

# The spread of *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents

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Within eight years of its discovery in the Cape Peninsula in 1994, the Eurasian woodwasp, *Sirex noctilio*, has spread up to 380 km along both the western and southern coasts of South Africa. A biological control programme was begun within the first year with the importation of the Kamona strain of the parasitic nematode, *Deladenus siricidicola*, which had originally been imported into Australia from Hungary. In 1995 and 1996 a total of 70 million nematodes were imported and inoculated into 296 *S. noctilio*-infested trees in a 90km arc around Cape Town. The parasitism rate increased from 22.6 % in 1996, to 54 % in 1997, and 96.1 % in 1998. The early larval parasitoid, *Ibalia leucospoides*, was imported into South Africa in 1998 from Uruguay, where it had arrived with its *S. noctilio* host. A total of 456 parasitoids was released in plantations from Cape Town to Riversdale from 1998–2001. By 2002 it was confirmed to be established at Stellenbosch. *Megarhyssa nortoni*, a late larval parasitoid originally from North America, was imported from Australia into South Africa in 1998 and 38 mated females were released on the Gifberg overlooking Vanrhynsdorp a year later. No recoveries from this site have been made and it is unknown whether it has become established. Since 1994, the numbers of the European cerambycid, *Arhopalus syriacus*, had increased because they were able to breed in the lower trunk of trees killed by *S. noctilio*. Their numbers have since declined with those of *S. noctilio* following the introduction of the natural enemies. At no stage did the loss of trees exceed 3.2 % of a *Pinus* compartment and effective biological control was achieved during this period within the southwestern Cape.

**Key words:** *Sirex noctilio*, biological control, *Deladenus siricidicola*, *Ibalia leucospoides*, *Megarhyssa nortoni*, South Africa, pine plantations.

## INTRODUCTION

The woodwasp, *Sirex noctilio* Fabricius (Hymenoptera: Siricidae) originates from Eurasia and North Africa where it is considered a minor pest of *Pinus* species, but it has become a major problem in countries in the Southern Hemisphere where it may destroy up to 70 % of a compartment (Neumann *et al.* 1987). A phytotoxic mucus and the symbiotic fungus, *Amylostereum areolatum* (Fr.) Boidin, are injected into stressed trees during oviposition; the mucus causing the stomata to open and the tree to wilt, thus allowing the weakly pathogenic fungus to germinate (Bedding 1984). The initial egg content of a female varies from 30–450 depending on size (Madden 1974) and up to three eggs are deposited at each oviposition site as the wasp moves along the tree trunk. The hatching larvae feed on the fungus growing within the dead tree.

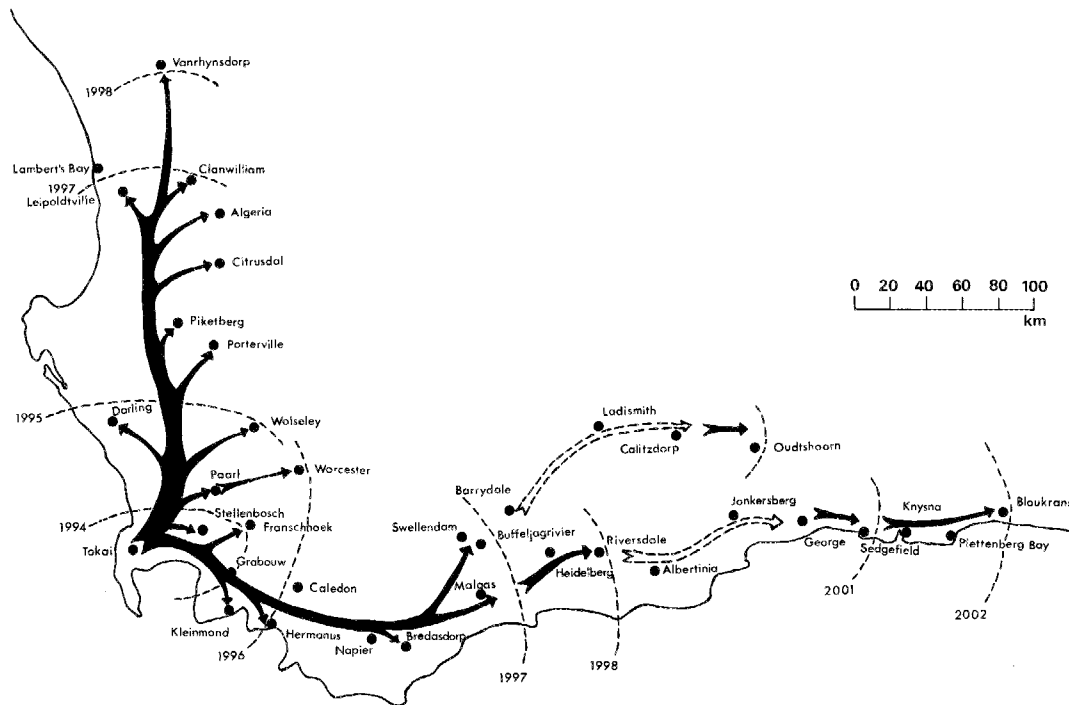
In April 1994, *S. noctilio* was discovered in Tokai

