Sensilla on the Antennal Flagellum of *Sirex noctilio* (Hymenoptera: Siricidae)

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ABSTRACT   The antennal receptors of *Sirex noctilio* F. (Hymenoptera: Siricidae) were examined using scanning and transmission electron microscopy. Male and female antennae share five sensillum types: Böhm bristles, sensilla chaetica, sensilla basiconica, sensilla ampullacea, and uniporous contact chemoreceptors. Contact chemoreceptors make up ≈85 and 78% of the total sensilla on male and female antennae, respectively. On the most proximal flagellomere of the antennae, contact chemoreceptors are located in a shallow depression on the ventral surface. The number of contact chemoreceptors increases toward the distal end, covering two thirds of the circumference of each flagellomere. Contact chemoreceptors seem to be innervated by two sensory dendrites that terminate near the tip. In longitudinal section, a single subterminal pore is seen to be associated with each sensillum. Males had significantly more uniporous sensory pegs than females on the proximal half of the antennae. These receptors may play an important role in mate identification, suggesting that a female-released contact pheromone may be used by this insect. The putative function of these sensilla types is discussed.

KEY WORDS   sensilla, antennae, contact chemoreceptors, electron microscopy

Sirex noctilio F. (Hymenoptera: Siricidae) is considered a major pest of pine (*Pinus* spp.) where it has been introduced. In 2005, an established population of *S. noctilio* was confirmed in Oswego County, NY (Hoebeke et al. 2005). Although not considered a serious pest in its native range of Europe, Asia, and northern Africa (Hurley et al. 2007), this Old World woodwasp has had a major economic impact in Southern Hemisphere countries, such as New Zealand (Nuttall 1989), Australia (Haugen 1990), Brazil (Iede et al. 1998), and South Africa (Tribe and Cilliè 2004). For a full history of biological invasions by *S. noctilio*, see Hurley et al. (2007). Most of the plantations in these Southern Hemisphere countries consist of North American pine species, especially Monterey pine (*Pinus radiata* D. Don) and loblolly pine (*Pinus taeda* L.). *S. noctilio* has therefore been assessed as being a high risk to native pine forests in North America (Haugen and Hoebeke 2005, Carnegie et al. 2006).

The severe economic impact on pines in the Southern Hemisphere is mainly due to *S. noctilio* taking advantage of trees that have been stressed by environmental or silvicultural factors, such as heavily stocked stands (Madden 1988, Hurley et al. 2007).

The wasp also has an interesting relationship with a symbiotic fungus *Amylostereum areolatum* (Chaillet) Boiden. The wasp injects both toxic mucus and *A. areolatum* into pine trees during oviposition. The com-

bination of mucus and fungus kills the tree (Hurley et al. 2007). The fungus and mucus work together to break down cellulose and provide nutrients for developing larvae (Talbot 1977, Spradbery and Kirk 1978, Madden 1988). The life cycle of *S. noctilio* in North America is summarized by Haugen and Hoebeke (2005).

Despite its reputation in the Southern Hemisphere as being one of the most damaging pests of pine forestry, few studies have examined the chemical ecology of *S. noctilio*. Females primarily attack stressed trees (Madden 1968). This has been attributed to attractant host tree volatiles in the cambium-phloem (Madden 1971, Simpson 1976), particularly α- and β-pinene, along with other monoterpene hydrocarbons (Simpson and McQuilkin 1976). There is currently no evidence that *S. noctilio* has a long-range sex pheromone. Observations of *S. noctilio* reared from infested wood material at the USDA APHIS quarantine facility (Otis ANGB, MA) have shown that mating is initiated by males but only after rapid antennation on the surface of a female body has taken place (D.J.C., unpublished observations). Morgan and Stewart (1966) also reported that mating was more likely after being "disturbed" by contact with one another.

Given the apparent importance of chemical cues in both host location and mating, information on the olfactory receptors of *S. noctilio* is important for understanding the chemical ecology of this species. The primary aim of this study was to describe the types and distribution of sensilla on the antennae of *S. noctilio*, giving particular reference to the presence and structure of contact re-

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Fig. 1. Scanning electron micrograph of *S. noctilio* antenna (male).

ceptors. Differences between the sexes also were investigated in this regard. It is hoped that this research will be a basis for further behavioral and chemical ecology studies on this important invasive pest.

Materials and Methods

Insects. Scots pine (*Pinus sylvestris* L.) trees infested with *S. noctilio* were felled 28 February 2006 in Fulton, Oswego, NY. Half-meter length sections were then cut and shipped to the USDA, APHIS, PPQ, CPHST quarantine lab at Otis ANGB and stored in plastic barrels covered with metal screening (at room temperature). Adults emerged 20–29 June 2007. Adults used for microscopic examination were between 2–3 d old.

