

Bernard Slippers · Peter de Groot  
Michael John Wingfield *Editors*

# The Sirex Woodwasp and its Fungal Symbiont

Research and Management  
of a Worldwide Invasive Pest

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# Dedication



Peter de Groot on top of Table Mountain during a visit to South Africa in May 2010 to work on editing of the book

The decision to assemble this book was that of our dear friend and colleague Dr. Peter de Groot. Peter who was passionate about this project and was determined to keep the other two editors continuously fired up to take it to its completion. Some years into the venture, Peter was diagnosed with cancer, but this did not quell his determination to complete the project. He fought his cancer courageously, convincing us that it would not conquer him. We were buoyed by his determination and he continued to work on revising and writing chapters, often under difficult circumstances. As a final burst of determination he visited us in South Africa in May 2010 in order to work on final elements of the project. At that time, we knew Peter was seriously ill, but he did not let this dull his enthusiasm. Sadly, the cancer caught up with Peter before the final touches had been put to this work. He would have loved to see it completed and we would have loved to celebrate this accomplishment with him. This was not to be, but we know that he is close and that he will be happy to see his work and that of many dear friends brought to conclusion.

This book is dedicated to the early pioneers of *Sirex noctilio* research, but especially to Peter de Groot (14 August 1954 to 22 October 2010), a giant of a man with a heart of gold and a dear friend and motivator to us all. May he rest in peace.

Bernard Slippers and Michael John Wingfield



# Preface

The Sirex woodwasp, *Sirex noctilio*, first appeared outside its native range around 1900 in pine plantations of New Zealand. Since then this alien invasive pest, together with its fungal symbiont, *Amylostereum areolatum*, gradually spread, first to Australia (1950s) and later, in the 1980s to South American countries including Uruguay, Brazil, Argentina, and Chile. In the early 1990s the woodwasp appeared for the first time in South Africa. In 2004 *S. noctilio* was discovered in the USA and the following year in Canada. In every country where this woodwasp has become established, it has resulted in considerable economic and ecological damage, or it has the potential to do so. There is no doubt that the global spread of the Sirex woodwasp will continue. With this spread, there is an increased need for new research to address its behaviour, impact and management in novel environments.

Information on the Sirex woodwasp was scant until its appearance in the Southern Hemisphere, which led to the first period of intensive research on this pest. This included important fundamental studies on the biology of *Sirex* and its fungal symbiont. Substantial attention was given to control options, which included the discovery and deployment of various biological control agents, including wasp parasitoids and a parasitic nematode. These agents, together with silvicultural practices to reduce stress in plantations, have yielded impressive control in New Zealand and Australia. However, when biocontrol was first attempted in South America and South Africa, the initial results were variable and disappointing. Likewise, the situation in North America with its diverse and complex conifer ecosystems consisting of mostly native species with well-developed arthropod, plant and diseases communities, including natural guilds of insect parasitoids and competing insect communities, was very different to that in Southern Hemisphere plantations of even-aged single species. How much impact the woodwasp will have in North American forests is still an open question.

An International Sirex Symposium and Workshop was held in South Africa from 9 to 16 May 2007 in recognition of the continuing global threat from the woodwasp and the realization that a sustained research effort would be required to deal with the pest across its growing distribution range. Approximately 80 researchers and foresters from 18 different countries convened in Pretoria and later in Pietermaritzburg, to discuss research on the Sirex woodwasp and its control. The meeting was jointly organized by researchers at the Forestry and Agricultural Biotechnology Institute (FABI) at the University of Pretoria and the Institute for Commercial Forestry Research in Pietermaritzburg.

The Sirex meetings in Pretoria and Pietermaritzburg succeeded remarkably in bringing together a diverse mosaic of practical and academic experience from virtually all groups working in this domain around the world. The foremost researchers and foresters from Australia, Europe, Japan, Brazil, Chile and Argentina shared their extensive experience regarding Sirex woodwasp biology, its fungi, and especially its management. Furthermore, the meeting was attended by a large group of



researchers and control managers from North America and where much work is currently being done to better understand and manage this complex problem. The shared experience from that meeting, as well as the research and management work undertaken subsequently to it, is the genesis of this book.

This book contains 20 chapters covering all aspects of *Sirex* woodwasp biology, ecology and management. It is organized thematically along these topics starting with four chapters on the insect's taxonomy, life history, host-plant relationships, and population dynamics. The woodwasp's fungal mutualist is discussed in the next three chapters addressing far ranging issues such as the nature of the symbiosis, and its distribution, diversity and biology in native and non-native areas. The following three chapters deal with insect and nematode parasites, two critical cornerstones of an integrated pest management system for this pest. The woodwasp and some of its parasites use chemicals emitted from the tree, the symbiotic fungus or the insect itself to find hosts or mates, which is covered in two chapters. These chemicals can be used in traps to provide an early warning system that the *Sirex* woodwasp has recently invaded the area. Early detection is critical to the success of all pest management programs. Seven chapters follow that show how each country or region has responded to the new invasions, in terms of detection and monitoring, quarantine, biological and silvicultural control, and public awareness. These chapters identify the current and emerging issues and challenges each region faces. It should be abundantly clear from reading these chapters that "silver bullets" do not exist for controlling the *Sirex* woodwasp. More importantly, that local adaptation of pest management strategies and tactics is needed to achieve this goal. In the final chapter, the editors have pulled together the major themes and issues of pest management and have identified many exciting opportunities for basic and applied research, and for international collaboration. Indeed, the global community need to face the increasing threats to forests from the *Sirex* woodwasp, and many other pests, together.