Plantation (34°03'S 18°25'E) in the Cape Peninsula where it was believed to have been present at least two years before its discovery (Tribe 1995). Using vegetative incompatibility testing, the *A. areolatum* fungus from South America and South Africa were shown to share a common origin but were not related to that from Australasia (Slippers 1998; Slippers *et al.* 2001). *Sirex noctilio* has since dispersed from the Cape Peninsula and three biological control agents have been introduced against it. This paper records the dispersal of *S. noctilio*, the origins of its biological control agents, their introduction, establishment, dispersal, and effectiveness.

## DISPERSAL OF SIREX NOCTILIO

A survey carried out in 1994 revealed that *S. noctilio* was to be found in pine plantations within a 90 km arc around Cape Town (33°55'S 18°25'E), with Grabouw (34°12'S 19°07'E) and Kluitjieskraal (33°25'S 19°11'E) (near Wolseley)

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**Fig. 1.** Direction and rate of dispersal (indicated in years) of *Sirex noctilio* from the Cape Peninsula where it was first discovered in April 1994. Most likely paths are indicated by black trunks and arrows; empty arrows represent locations where *S. noctilio* was not recorded.

plantations representing the extremities of the distribution (Tribe 1995). By 1997 *S. noctilio* was found near Leipoldtville ( $32^{\circ}13'S$   $18^{\circ}29'E$ ) along the west coast and at Swellendam ( $34^{\circ}01'S$   $20^{\circ}26'E$ ) and Malgas ( $34^{\circ}17'S$   $20^{\circ}35'E$ ) along the south coast (Fig. 1). In 1999 it was discovered on the Gifberg overlooking the town of Vanrhynsdorp ( $31^{\circ}36'S$   $18^{\circ}44'E$ ) but except for isolated pines near farmsteads, few trees occur in the semi-arid Knersvlakte further north. It was present at Jonkersberg (Pinegrove and Ruitersbos) Plantation ( $33^{\circ}55'S$   $22^{\circ}14'E$ ) near George and at Sedgefield ( $34^{\circ}00'S$   $22^{\circ}48'E$ ) in July 2001, and on the Swartberg Pass near Oudtshoorn ( $33^{\circ}35'S$   $22^{\circ}12'E$ ) in March 2002. Further surveys revealed *S. noctilio*-infested trees at Keurboomsrivier ( $33^{\circ}55'S$   $23^{\circ}26'E$ ) and Bloukrans Plantations ( $33^{\circ}57'S$   $23^{\circ}38'E$ ) in July 2002. In May 2002, 260 ha of 12-year-old *Pinus radiata* D. Don trees were killed by *S. noctilio* at Bergplaas Plantation ( $33^{\circ}54'S$   $22^{\circ}40'E$ ), near Wilderness. This dispersal of about 380 km from the nearest point to Sedgefield in eight years represents an annual rate of 48 km. A dispersal rate of up to 30 km per year was recorded in Victoria, Australia (Neumann *et al.*