Scanning Electron Microscope Preparation. All samples were gently sonicated in 70% ethanol for 1 min to clean off any debris. Isolated heads were air-dried, mounted on specimen stubs with silver adhesive, and coated in a Samsputter 2a (Tousimis Research, Rockville, MD) with gold/palladium for 3 by 1 min. Specimens were rotated between each run to distribute an equal amount of coating and reduce subsequent charging. Specimens were coated without using freeze drying or critical point drying techniques as these methods damage the antennal sensilla. Six

wasp antennae of each sex were examined with a JSM-840 scanning electron microscope (JEOL, Peabody, MA) at an accelerating voltage of 15 kV. Photographs were taken using an AMT 1k × 1k digital camera and software system (Advanced Microscopy Techniques, Danvers, MA).

Transmission Electron Microscope Preparation. Whole antennae were individually fixed for 1 h in 2.5% glutaraldehyde buffered in 0.13 M Millonig's phosphate buffer. The antennae were then washed in buffer (pH 7.4), postfixed in aqueous 1% osmium tetroxide (OsO_4) for 2 h, dehydrated in a series of alcohols, and transferred via two changes of 100% propylene oxide and a 50:50 mix of propylene oxide and epoxy, before being embedded in araldite epoxy resin for 24 h at 65°C. Silver sections were cut using a diamond knife (Diatome, Electron Microscopy Sciences, Hatfield, PA), picked up on grids, stained with uranyl acetate and lead citrate, and examined at 80 Kv on a 10CA TEM microscope (Carl Zeiss, Thornwood, NY). Micrographs were recorded with an AMT camera.

Results

The antennae of male *S. noctilio* consist of a large scape, pedicel, and antennal flagellum that consists of 15 flagellomeres (Fig. 1). Female antennae are almost

Table 1. Distribution and mean (range) of sensilla on the antennae of male *S. noctilio* ($n = 4$)

	Sensilla chaetica	Contact chemoreceptors	Sensilla basiconica	Sensilla ampullacea	Böhm bristles
Scape	32 (25–38)	0	0	0	0
Pedicel	12 (10–13)	0	0	0	16 (11–20)
1st	30 (17–35)	116 (104–135)	13 (9–16)	3 (2–4)	0
2nd	20 (16–21)	123 (105–161)*[a]	14 (11–18)	5 (4–6)	0
3rd	20 (14–23)	153 (128–180)*	15 (10–20)	5 (4–7)	0
4th	16 (12–20)	163 (148–180)*	14 (10–21)	4 (3–5)	0
5th	16 (12–20)	157 (151–170)*	16 (13–21)	4 (2–6)	0
6th	14 (7–17)	178 (143–211)*	17 (13–22)	3 (3)*	0
7th	17 (13–19)	168 (131–208)*	13 (11–15)	0.3 (0–1)	0
8th	12 (7–15)	183 (146–230)	13 (11–15)	0.3 (0–1)	0
9th	12 (9–15)	190 (162–225)	13 (9–17)	1 (0–2)	0
10th	10 (9–11)	196 (168–242)	14 (12–15)	1 (0–3)	0
11th	10 (7–11)	226 (193–260)	11 (10–13)	0	0
12th	10 (7–13)	234 (205–265)	13 (11–15)	0	0
13th	8 (6–10)	223 (194–242)	14 (10–19)	0	0
14th	7 (5–10)	201 (186–219)	11 (8–13)	0	0
15th	16 (13–18)	264 (237–309)	16 (11–26)	0	0

[a] Asterisk (*) indicates a significant difference in the number of sensilla between the sexes ($P < 0.05$; *t*-test).

Table 2. Distribution and mean (range) of sensilla on the antennae of female *S. noctilio* (*n* = 6)

	Sensilla chaetica	Contact chemoreceptors	Sensilla basiconica	Sensilla ampullacea	Böhm bristles
Scape	32 (14–49)	0	0	0	0
Pedicel	10 (6–15)	0	0	0	21 (18–24)
1st	28 (17–37)	101 (75–161)	8 (5–11)	3 (2–4)	0
2nd	25 (14–35)	100 (77–130)	13 (10–18)	6 (4–7)	0
3rd	30 (21–43)*[a]	121 (101–160)	11 (9–15)	4 (3–5)	0
4th	30 (19–36)*	115 (100–137)	13 (10–17)	4 (0–6)	0
5th	30 (18–39)*	88 (41–120)	14 (8–17)	2 (0–4)	0
6th	27 (17–36)*	74 (46–107)	14 (12–15)	1 (0–3)	0
7th	23 (12–32)	83 (52–120)	13 (10–19)	0.2 (0–1)	0
8th	23 (14–28)*	104 (75–140)	14 (8–21)	1 (0–3)	0
9th	23 (13–35)*	125 (98–165)	13 (10–19)	0	0
10th	20 (14–25)*	168 (125–248)	13 (9–16)	0.3 (0–2)	0
11th	21 (14–32)*	192 (147–220)	14 (9–17)	0.3 (0–2)	0
12th	18 (13–23)*	199 (175–230)	13 (7–18)	0	0
13th	17 (12–21)*	218 (164–266)	13 (10–20)	0	0
14th	17 (9–21)*	229 (128–287)	13 (8–20)	0	0
15th	14 (12–17)	224 (152–286)	11 (8–18)	0	0
16th	17 (9–21)	185 (102–268)	14 (11–18)	0	0
17th	19 (17–22)	138 (84–210)	15 (9–21)	0	0