Some notes regarding common use of organism names are needed. There is uncertainty at present about the taxonomic position of the nematode biological control agent of *Sirex noctilio*, with both *Deladenus siricidicola* and *Beddingia siricidicola* being used in literature. The confusion results from the most recent taxonomic work suggesting that the latter genus is not valid, a view that is not shared by all researchers in the field. Until this uncertainty has been resolved, the original name should take precedence and is, therefore, used throughout the book. Furthermore, there is no official common name for *S. noctilio*. We have used the most common version, the *Sirex* woodwasp, throughout the book.

The authors are indebted to a number of organizations and individuals who have contributed to making this project possible. The South African forestry industry, through the Tree Protection Co-operative Programme, and University of Pretoria in South Africa have sponsored intensive *Sirex* research for many years, including the symposium that initiated this book project. We are also grateful to the authors who have unselfishly shared their expert knowledge and worked hard to produce a product of high quality.

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# Memories from the International Sirex Symposium

The images on this page and next page capture the spirit of the International Sirex Symposium held in South Africa from 10 to 16 May 2007 and that brought together approximately 80 researchers and foresters from 18 different countries. The meeting began with 2 days of presentations and intensive discussions at the University of Pretoria, including 'team building' fun with African drumming and dancing, where after the participants set off on a field trip.





The interactions in Pretoria established an incredibly congenial atmosphere prior to participants engaging in a 4 day field trip through forestry areas and the Kruger National Park, while concurrently continuing the intensive discussions. The week ended with a workshop to review Sirex management and research in South Africa and around the world. Those discussions were the genesis of this book.

# Chapter 1

## *Sirex* Systematics; Problems and Solutions

Henri Goulet

**Abstract** Earlier literature on the species of *Sirex* is confusing, also for North American species. Among the traditionally recognized species most are in need of some change in concepts. Fourteen species are known to occur in the Western Hemisphere and only one of these, *Sirex noctilio* F., is introduced. This review discusses characters that helped to clarify the species concepts in North America based independently on classical morphological and mitochondrial DNA (cytochrome c oxidase subunit 1 – CO1) data. Significant structural characters, especially the ovipositor pits in females, are discussed and illustrated based on this study of Western Hemisphere *Sirex* species.

### 1.1 Introduction

Key concepts on the systematics of the New World Siricidae have previously been published in Benson (1943; Benson 1962, 1963), Bradley (1913), Cresson (1880), Middlekauff (1960), Smith (1978, 1979, 1988), Smith and Schiff (2002) and Schiff et al. (2006). These concepts are currently under revision (Schiff et al. 2011) and will include numerous changes in the species numbers and concepts relative to previous works. This review contains a brief comparison of differences between the old and new concepts.

A number of examples are cited to illustrate some of the difficulties with previous concepts in the New World Siricidae. A first example is that of *Sirex juvencus juvencus* Linnaeus. Although this is a European species not found in North America, many

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papers applied this name to North American specimens (Benson 1963, Smith 1979; Smith and Schiff 2002; Schiff et al. 2006). Females of *S. juvenus* have a unique type of ovipositor not seen in any American specimens.

A second confusing species is *S. cyaneus* F., a North American species. The first problem with this taxon is that the type was unknown until lately (images of the ovipositor of the type specimen studied by the author, specimen in the Hunterian Museum in Glasgow, Scotland). For this reason, there has been lack of clarity regarding the identification of this species. The second problem is that five species in North America and one in Europe fall under this name. All have reddish brown femora and females are dark blue with black antennae.

Contrary to Benson (1945), the name *S. juvenus californicus* (Ashmead) is distinct from and not closely related to *S. juvenus*. Associated with *S. californicus* are three more species (*S. obesus* Bradley and two new ones). Moreover, females of *S. californicus* exist in two distinct color forms, dark and pale legged. This last color form is confused with *S. cyaneus* of previous authors.

Finally, classically distinct species, *S. edwardsii* Brullé and *S. nigricornis* F., are nothing more than discreet color forms of one species, *S. nigricornis* (based on our morphological and DNA results). Four species from previous studies remains the same (i.e., *S. areolatus* Cresson, *S. longicauda* Middlekauff, *S. behrensii* Cresson, and *S. noctilio* F.). Surprisingly, out of 14 species known from North America, meso-America and the Greater Antilles, four are new to science and only one, *Sirex noctilio*, is an accidental introduction.

## 1.2 Important Features for Solving Identification Problems

Three important features underpin the solution to resolving the systematics of the New World species: the discovery of the significance of the ovipositor structures, mitochondrial DNA, and large collections of reared specimens.