1987) and about 40 km in New South Wales (Eldridge & Taylor 1989). In May 2002, *S. noctilio* larvae were found in *Pinus patula* Schlecht. et Cham. trees at Umtata ( $31^{\circ}36'S$   $28^{\circ}47'E$ ) which was about 673 km from the nearest known infestation at Bloukrans plantation ( $33^{\circ}57'S$   $23^{\circ}38'E$ ). It is therefore unlikely that *S. noctilio* arrived there unassisted. *Sirex noctilio* was recorded at Weza plantation ( $30^{\circ}36'S$   $29^{\circ}43'E$ ) in January 2003 (Hurley, pers. comm.).

The spread of *S. noctilio* could also have been facilitated by the sale of untreated poles from several small sawmills in the Western Cape Province. *Sirex noctilio* wasps did emerge from infested *P. radiata* poles which had been pressure treated with the stomach poison copper-chromium-arsenate at a commercial treatment plant, but failed to emerge from poles similarly treated with creosote (Tribe & Cillié, unpubl.). However, *S. noctilio* emerged only from test poles that contained larvae that had already completed their feeding – poles that would normally be rejected because the damage would be readily apparent. Eldridge and Taylor (1989) found that later-stage

*S. noctilio* larvae can survive the vacuum/pressure impregnation of their host timber with copper-chromium-arsenate salts and emerge as apparently normal adults.

A survey in 1996 recorded 96 *P. radiata* trees killed by *S. noctilio* in Tokai compartment C17b which consisted of 8.1 ha planted at 362 stems per ha. This represented 3.27% mortality at a cost of R20 943 (where the average tree volume was 2.16 m<sup>3</sup> and the average price was R101 per m<sup>3</sup>). From the time *S. noctilio* was discovered at Tokai, until the first inoculations of natural enemies, SAFCOL (South African Forestry Company Limited) removed all infested trees by felling and burning. The older compartments (>40 years) which had been attacked were clearfelled to deny *S. noctilio* access to these senescent trees to which they were most attracted. This operation was responsible for destroying a large number of wasps.

#### SEASONAL EMERGENCE OF *S. NOCTILIO*

To synchronize the importation of biological control agents against the various life stages of *S. noctilio* it was necessary to establish when the adults emerge from infested logs. Most *S. noctilio* undergo a year-long development, with the pupa spending a part of the year in the log. Larvae hatch and feed on the symbiotic fungus growing on the tree nutrients as they tunnel ever deeper into the wood. When the less nutritious heartwood is reached, the larvae make U-turns and eventually pupate below the bark where they await the relevant cues before emerging as adults. Trees containing *S. noctilio* larvae, wherever they could be found within their distribution in the Western Cape Province in 1994, were felled in May and approximately 150 trunks of all sizes were placed in an emergence cage during July. The psylla net-covered, walk-in cage was monitored daily and the number and sex of the emerging *S. noctilio* were recorded.

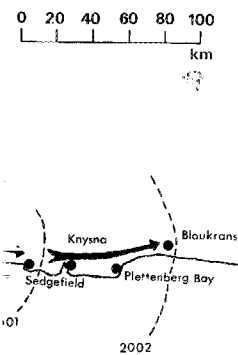
*Sirex noctilio* wasps emerged from the caged logs over a period of 24 weeks from mid-November until the end of April, with a peak in March (Fig. 2) representing 39.5% ( $n = 3205$ ) of annual emergences. Between weeks 8 and 14 (February–April 1995), 57.4% of the emergences for the year occurred. The sex ratio of 10.2 males : 1 female ( $n = 3205$ ) recorded in 1994 indicated a reduced mating frequency but this decreased to 5 males : 1 female ( $n = 402$ ) in 1996, and 3.3 males : 1 female in 2002

( $n = 215$ ). Both the emergence period and the 3:1 sex ratio conformed to that recorded in Australia (Taylor 1981; Neumann & Morey 1984) and was comparable to the 1.8 males : 1 female sex ratio recorded in Europe (Spradbery & Kirk 1978).