[a] Asterisk (*) indicates a significant difference in the number of sensilla between the sexes (*P* < 0.05; *t*-test).

identical in structure to that of males, but they have two extra flagellomeres. Total male antennal length ranged from 6,000 to 6,110 μm compared with 6,860–7,220 μm for females. The scape is the longest part of the antenna, measuring ≈750 μm for both the male and female. The pedicel measures 160 μm on both male and female antennae. For both sexes, flagellomeres are similar in shape but become progressively shorter toward the distal tip (Fig. 1). The most proximal of these are ≈550 μm in length, whereas the most distal tip measures 220 μm.

Types of Sensilla. Sensilla morphology is based upon common terminology of Altner and Prillinger (1980) and Zacharuk (1980). *S. noctilio* male and female antennae have five different types of sensilla: Böhm bristles, sensilla chaetica, sensilla basiconica, sensilla ampullacea, and uniporous contact chemoreceptors. Distributions and mean counts of all sensilla types on both male and female antennae are shown in Tables 1 and 2.

Böhm Bristles (Mechanoreceptor). These sharp-tipped receptors are situated on the base of the pedicel, where they project laterally toward the proximal portion of the scape/pedicel junction (Fig. 2). These small sensilla range from 25 to 30 μm in length.
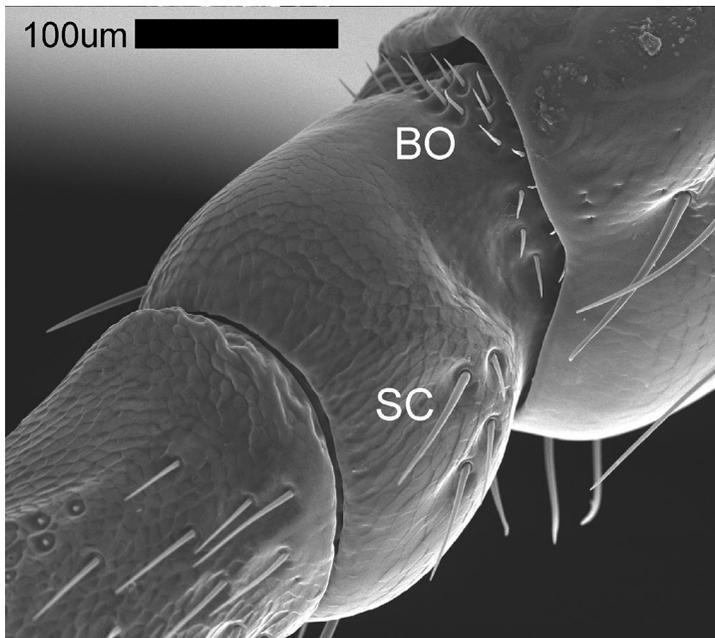

Fig. 2. Scanning electron micrograph showing the pedicel of a female *S. noctilio* antenna. Note the Böhm bristles (BO) arranged around the dorsal edge of the pedicel-scape junction. Several sensilla chaetica are also present (SC).
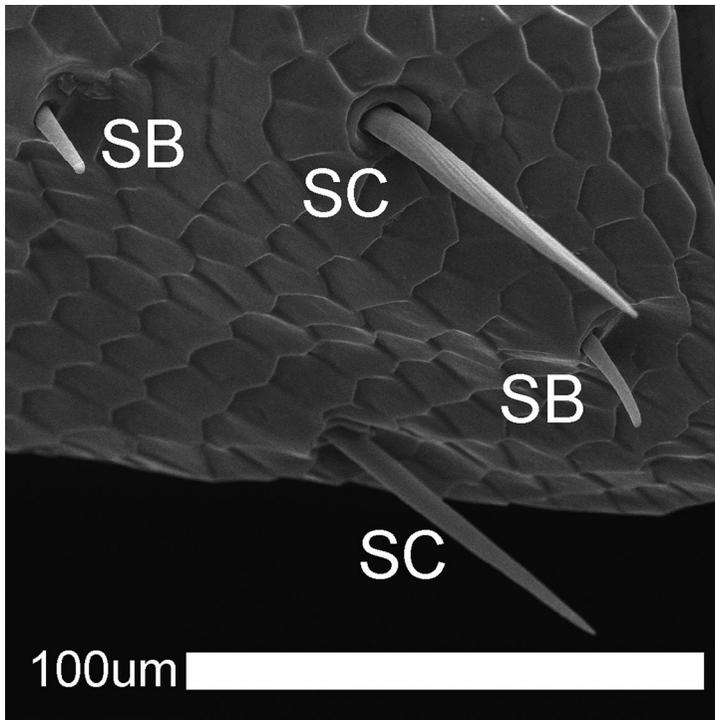
Fig. 3. Scanning electron micrograph showing the fifth flagellar segment of a male *S. noctilio* antenna. Sensilla basiconica (SB) and sensilla chaetica (SC).