### 1.2.1 Ovipositor Morphology

Viitasaari (1984) published on the fauna of Siricidae of Finland and nearby countries. In his work, he consistently used a structure apparently not used frequently before, namely the pits on the ventral portion (lancet) of the ovipositor. This character was used for the first time by Kjellander (1945) to segregate females of *S. juvenus* from those of *S. noctilio*. Kjellander's discovery remained unknown as it was published in a Swedish journal that was difficult to locate. Viitasaari's paper was in Finish, but it was excellently illustrated. The character had great potential for resolving taxonomic problems of *Sirex* in the New World. In 1989, an English key was published by Viitasaari and Midtgaard confirming the interpretation of Viitasaari (1984).

It is curious that the ovipositor pits were not noticed by the numerous sawfly experts. After all, sawfly taxonomists have a special predilection for ovipositor details, especially those along the ventral edge. A likely reason is the lack of saw-like structures on the ventral edge of the lancet. Moreover, pits on the lateral surface of the lancet are difficult to observe unless one uses a diffused light source.

### 1.2.2 *Mitochondrial DNA*

The results of the mitochondrial DNA (cytochrome c oxidase subunit 1 – CO1) sequencing are promising to be very useful in distinguishing Siricid species. The establishment of *S. noctilio* around the east end of Lake Ontario (Hoebeke et al. 2005) in New York and Ontario was the trigger for our revision. The question was how one might distinguish a *S. noctilio* specimen from other North American species. For this purpose, one study developed a barcoding approach based on CO1 sequence data to distinguish *S. noctilio* from other native Siricid species (Wilson and Schiff 2010). This study is based on 22 native and non-native species of wood boring sawflies (Anaxyelidae, Siricidae and Xyphidiidae), in addition to *S. noctilio*. Ongoing work on the North American Siricids now include sequence data for 12 species of *Sirex*. The recognition of species by mitochondrial DNA and classical morphological studies are in complete agreement.

Not only did mitochondrial DNA data allow for the accurate identification of adults of both sexes, it is also useful for associating specimens with distinct color forms of the same species (e.g., the dark abdomen *S. edwardsii* and pale abdomen *S. nigricornis*). Furthermore, it segregates larvae accurately, which is important for screening intercepted specimens by quarantine systems.

### 1.2.3 *Collections*

The importance of having large and representative collections must be stressed. The Canadian National Collection in Ottawa, Ontario, holds over 2,000 specimens of *Sirex*, about 70% of which were reared specimens from identified host trees. As part of current studies, the author organized the collection (in 2007) by obvious species, then by provinces and states for the United States and Canada, and finally by field collected versus reared specimens. All original series were reassembled and reared specimens were organized by host trees from which they had emerged. This process included checking each specimen and dissecting many during the curatorial process. Most of the species now recognized were segregated during the curatorial process.

The Smithsonian Institute (Washington, DC) contains a large collection of Siricidae, with more species from the New World and Eurasia and more intercepted specimens at various ports of entry. Except for the Smithsonian collection, other collections were not so rich in number of field-collected and reared specimens of



*Sirex*. During five visits to the Smithsonian collection (2008–2010), the author discovered two more species, one from the Southwest United States and the nearby state of Chihuahua in Mexico and one from the Mexico City area. Recently, the author recognized another species from the Dominican Republic. Altogether, there are thus 14 species of *Sirex*, based on more than 4,000 specimens from the New World.

### 1.3 Diversity and Biogeographic Coverage

In the New World, the range of *Sirex* covers all coniferous regions of Canada, the United States, and as far south as Guatemala in Central America. The species of *Sirex* from the Dominican Republic was collected in the pine forest zone above 1,000 m. The fauna of Canada and the United States is quite satisfactorily sampled and obvious new species are not likely, but many species are likely to be discovered in Mexico and Guatemala wherever conifers grow in temperate and montane regions. The discovery of a species in the Greater Antilles suggests that other species may be found, perhaps in Cuba at higher elevations in places where pines and junipers grow.