#### INTRODUCTION OF *DELADENUS SIRICIDICOLA*

The nematode *Deladenus siricidicola* Bedding (Nematoda: Neotylenchidae) was imported from Europe into Australia for the biological control of *S. noctilio* where it proved to be most effective (Bedding 1993). It has a free-living form which feeds on the *A. areolatum* fungus in the wood (Bedding 1967). On encountering a *S. noctilio* larva, the high CO<sub>2</sub> and low pH levels in the microenvironment surrounding the larva results in the production of a parasitic form of *D. siricidicola* with a stylet which is able to penetrate the cuticle of the larva (Bedding 1993). The nematodes feed in the haemocoel of *S. noctilio*, increase 1000 fold in size and produce as many as 10 000 eggs each, the hatching juveniles migrating to the reproductive organs of both sexes and the emerging wasp deposits her eggs, each containing 50–200 juvenile nematodes, into stressed trees (Bedding 1984). Because other non-parasitised *S. noctilio* females are also attracted to these same trees, the nematode becomes further dispersed. Following a *S. noctilio* outbreak in southern Australia in 1979 after a fire, it was discovered that the *D. siricidicola* strain inoculated into trees containing *S. noctilio* larvae was no longer as effective due to years of continually culturing only the free-living form; this led to the re-selection of a virulent strain of the nematode originating from Hungary that had been initially released in Tasmania, to be registered as the Kamona strain (Bedding 1993).

The right to use the Kamona strain in South Africa south of latitude 32°S was purchased from the Australian CSIRO (Commonwealth Scientific and Industrial Research Organization) in 1995. It was found to be more cost-effective to purchase *D. siricidicola* nematodes from Australia than to rear them in South Africa when tree mortality was only 3.2%. The first consignment of 100 000 nematodes was sent directly to the Division of Plant and Quarantine Control in Pretoria where they were checked for any contaminants. Samples were then taken from every subsequent consignment to be similarly tested at the Division's



peninsula where it was first  
arrows represent locations

in New South Wales  
in May 2002, *S. noctilio*  
*atula* Schlecht. et Cham.  
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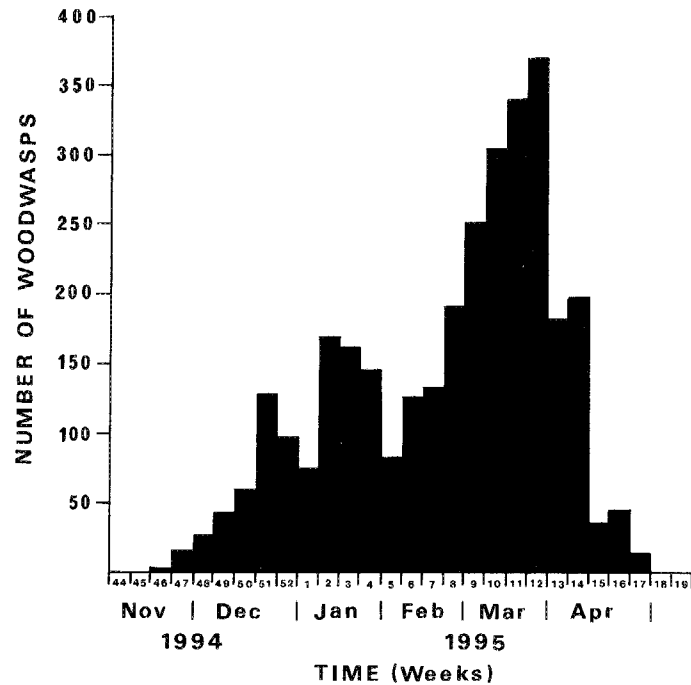


Fig. 2. Number of *Sirex noctilio* adults emerging weekly from logs collected throughout the southwestern Cape in July 1994 and placed in a cage.