Sensilla Chaetica (Mechanoreceptor). These receptors vary between 66 and 120 μm in length. Each sensillum arises from a clearly defined socket (Fig. 3). Sensilla chaetica are longer on the more proximal flagellomeres of the antennae. Numbers typically range between 7 and 36 on each flagellomere, with counts decreasing toward the tip (Tables 1 and 2). These receptors are arranged around the proximal, mid-, and distal parts of each flagellomere (groups of three to five around the circumference at each point). In general females were seen to have significantly more sensilla chaetica than males on most antennal flagellomeres ($P < 0.05$; t-test).

Sensilla Basiconica (Olfactory Receptor). These peg like receptors arise from a shallow socket and are $\approx$20 μm in length (Fig. 3). They are located in small numbers (10–21) on every part of the antennae except the scape and pedicel. These receptors are usually arranged around the circumference of the proximal and mid-portion of each flagellomere. They are occasionally found on the distal portion of the flagellomere. There was no detectable difference in the number of sensilla basiconica for either male or female antennae.

Sensilla Ampullacea (Olfactory/Thermoreceptor). Between two and seven small pore openings are located on each flagellomere on the proximal half of the antenna (Figs. 4 and 5). These pit organs are located among the numerous uniporous sensory pegs. The small pore opening is situated in a shallow pit 10 μm in width. There was no detectable difference in the number of sensilla ampullacea between male and fe-

male antennae except for the sixth flagellomere. Males consistently had three sensilla on their sixth flagellomere compared with zero three for females.

Uniporous Sensory Pegs (Contact Chemoreceptor). These receptors are located along the entire length of the antenna except the scape and pedicel. Numbers per flagellomere range from 41 to 287 (female) and from 104 to 309 (male). Males were seen to have significantly more uniporous sensory pegs than females on the proximal half of the antennae ($P < 0.05$; t-test). Female antennae have between 84 and 210 of these receptors on their distal tip (17th flagellomere), whereas males have between 237 and 309 on their distal tip (15th flagellomere).

Uniporous peg sensilla generally increased in number toward the distal tip for both sexes. At the proximal end of the antennae, these sensilla are located in a shallow depression ($\approx$150 μm in width by 500 μm in length) on the ventral surface of the flagellomere (Fig. 4). As numbers increase toward the distal end, the sensilla cover two thirds of the circumference of each flagellomere (Figs. 5 and 6). Each blunt sensillum (4–5 μm in height) is situated within a shallow socket (Fig. 7) located within a small crater-like depression ($\approx$10 μm in width). These crater-like depressions give the most distal flagellomeres a pitted appearance (Fig. 6).

In section, these sensilla have an outer wall between 500 and 600 nm in thickness. A single pore (400–500 nm in width) is evident near the subterminal region of each sensillum (Fig. 8). This pore is open to the en-
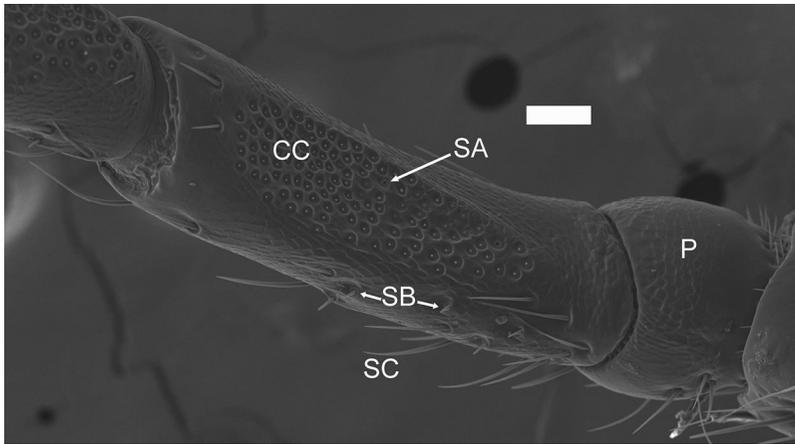
Fig. 4. Scanning electron micrograph showing the first flagellar segment of a male *S. noctilio* antenna. Contact chemoreceptors (CC), sensilla basiconica (SB), sensilla chaetica (SC), sensilla ampullacea (SA), and pedicel (P). Scale bar = 100 μm.

vironment and leads directly to the inner sensillar lumen. When cut proximally, ≈3 μm below the tip, there seem to be two sensory dendrites entering the short sensillum shaft (Fig. 9). One dendrite seems to be more electron dense than the other dendrite, indicating it to be the proximal region of a tubular body. The electron-dense tubular body expands and surrounds the other sensory dendrite as it branches and progresses toward the tip. In oblique sections cut nearer the distal tip, branched dendrites are surrounded by an electron-dense sheath that also seems to contain at least one vacuole (Fig. 8). It is also interesting to note that the lumen of the sensillum extends, via channels, into the sensillum outer wall, to within 100 nm of the surface. We did not observe these channels penetrating through the cuticular surface;

thus, they were not considered to be pore channels associated with pore openings.