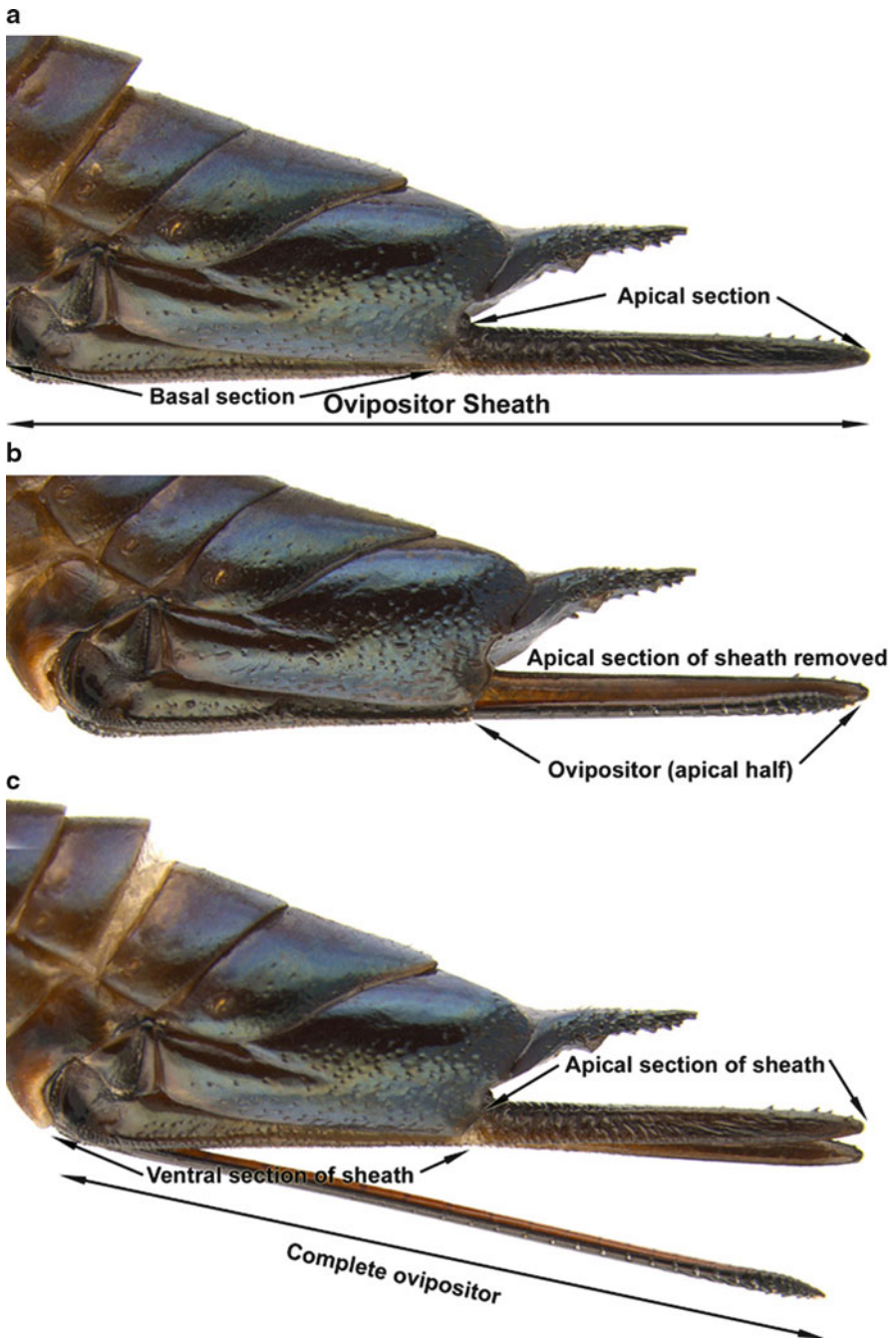
Regarding Old World specimens, more time and resources will be needed to resolve systematic issues. The species in Europe are quite well defined, but eastward they become very confusing. In eastern Asia, *Sirex* is greatly in need of study. This work must be done with large collections of specimens covering the Palaearctic region systematically using an approach similar to that used in the New World and Viitasaari (1984).

### 1.4 Morphological Characters Used to Recognize Species

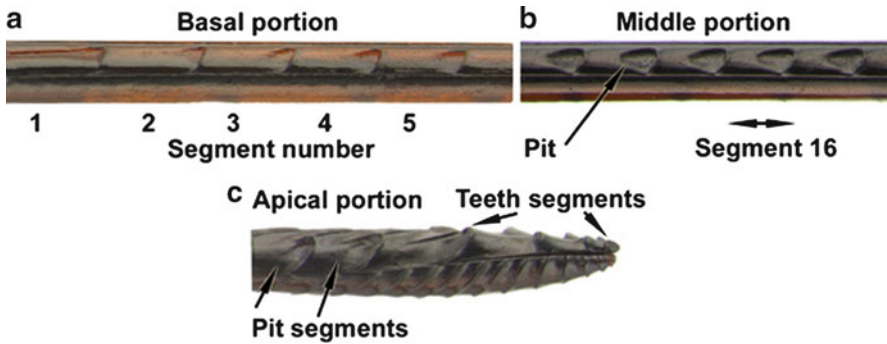
The aim of the following section is to stress practical aspects of the morphological characters that can be readily assessed by researchers using only a dissection microscope. The ovipositor is the key character in distinguishing most species. In the New world, each species has an ovipositor with special attributes. Building on this foundation, other characters are useful in recognizing species. Once females are segregated and identified, males can be associated.

#### 1.4.1 Ovipositor Characters

The structures associated with egg laying are illustrated in Fig. 1.1c. The ovipositor consists of a dorsally fused section, the lance, and ventrally of two isolated and parallel sections, the lancets. The lancets slide back and forth independently to move the egg and to penetrate the wood (Figs. 1.1c, and 1.2a–c). The important characters



**Fig. 1.1** Female external reproductive structures of *Sirex nitidus* (Harris); (a) ovipositor hidden by sheath, (b) apical half of ovipositor visible after breaking off apical section of sheath, (c) sheath and complete ovipositor visible after dissection



**Fig. 1.2** Basal middle and apical sections of ovipositor; (a) and (b) basal and middle section of *S. noctilio*, (c) apical section of *S. longicauda*

are pits found along the lancet from the base to about the middle (Fig. 1.2a, b). The apical teeth segments do not usually show specific characters (Fig. 1.2c). The sheath covers the ovipositor. The sheath consists of two obvious sections, the basal and apical sections separated by a narrow membrane about half way (Fig. 1.1a). Apart from the relative length between the apical and basal sections and its total length relative to fore wing length, we found no structural difference.

