 58–59.

Williams, D. W., K. E. Zylstra, and V. Mastro. 2012. Ecological considerations in using *Deladenus* (=*Beddingia*) *siricidicola* for the biological control of *Sirex noctilio* in North America, pp. 135–148. *In* Slippers, B., P. deGroot, and M. J. Wingfield (eds.). *The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest*. Springer, Dordrecht, The Netherlands.

Yu, Q., P. de Groot, I. Leal, C. Davis, W. Ye, and B. Foord. 2009. Characterization of *Deladenus siricidicola* (Tylenchida: Neotylenchidae) associated with *Sirex noctilio* (Hymenoptera, Siricidae) in Canada. *International Journal of Nematology* 19: 23–32.

Zondag, R. 1962. A nematode disease of *Sirex noctilio*. Interim Research Release. New Zealand Forest Service, Rotorua, New Zealand, 6 pp.

Zondag, R. 1979. Control of *Sirex noctilio* (F.) with *Deladenus siricidicola* Bedding, Part II. Introduction and establishments in the South Island 1968–1975. *New Zealand Journal of Forestry Science* 9: 68–76.

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