Discussion

Contact chemoreceptors make up ≈85 and 78% of the total sensilla on male and female antennae, respectively. Contact chemoreception is clearly an important sensory function in *S. noctilio* behavior and ecology. The uniporous sensilla of *S. noctilio* possess the characteristics of "gustatory" or "contact chemoreceptors" as defined by Altner and Prillinger (1980), Chapman (2003), and Zacharuk (1980) in that there are a small number of sensory neurons inside a cone of cuticle that terminate in a single pore near the tip. During contact of a suitable surface, stimulating chem-
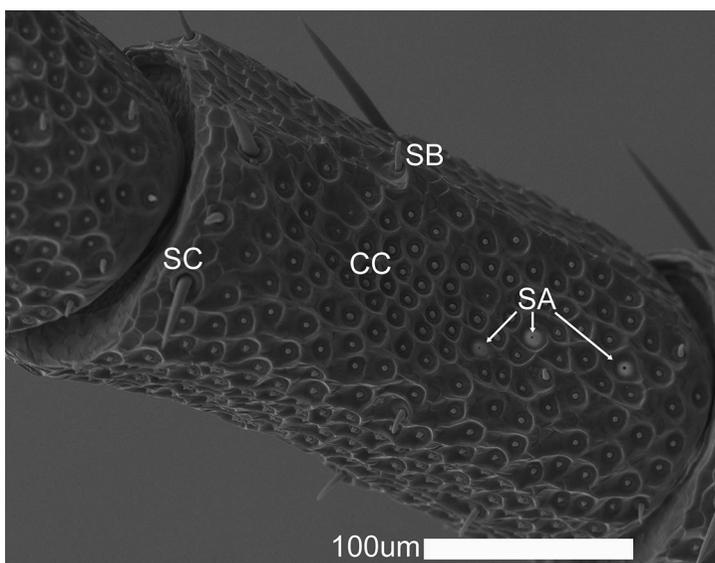

Fig. 5. Scanning electron micrograph showing the 11th flagellar segment of a male *S. noctilio* antenna. Contact chemoreceptors (CC), sensilla basiconica (SB), sensilla chaetica (SC), and sensilla ampullacea (SA).
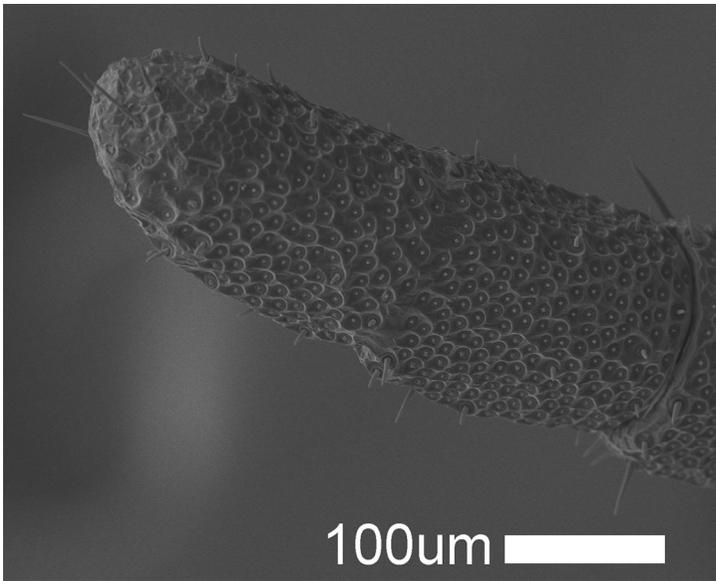
Fig. 6.   Scanning electron micrograph showing the distal tip of a male *S. noctilio* antenna.

icals reach the dendrites through this terminal/sub-terminal pore (Altner and Prillinger 1980, Chapman 2003). Although there is no obvious sexual dimorphism with respect to sensilla types or their distribution, males did possess more contact chemoreceptors than females. This indicates that these receptors play an important role in mate identification and suggests that a female-released contact pheromone may be used by this insect.

S. noctilio are facultatively parthenogenetic (Rawlings 1953). Unfertilized females produce viable eggs that develop into male insects (arrhenotoky). This has been postulated as being responsible for the male:

female ratio in adults being almost always overwhelmingly in favor of males. For example, in South African pine plantations a male:female ratio of 10.2:1 was recorded in 1994 (Tribe and Cillié 2004). Mating frequency was seen to improve in 1996 with a male: female ratio of 5:1. In 2002, the authors reported a ratio of 3.3:1. In New Zealand, male wasps outnumbered females by an average of 7:1 over a 4-yr period (Morgan and Stewart 1966). A 3:1 ratio in favor of males also has been reported in Australia (Taylor 1981, Neumann and Morey 1984), as well as a 1.8:1 ratio in Europe (Spradberry and Kirk 1978). Males tend to emerge before females and have been observed to form
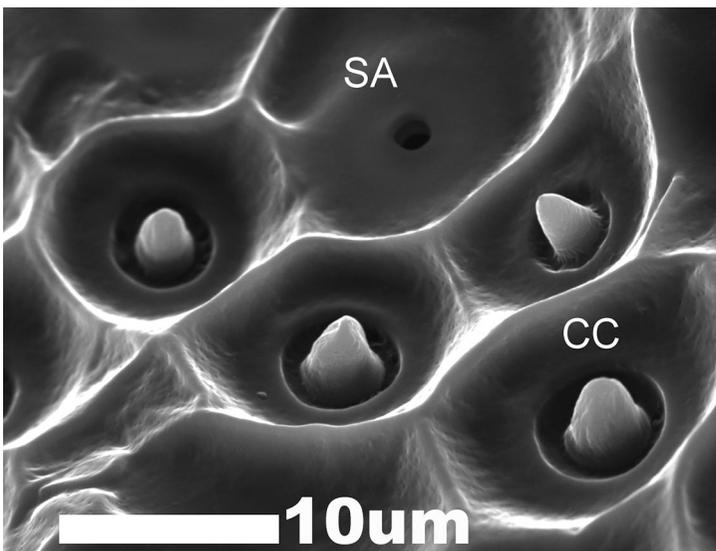

Fig. 7.   Scanning electron micrograph showing sensilla ampullacea (SA) and contact chemoreceptors (CC) on a male *S. noctilio* antenna.
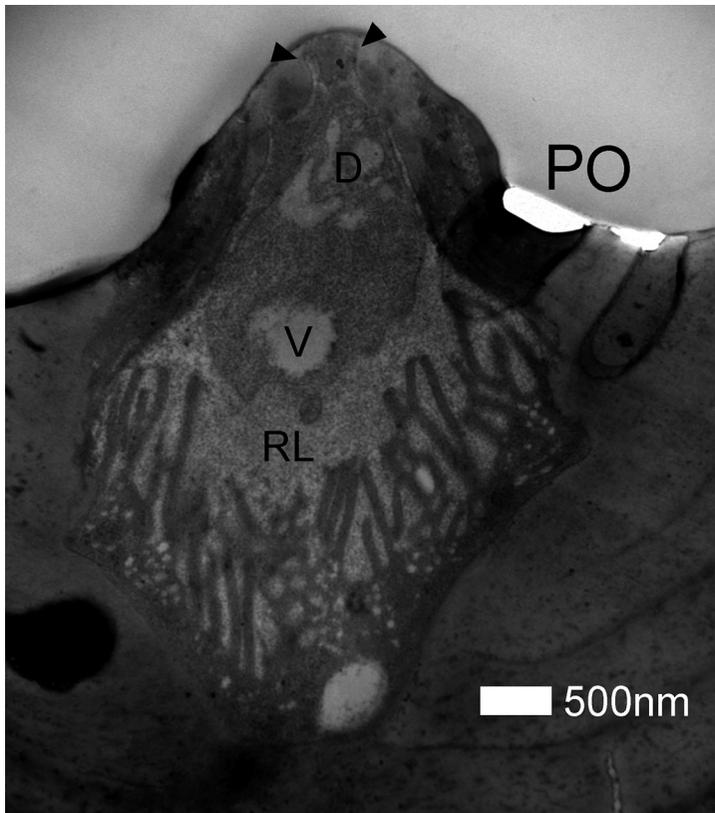
Fig. 8. Transmission electron micrograph showing a longitudinal section of a contact chemoreceptor (male) of *S. noctilio*. Dendrites (D), pore (PO), receptor lumen (RL), and vacuole (V). Black arrowheads indicate lumen channels.

swarms over the tree canopy around the eclosion site (Morgan and Stewart 1966, Madden 1988, Taylor 1981). When females do eventually emerge from trees, they exhibit a strong photopositive response and fly up into the male swarms. After mating in the upper canopy, females leave the swarm to find suitable oviposition sites (Morgan and Stewart 1966, Madden 1988). Therefore, it is reasonable to assume that a strong short-range contact cue is all is that required for mating success in *S. noctilio*. The behavior of females flying into male swarms seems to negate the requirement for a long-distance female-produced pheromone.

Our results show that uniporous contact chemoreceptors are also abundant on the antennae of females. Females also may use these receptors during initial mating behavior to help them accept or reject potential mates. They also may be used in choosing potential hosts, although it seems probing for a suitable oviposition substrate is done mainly with the ovipositor and not the antennae (Madden 1974, Madden 1988). *S. noctilio* females are known to be attracted to physiologically stressed trees (Madden 1988, Haugen 2000). Factors, such as drought and overcrowding, cause hosts to release specific volatiles that identify them as stressed trees (Madden 1968, 1977). When a tree is stressed by artificial means, such as a mechanical girdle (removing a ring of bark around the full circumference of the tree) the osmotic pressure decreases. This results in changes in bark permeability, which causes more volatiles to be released from the phloem and cambial sap (Madden 1968, 1971, 1988). *S. noctilio* females have been shown to be highly attracted to the area directly below girdle wounds ≈10 d after the
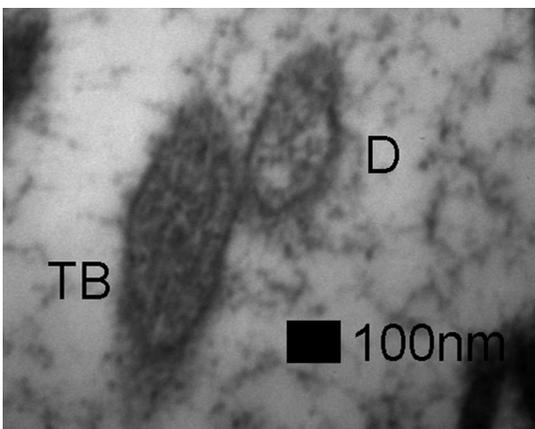