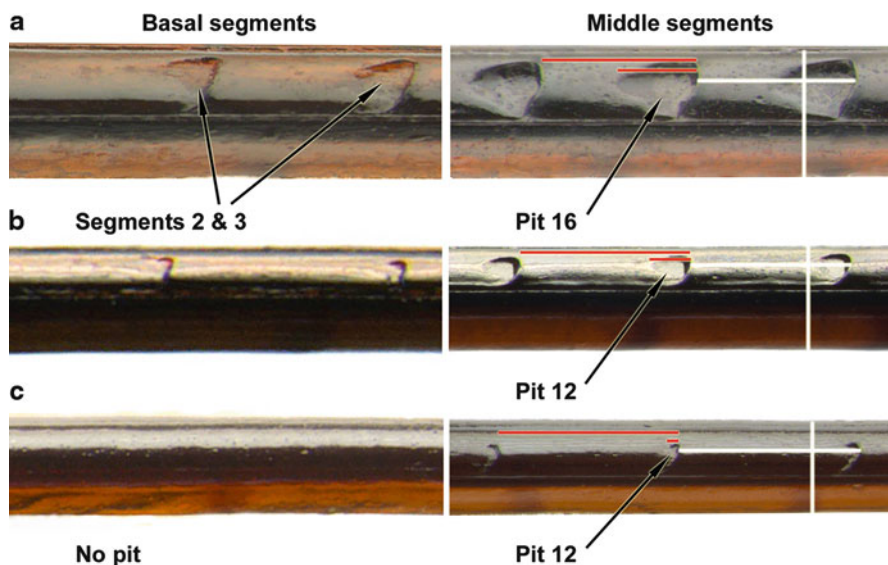
There are three ways to study the ovipositor, namely from a dry specimen, a relaxed specimen, and a specimen in liquid preservative.

#### 1.4.1.1 Dry Specimen

The apical half of the ovipositor can be seen by popping out one (either right or left) of the apical sections of the sheath (Fig. 1.1b). This is done by sliding an entomological pin at the end of the sheath between the ovipositor and the sheath. Then, the pin is pushed basally until the apical section breaks off. If the visible portion of the ovipositor is dirty, it can be cleaned with a paintbrush dipped in ethanol (70–95%). This is a practical and rapid method, but it is not possible to observe the ovipositor under the basal section of the sheath.

#### 1.4.1.2 Relaxed Specimen

After 24–48 h in a very humid atmosphere a dry specimen becomes soft and it can be easily dissected. A container with a moist to almost wet cloth will relax the specimen. The specimen is pinned on a foam surface put above the moist cloth. The jar is sealed and kept away from the sun for a day or two. An entomological pin can then be used to tease out the ovipositor away from the sheath while the specimen is secured between the fingers of the observer. The pin can then be moved towards the base of



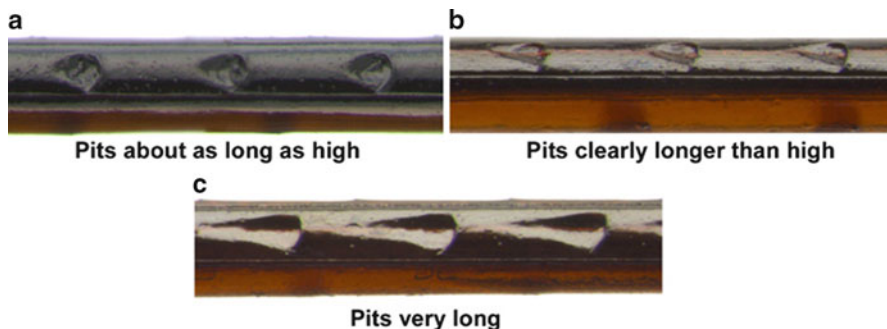
**Fig. 1.3** Basal and middle section showing pits on lancet (in middle section, red lines compare the length of pit with that of segment; white lines compare length of segment with width of ovipositor; pit segment number refers to alignment of pit with the junction of basal and apical section of sheath); (a) *S. noctilio*, (b) *S. nitidus*, (c) *S. cyaneus*

the ovipositor without too much effort (the ovipositor could break). At this point, it is possible to observe all of the pits on the ovipositor. If the ovipositor is dirty, it can be cleaned with a paintbrush dipped in ethanol (Fig. 1.1c).

#### 1.4.1.3 Specimen in Preservative

The technique used to study specimens stored in preservative is similar to that for examining relaxed specimens other than the fact that the ovipositor is teased out as soon as the excess of preservative has been removed (Fig. 1.1c).