Stellenbosch laboratories. Sachets, each containing five million nematodes, were imported during 1995 and 1996 for release. The nematodes require a water and oxygen suspension to survive while being inoculated into the stem and this was achieved by adding 100 ml of water to one gram of poly-acrylamide gel Synpol™ to which 200 000 nematodes were added to provide 2000 nematodes per millilitre of gel. Trees containing *S. noctilio* larvae were felled and two rows of holes were punched in the stem at 300-mm intervals between each hole, with specially designed hammers purchased in Australia which do not cauterize the vessels in the phloem (Bedding & Akhurst 1974). The nematode suspension was poured into plastic bottles and squirted at a concentration of approximately 2000 nematodes per hole, into approximately 50 holes per tree. As the gel dried, the nematodes migrated into the phloem vessels.

There were three nematode consignments in 1995, in May (25 million), June (15 million), and July (10 million), which were inoculated into all *S. noctilio*-infested trees that could be located within their distribution arc of 90 km around Cape Town (Table 1). In May and June 1996 two further consignments each of 10 million nematodes were

received and additional trees were inoculated. The establishment of *D. siricidicola* was confirmed by felling *S. noctilio*-infested trees within Tokai plantation in June, placing them in walk-in cages, dissecting the emerging wasps of both sexes and recording the presence or absence of the nematode. In 1996 the parasitism rate was 22.6 % ( $n = 402$  wasps), in 1997 it was 54 % ( $n = 89$ ) and 96.1 % ( $n = 77$ ) in 1998.

The nematode achieved the required control in the third year after inoculation and this was representative throughout Tokai plantation. Its dispersal from the nearest release site in Cecilia plantation was very slow because they were not recovered from dying 44 year old *Pinus pinea* Linnaeus trees at Rhodes Memorial about 4 km away in 1999 ( $n = 131$  wasps dissected). The establishment of the nematode was confirmed from August-October 2002 in Jonkershoek and Cecilia plantations from 41 and 31 trees respectively that had been killed by *S. noctilio*. Nematodes emerged from wedges of wood that were removed from the trees and placed overnight in water (National *Sirex* Co-ordination Committee 1991). In both plantations just over 80 % of the trees (33 and 25, respectively) contained nematodes (and there-

**Table 1.** The number of *Pinus radiata* trees inoculated with *Deladenus siricidicola* in various plantations during 1995 and 1996.

Plantation	Latitude south	Longitude east	Number of trees inoculated	
			1995	1996
Tokai	34°03'	18°25'	113	7
Cecilia	34°00'	18°25'	49	—
La Motte	33°54'	19°07'	7	—
Jonkershoek	33°58'	18°56'	13	—
Grabouw	34°12'	19°07'	41	—
Kluitjieskraal	33°25'	19°11'	11	6
Papegaaiberg	33°56'	18°51'	3	2
Lourensford Estate	34°06'	18°50'	6	—
Somersset West	34°05'	18°50'	7	—
Newlands Forest	34°00'	18°25'	—	2
Cape Point	34°20'	18°29'	—	18
Steenbrasdam	34°12'	19°07'	—	4
Wemmershoekdam	33°54'	19°06'	—	2
Silvermine Reserve	34°04'	18°26'	—	2
Total			0	46

fore, sterilized *S. noctilio* adults). Their presence was not confirmed at any of the other release sites because of the subsequent absence of *S. noctilio*-infested trees. Logs collected in Tokai and confirmed to contain *S. noctilio* larvae infected with *D. siricidicola* were placed in the Swellendam and Garcia (34°00'S 21°17'E) plantations to facilitate natural dispersal after *S. noctilio* was discovered there in 1998. Similarly, a consignment of 52 logs collected in the southwestern Cape and confirmed to contain *S. noctilio* larvae parasitized by *D. siricidicola* were placed within Bergplaas plantation in November 2002. In January 2003, *D. siricidicola* was extracted from *S. noctilio* adults emerging from logs collected in Kluitjieskraal plantation, confirming their establishment there. The nematodes also retard the expansion of *S. noctilio* into new areas by decreasing host size. The largest female *S. noctilio* is likely to fly up to 50 times as far as the smallest and there is a direct relationship between decrease in size of the host and the presence of nematodes (Bedding 1984).