Fig. 9. Transmission electron micrograph showing an oblique section through the proximal region of a contact chemoreceptor (male) of *S. noctilio*. Sensory dendrite (D) and tubular body (TB).

wound was created (Madden 1988). Olfactory attraction to stressed trees is supported by electrophysiological studies that have shown that *S. noctilio* antennae have the ability to respond to a range of host volatiles (Simpson 1976; Simpson and McQuilkin 1976; D.J.C., unpublished results).

The external morphology of sensilla basiconica found on *S. noctilio* have characteristics typical of sensilla that respond to olfactory stimuli (Altner and Prillinger 1980). We hypothesize that for *S. noctilio*, sensilla basiconica are important olfactory apparatus for detecting host tree volatiles.

Böhm bristles are described as classical mechanoreceptors (Merivee et al. 1999). Their location between the scape and pedicel suggests that Böhm bristles are proprioreceptors that monitor movements and vibrations of the antennae (Usha Rani and Nakamuta 2001).

Sensilla chaetica are generally more abundant on female antennae. The reasoning for this remains unclear at present. These mechanoreceptors are mainly located at flagellomere junctions, so their probable role is to detect and prevent over flexing of the antenna. They may also help protect the underlying olfactory sensilla and detect changes in air movement during flying (Crook et al. 2003). There is currently no evidence to suggest that *S. noctilio* use sensilla chaetica to orient to sound.

Our conclusion that the porous openings on *S. noctilio* antennae are sensilla ampullacea is based on scanning electron micrographs alone, as sections were not obtained for this sensillum type. External pores cannot be assigned to the sensilla ampullacea with certainty, because sensilla coeloconica also share very similar external features (Kleineidam et al. 2000). That sensilla ampullacea are common in Hymenoptera (Kleineidam et al. 2000) and are usually observed in low numbers along the entire length of an antenna (Altner and Prillinger 1980), supports our tentative identification with regards to *S. noctilio*. In other Hymenoptera, sensilla ampullacea are single innervated cones situated within an ampulla, which connects to the outside via a narrow opening in the cuticle surface (Schneider 1964, Kleineidam et al. 2000). Sensilla ampullacea have been described in detail for Diptera (mosquitoes and biting midges), where their role as potential temperature and/or humidity receptors has been discussed (Blackwell et al. 1992, Cribb 1997, McIver 1982, Sutcliffe 1994). Further histological studies are needed to accurately define the structure and function of these particular receptors with respect to *S. noctilio*.

Future studies will aim to describe *S. noctilio* contact/mating behavior and to identify the important components of the female-produced contact pheromone.

Acknowledgments

References Cited

Altner, H., and L. Prillinger. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. Int. Rev. Cytol. 67: 69–139.

Blackwell, A., A. J. Mordue (Luntz), and W. Mordue. 1992. Morphology of the antennae of two species of biting midge: *Culicoides impunctatus* (Goetghebuer) and *Culicoides nubeculosus* (Meigen) (Diptera, Ceratopogonidae). J. Morphol. 213: 85–103.

Carnegie, A. J., M. Matsuki, D. A. Haugen, B. P. Hurley, R. Ahumada, P. Klasmer, J. Sun, and E. T. Iede. 2006. Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. Ann. For. Sci. 63: 119–128.

Chapman, R. F. 2003. Contact chemoreception in feeding by phytophageous insects. Annu. Rev. Entomol. 48: 455–484.

Cribb, B. C. 1997. Antennal sensilla of the female biting midge: *Forcipomyia* (*Lasiohelea*) *townsvillensis* (Taylor) (Diptera: Ceratopogonidae). Int. J. Insect Morphol. Embryol. 25: 405–425.

Crook, D. J., R. A. Higgins, and S. B. Ramaswamy. 2003. Antennal morphology of the soybean stemborer *Dectes texanus texanus* LeConte (Coleoptera: Cerambycidae). J. Kans. Entomol. Soc. 76: 397–405.

Haugen, D. A. 1990. Control procedures for *Sirex noctilio* in the green triangle: review from detection to severe outbreak (1977–1987). Aust. For. 53: 24–32.

Haugen, D. A. 2000. *Sirex noctilio. In* Exotic Forest Pest Information System for North America. (http://spfnic.fs.fed.us/exfor/data/pestreports.cfm?pestidval=33&langdisplay=English).