To study the pits on the ovipositor, a diffuse light source is required. A semi opaque plastic sheet is then placed between the light source and the specimen, positioned about 20 mm from the specimen, or a 13 W desk fluorescent lamp can also be used. The specimen must be shifted until the shadow and lit area reach the middle of pits (as in Fig. 1.4c). The diffuse light renders the pits sharply and clearly visible without glare. The researcher will typically record the size of pits near the middle where the apical and basal section of sheath normally meet. The relative size of pits is a function of the segment length (see red lines in Fig. 1.3a–c). It can then be ascertained whether the size of pits changes little or markedly toward the base of the



**Fig. 1.4** Proportion of pits based on middle segments; (a) *S. nigricornis*, (b) *S. californicus*, (c) *Sirex* sp. (from Chihuahua, Mexico)

ovipositor. They may even disappear several segments before the base (compare basal and middle segments in each of Fig. 1.3a–c). It is then necessary to record the segment number of the ovipositor where the basal and apical section of the sheath would normally meet (as in Fig. 1.3a (pit 16), b (pit 12), c (pit 12)). For some species it is useful to note the segment length relative to ovipositor (lance and lancet) diameter at this segment (see white lines in Fig. 1.3a–c). There have been similar measurements done between segment 1 and 2, 4 and 5, and 9 and 10 (Viitasaari 1984; Viitasaari and Midtgaard 1989). Furthermore, the pit proportions at the middle and base of the ovipositor must be recorded. Pits are commonly about as long as high, but they could be elongate and almost look gutter-like (Fig. 1.4a–c). Finally, for some species the number of pits is exceptionally high (35–43, as opposed to 26–33). All New World species were separated using the above approaches.

### 1.4.2 Other Characters

Once species are recognized using the ovipositor, other characters (e.g., pits on the head and the mesoscutum, proportions of tarsomeres and tarsal pads in females, and color patterns on the legs, abdomen and antennae) are usually found. Moreover, as females become clearly identified, males of most species are quite easily associated and their characters (e.g., structural characters shared usually by both sexes, and color patterns that are often peculiar to each sex) are also discovered.

There are many informative structural characters and significant color patterns. Color patterns that are useful are those on the antennae (Fig. 1.5a–c), the side of the head (Figs. 1.6a, b), the wings after considering the sex of the specimen (Fig. 1.8a–c), the abdomen (Fig. 1.9a–c), and legs (especially femora and tibia of the hind leg) (in males see Fig. 1.7a–d, in females see Fig. 1.10a–d). The main



Fig. 1.5 Antenna in male; (a) *S. obesus*, (b) *S. californicus*, (c) *Sirex* sp. (Chihuahua, Mexico)

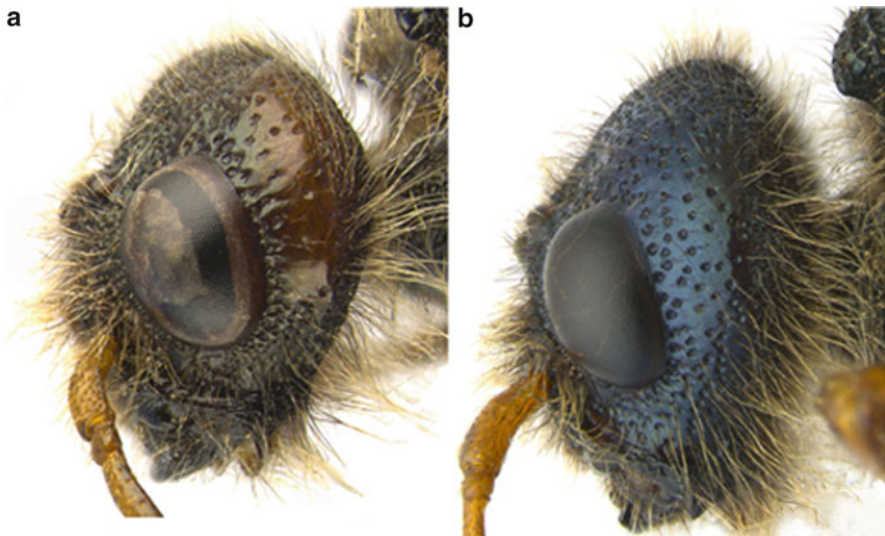
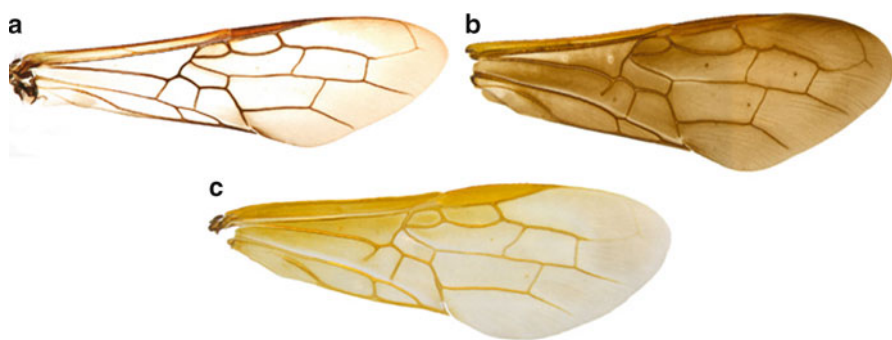
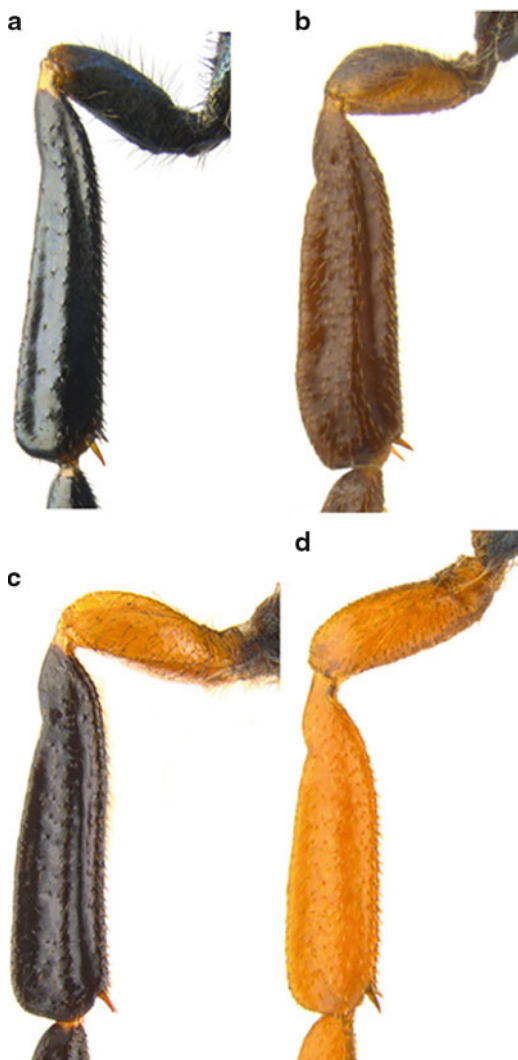