#### INTRODUCTION OF *IBALIA LEUCOSPOIDES*

The successful control of *S. noctilio* in Australasia was achieved through the introduction of a complex of natural enemies, including hymenopteran parasitoids (Taylor 1976). Of these, three were selected for importation into South Africa, two of which were eventually introduced. It was

decided to introduce the nematodes before the hymenopterans because they were regarded as the key factor in the natural enemy complex and because the hymenopteran parasitoids may parasitize nematode-infested hosts without themselves becoming infested (Zondag 1969; Neumann & Morey 1984). *Ibalia leucospoides* (Hochenwarth) (Hymenoptera: Ibalidae) locates the oviposition channel bored by the *S. noctilio* wasp from the odour of the symbiotic fungus when it begins to grow 14 days after deposition and which coincides with the hatching of the host egg; *I. leucospoides* oviposits down the oviposition channel into the egg or newly hatched *S. noctilio* larva (Spradbery 1974). Chrystal (1930) estimated that large female *I. leucospoides* produced more than 600 eggs. The first three larval instars are endoparasitic but the final instars are ectoparasitic. The predominantly univoltine life cycle is completed almost in synchrony with that of the host with the flight season commencing in mid-summer and terminating in mid-autumn (Neumann *et al.* 1987).

*Ibalia leucospoides* was imported into South Africa in February 1998 from Uruguay where it had arrived together with its host. From the 18 males and 19 females initially imported into quarantine, a total of 456 parasitoids were released from the beginning of December 1998 until the end of February 2001 in plantations from Cape Town to Garcia near Riversdale (Table 2). A sex ratio of 1.15

**Table 2.** The number of *Ibalia leucospoides* (unsexed) released on *Sirex noctilio*-infested trees at various localities between December 1998 and February 2001.

Year	Locality	Latitude south	Longitude east	Number of <i>Ibalia</i>
1998	Rhodes Memorial	33°57'	18°27'	28
	Citrusdal	32°35'	19°00'	6
	Cecilia Forest	34°00'	18°25'	32
1999	Cecilia Forest	34°00'	18°25'	59
	Cape Point	34°20'	18°29'	62
	Zonnestraal	33°56'	18°29'	79
	Rondebosch Common	33°57'	18°28'	19
	Rosebank	33°56'	18°28'	3
	Jonkershoek	33°58'	18°56'	12
	2000	Tokai Plantation	34°03'	18°25'
Rosebank	33°56'	18°28'	2	
Garcia Plantation	34°00'	21°17'	86	
Algeria Plantation	32°21'	19°05'	48	
2001	Cape Point	34°20'	18°29'	8
	Stellenbosch	33°56'	18°51'	3
Total				456

males:1 female has been recorded (Spradbery & Kirk 1978). Because *I. leucospoides* and its *S. noctilio* host are in synchrony, it usually takes a complete year for both species to complete their cycles and emerge from infested logs. A number of *S. noctilio* and *I. leucospoides* adults emerged after only three months in quarantine and the first releases were made below Rhodes Memorial on *S. noctilio*-killed *P. pinea* trees.

Eleven *I. leucospoides* emerged in January/February 2002 from *S. noctilio*-infested trees felled at Papegaaiberg (Stellenbosch) (33°56'S 18°51'E) in July 2001, thus confirming the establishment of this parasitoid species. The nearest release had been at Jonkershoek in 1999 of 12 adults. Nine of these parasitoids were subsequently released at Brenton-on-Sea (34°02'S 23°02'E) near Knysna where *S. noctilio* had recently appeared. In January 2003 a further four *I. leucospoides* wasps emerged from logs collected in Kluitjieskraal plantation. Again, the nearest release had been at Jonkershoek of 12 adults in 1999. Because so few trees had been invaded by *S. noctilio*, it was not possible to establish the percentage parasitism. However, field parasitism can be expected to approximate that recorded in Australia which varied between 12.7 and 28.9 % in commercial plantations and up to 40 % in small plantations in Victoria (Neumann *et al.* 1987). Between 26 and

64 % parasitism was recorded in Japan (Fukuda & Hiji 1996) and a mean of 21.8 % parasitism in Europe where *I. leucospoides* appeared to be more adapted to the Mediterranean and cold axeric bioclimatic zones than to the temperate zone (Spradbery & Kirk 1978).