Haugen, D. A., and E. R. Hoebeke. 2005. Pest alert: *Sirex* woodwasp–*Sirex noctilio* F. (Hymenoptera: Siricidae). U.S. Dep. Agric. Forest Service NA-PR-07-05.

Hoebeke, E. R., D. A. Haugen, and R. A. Haack. 2005. *Sirex noctilio:* discovery of a Palearctic siricid woodwasp in New York. Newsl. Mich. Entomol. Soc. 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. Agric. For. Entomol. 9: 159–171.

Iede, E. T., S.R.C. Penteado, and E. G. Schaitza. 1998. *Sirex noctilio* problem in Brazil–detection, evaluation and control, pp. 45–52. *In* E. Iede, E. Shaitza, S. Penteado, R. Reardon, and T. Murphy [eds.], Proceedings of a Conference: Training in the control of *Sirex noctilio* by use of natural enemies, FHTET 98-13. U.S. Dep. Agric. Forest Service, Morgantown, MV.

Kleineidam, C., R. Romani, J. Tautz, and N. Isidoro. 2000. Ultrastructure and physiology of the CO_2 sensitive sensillum ampullaceum in the leaf-cutting ant *Atta sexdens.* Arthropod Struct. Dev. 29: 43–55.

Madden, J. L. 1968. Physiological aspects of host tree favourability for the woodwasp, *Sirex noctilio*. F. Proc. Ecol. Soc. Aust. 3: 147–149.

Madden, J. L. 1971. Some treatments which render Monterey pine (*pinus radiata*) attractive to the wood wasp *Sirex noctilio*. F. Bull. Entomol. Res. 60: 467–472.

Madden, J. L. 1974. Oviposition behavior of the woodwasp, *Sirex noctilio*. F. Aust. J. Zool. 22: 341–351.

Madden, J. L. 1977. Physiological reactions of *Pinus radiata* to attack by woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae). Bull. Entomol. Res. 65: 405–426.

Madden, J. L. 1988. Sirex in Australasia, pp. 407–429. *In* A. A. Berryman [ed.], Dynamics of forest insect populations. Plenum, New York.

McIver, S. B. 1982. Sensilla of mosquitoes (Diptera: Culicidae). J. Med. Entomol. 19: 489–535.

Merivee, E., M. Rahi, and A. Luik. 1999. Antennal sensilla of the click beetle, *Melanotus villosus* (Geoffroy) (Coleoptera: Elateridae). Int. J. Insect Morphol. Embryol. 28: 41–51.

Morgan, F. D., and N. C. Stewart. 1966. The biology and behaviour of the woodwasp *Sirex noctilio* (F.) in New Zealand. Trans. R. Soc. N. Z. Zool. 7: 195–204.

Neumann, F. G., and J. L. Morey. 1984. Influence of natural enemies on the *Sirex* wood wasp in herbicide-treated trap trees of radiata pine in north-eastern Victoria. Aust. For. 56: 129–139.

Nuttall, M. J. 1989. *Sirex noctilio* F., sirex wood wasp (Hymenoptera: Siricidae), pp. 299–306. *In* P. J. Cameron, R. L. Hill, J. Bain, and W. P. Thomas [eds.], Review of Biological Control of Invertebrate Pests and Weeds in New Zealand from 1874 to 1986. CAB International Institute of Biological Control, London, United Kingdom.

Rawlings, G. B. 1953. Rearing of *Sirex noctilio* and its parasite *Ibalia leucospoides*. N. Z. For. Res. Notes 20–34.

Schneider, D. 1964. Insect antennae. Annu. Rev. Entomol. 9: 103–122.

Simpson, R. F. 1976. Bioassay of pine oil components as attractants for *Sirex noctilio* (Hymenoptera: Siricidae) using electroantennogram techniques. Entomol. Exp. Appl. 19: 11–18.

Simpson, R. F., and R. M. McQuilkin. 1976. Identification of volatiles from felled *Pinus radiata* and the electroantennograms they elicit from *Sirex noctilio*. Entomol. Exp. Appl 19: 205–213.

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. B. Entomol. Res. 68: 341–359.

Sutcliffe, J. F. 1994. Sensory bases of attractancy: morphology of mosquito olfactory sensilla–a review. J. Am. Mosq. Control 10: 309–315.

Talbot, P.H.B. 1977. The *Sirex–Amylostereum–Pinus* association. Annu. Rev. Phytopathol. 15: 41–54.

Taylor, K. L. 1981. The *Sirex* woodwasp: ecology and control of an introduced forest insect, pp. 231–248. *In* R. L. Kitching and R. E. Jones [eds.], The ecology of pests, some Australian case histories. Commonwealth Scientific and Industrial Research Organization, Hobart, Tasmania.

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

Usha Rani, P., and K. Nakamuta. 2001. Morphology of antennal sensilla, distribution and sexual dimorphism in *Trogossita japonica* (Coleoptera: Trogossitidae). Ann. Entomol. Soc. Am. 94: 917–927.

Zacharuk, R. Y. 1980. Ultrastructure and function of insect chemosensilla. Annu. Rev. Entomol. 25: 27–47.