Fig. 1.6 Gena behind eye in male; (a) *S. behrensii*, (b) *S. californicus*

structures are, in both sexes, pits on the vertex (Fig. 1.11a–c) and on the disc of the mesoscutum (Fig. 1.12a–e), and in females, the proportion of the metatarsomere 2 in lateral view (it is the easiest segment to see and measure and the character states are best expressed on this segment) (Fig. 1.13a–c), the relative size of its tarsal pad (Fig. 1.14a, b), and the proportion between the sheath sections.

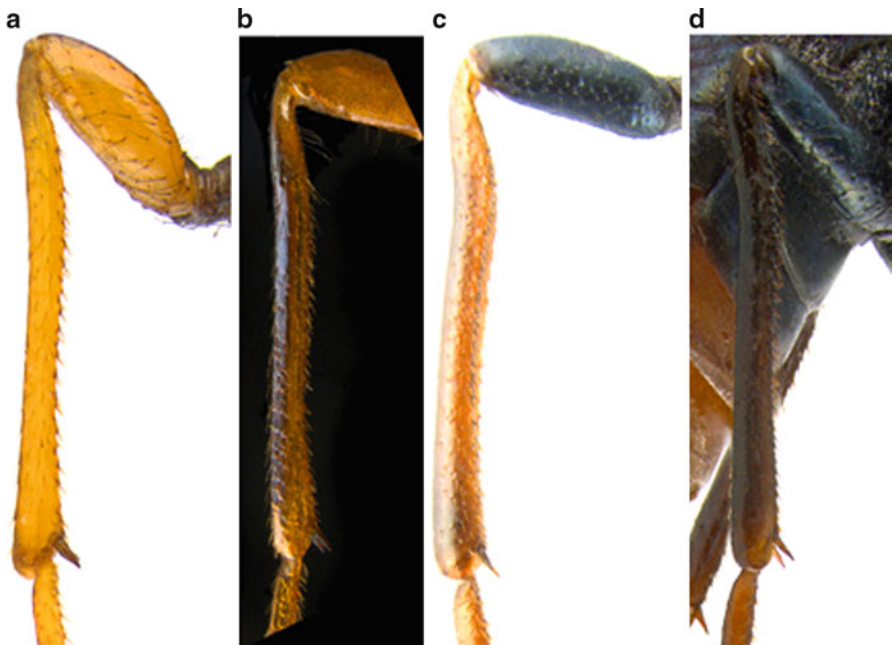
**Fig. 1.7** Hind leg in male; (a) *S. nigricornis*, (b) *S. behrensii*, (c) *S. nitidus*, (d) *S. californicus*