#### INTRODUCTION OF *MEGARHYSSA NORTONI* *NORTONI*

*Megarhyssa nortoni* (Cresson) (Hymenoptera: Ichneumonidae: Pimplinae) originates in California, from whence it was imported into Australia (Neumann *et al.* 1987). The wasp parasitizes later stage *S. noctilio* larvae by drilling a hole through the bark to a depth of 70 mm. The larvae of *M. nortoni* feed ectoparasitically on large *S. noctilio* larvae or pupae (Neumann & Morey 1984). They are predominantly univoltine having a larval diapause with a flight season between early October and mid-December but about 20 % of each generation of *M. nortoni* is non-diapausing, and this plays an important role in its rapid establishment (Taylor 1976). The sex ratio of adult *M. nortoni* emerging from field-collected logs in Australia was 1 male : 1.3 females (Haugen & Underdown 1990).

In October 1998, 10 males and 44 mated females were imported from Tasmania into South Africa. From these, the 41 males and 38 females reared in

ted trees at various localities

Number of *Ibalia*

28  
6  
32  
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#### **GARHYSSA NORTONI**

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quarantine were released in 1999 on the Gifberg overlooking the town of Vandrhyndorp on *S. noctilio*-infested *P. radiata* where prior sampling had indicated the absence of parasite species. This species has not been recovered from the field and it is as yet unknown if it has become established. Field parasitism in Australia has varied from 12-22.7 %, with dispersal from the nearest liberation point up to 19 km (Taylor 1976).

#### **THE INFLUENCE OF OTHER ORGANISMS ON TREES INFESTED WITH *S. NOCTILIO***

An association has developed in South Africa between *S. noctilio* and a previously minor pest of decaying timber, *Arhopalus syriacus* (Reitter) (Coleoptera: Cerambycidae) (Browne 1968). The nocturnal *A. syriacus* (in South Africa previously referred to as *Criocephalus pinetorum* Wollaston) occurs naturally throughout the Mediterranean region in *Pinus* spp. (Browne 1968) and since its discovery in South Africa in 1964 has only been found in discarded logs within plantations. The symbiotic dry rot fungus introduced by *S. noctilio* renders the tree attractive to *A. syriacus* which then lays its eggs in crevices in the bark. Although *A. syriacus* larvae feed initially on the inner bark, they later tunnel within the wood and the timber is totally destroyed. Pupation takes place within the wood after an exit tunnel has been extended to the surface of the bark which is then plugged with coarse strands of wood which project from the hole. The exit holes of *A. syriacus* are oval in shape and can be easily distinguished from the round exits of *S. noctilio*. Most *A. syriacus* complete their life cycle within a year and emerge during the summer months.

*Sirex noctilio* may inhabit the entire trunk in the absence of *A. syriacus* but when *A. syriacus* is present, the lower two metres (this length depending on the size of the tree) will be occupied by the cerambycid larvae, with *S. noctilio* usually occurring above them. Sections of trunks that were sampled revealed that the timber where *A. syriacus* occurs is heavier, indicating that more moisture is retained, probably because the symbiotic fungus is not deposited here and does not readily disperse from the deposition sites above, resulting in slower drying. Their numbers have increased greatly since their association with *S. noctilio* but they are expected to decline together with *S. noctilio* as the introduced biological control agents exert their influence. When *S. noctilio* and

*A. syriacus* larvae were extracted from the same log and dissected, only *S. noctilio* was parasitized by *D. siricidicola*.

Wood samples taken during these investigations to confirm the presence of *D. siricidicola* led unexpectedly to the discovery of five species of nematodes not previously recorded in South Africa (Swart & Heyns 1997; Braasch *et al.* 1998). The wider distribution of these nematode species, whether they are entirely secondary, or which insects serve as their vectors, is unknown.

*Sirex noctilio* larvae are most readily distinguished by the presence of a stout anal spine. Some confusion occurs with *Tenomerga leucophaea* (Newman) (Coleoptera: Cupedidae), a rare indigenous wood-boring beetle species which possesses a similar spine and whose larvae are occasionally found in rotten *P. radiata* logs in the southern Cape. *Tenomerga leucophaea* larvae feed on wood fibre and fungus (R. Oberprieler, pers. comm.) but except for the anal spine, the resemblance to *S. noctilio* is superficial.

Round exit holes made by the indigenous cerambycid *Delochilus prionoides* Thomson in discarded logs are easily mistaken for those of *S. noctilio*. However, only discarded logs are colonized and the tunnels within the log resemble those of *A. syriacus* and not those of *S. noctilio*.

#### **DISCUSSION**

*Sirex noctilio* is expected to become established wherever its host trees occur within southern Africa. Both *I. leucospoides* and *M. nortoni* are strong fliers which should follow in the wake of their host as it expands its distribution range, even though they are not particularly density dependent (Bedding 1993). Although these parasitoids rarely killed more than 30-40 % of the *S. noctilio* on mainland Australia (Neumann *et al.* 1987, 1993), their contribution in reducing *S. noctilio* numbers is significant. *Deladenus siricidicola*, however, is strongly density dependent (Bedding 1993) but disperses relatively slowly between plantations and to prevent tree losses, will have to be continually inoculated into areas newly colonized by *S. noctilio*. Population stability should be achieved once *S. noctilio* and its parasites occur throughout southern Africa. Sporadic outbreaks could then be expected only when environmental changes may temporarily favour *S. noctilio* proliferation, before the parasites resume control. These factors include

fire, drought, the actions of other insects or pathogens, and the thinning or pruning of trees during the flight season (Neumann *et al.* 1987; Madden 1988). Madden (1988) hypothesized that intermitent drought during the *S. noctilio* emergence season contributes significantly to outbreaks by increasing tree attractiveness and susceptibility through rapid physiological changes following rains of short duration. When *S. noctilio* invades a plantation the most susceptible trees are killed first which results in an increase in vigour of the remaining trees, accompanied by an increase in the proportion of trees possessing natural resistance (Madden 1975). However, even where the biological control agents were present in Australia, for example near Delatite in east-central Victoria, *S. noctilio* killed up to 77 % of trees in certain compartments (Neumann *et al.* 1987).

Should the present biological control agents be regarded as insufficient to counter sudden upsurges in the numbers of *S. noctilio*, the importation of a fourth natural enemy should be considered. *Rhyssa persuasoria* (Linnaeus) (Hymenoptera: Ichneumonidae) was imported into Australasia from Europe where it accounted for 28 % parasitism of siricid species (Kirk 1975). *Rhyssa persuasoria* was found parasitizing *S. noctilio* late instar larvae in increasing numbers as the trunk diameter de-

creased, while *M. nortoni* occurred more frequently in the lower, thicker part of the trunk (Taylor 1978). It appears to be more adapted to the cold axeric and temperate bioclimatic zones of Europe, where it recorded a mean parasitism rate of 33.7 %, than to that of the Mediterranean zone (Spradbery & Kirk 1978). Its behaviour complements that of *M. nortoni* and should be considered for importation.

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occurred more frequently of the trunk (Taylor 1978). Adapted to the cold axeric zones of Europe, where parasitism rate of 33.7%, than the Mediterranean zone (Spradbery & Tribe complements that of M. considered for importation.

## DISCUSSION

For the importation of the wasps came from SAFCOL Pty for the sustained support. Additional funding was provided by the Forest Owners Association. We thank colleagues who assisted in all aspects of the project and G. Crompton, thanked for their generous contribution on the course attended in the field. D. Bashford, Tasmania, kindly supplied the wasps. The collection of the wasps was facilitated by N. Prestal, Uruguay. *Arhopalus* by E. Grobbelaar, Biosystematics and Plant Protection Research

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