**Fig. 1.8** Fore wing; (a) female of *S. nitidus*, (b) female of *S. nigricornis*, (c) male of *S. obesus*

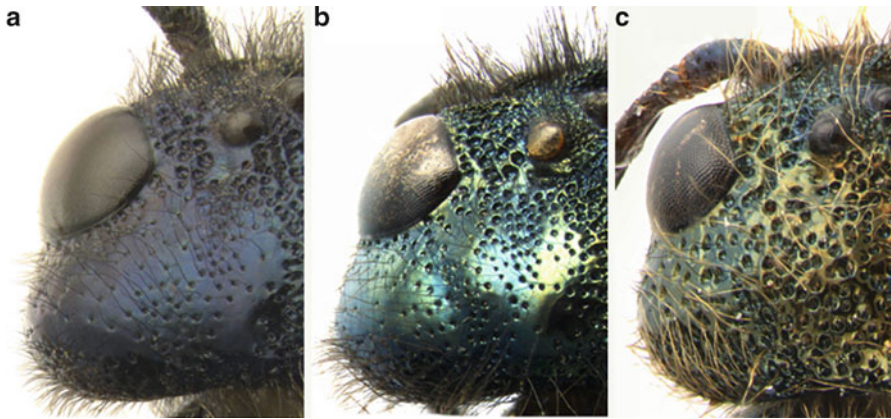


**Fig. 1.9** Abdomen in female; (a) *S. behrensii*, (b) *S. californicus*, (c) *S. nigricornis*

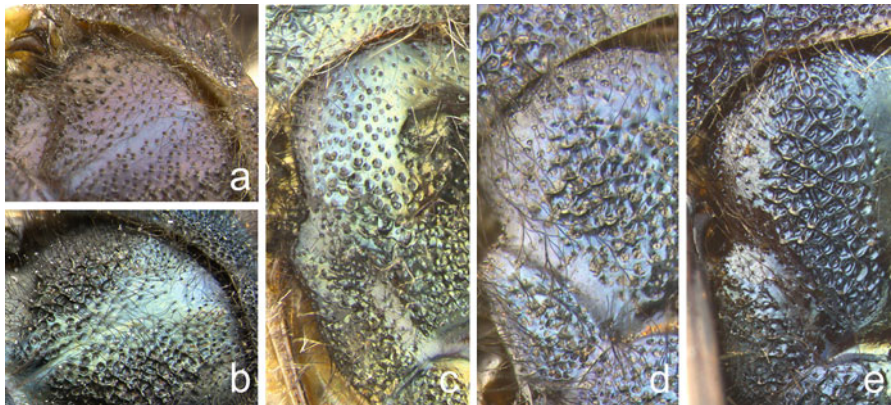


**Fig. 1.10** Metafemur and metatibia in female; (a) *S. nitidus*, (b) *S. varipes*, (c) *S. nigricornis* (light color form), (d) *S. nigricornis* (dark color form)





**Fig. 1.11** Pit development on dorsal surface of head; (a) fine and scattered pits, *S. noctilio*, (b) moderate size and dense pits, *S. nitidus*, (c) large and dense pits, *S. obesus*



**Fig. 1.12** Pit development on mesoscutum; (a) dorsolateral view of pit and associated tooth behind, *S. noctilio*, (b) dorsolateral view of pit development of net-like ridges, *S. nitidus*, (c) dorsal view, *Sirex* sp. (central Mexico), (d) dorsal view, *S. obesus*, (e) dorsal view, *Sirex* sp. (northern Mexico)



**Fig. 1.13** Proportion of metatarsomere 2 length relative to maximum height; (a) *S. obesus*, (b) *S. noctilio*, (c) *S. areolatus*

**Fig. 1.14** Proportion of tarsal pad (blue line) of metatarsomere 2 relative to maximum ventral length of tarsomere (red line); (a) *S. nitidus*, (b) *S. noctilio*



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## Chapter 2

# Life History and Biology of *Sirex noctilio*

Kathleen Ryan and Brett P. Hurley

**Abstract** The wood-boring wasp *Sirex noctilio* has an obligate mutualistic relationship with the basidiomycete fungus, *Amylostereum areolatum*. Female wasps carry the fungus in internal mycangia and introduce it into a relatively competition free environment inside the living stems of *Pinus* trees. The fungus and a phytotoxic mucus produced by the wasp act in concert to stress the host tree, creating an ideal environment for the fungus to develop. Fungal development is essential for the initiation of insect development and nutrition of the larvae. Favourable conditions for the fungus produce larger wasps and this influences their longevity, fecundity and flight potential, thus facilitating population growth and expansion. Trees that are physiologically stressed, for example by climatic factors, overcrowding, or other pests and pathogens, are more susceptible to attack. In susceptible stands, populations of the pest were long thought to be regulated by a number of parasites. As the pest complex continues to expand its range, it is becoming evident that a more complex interaction of various biotic and abiotic factors combine to regulate population dynamics. Addressing such knowledge gaps is important if successful control of *S. noctilio* is to be ensured into the future.

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## 2.1 Introduction

*Sirex noctilio* F. (Hymenoptera; Symphyta; Siricidae) is a woodboring wasp that has elicited considerable attention for its ability to kill pines, especially in regions where it has been introduced. This species has a wide host range and most pine species appear to be susceptible (e.g., Morgan and Stewart 1966a; Spradbery and Kirk 1978). *Sirex noctilio* is the only woodwasp species known to be capable of actually killing trees (Spradbery 1973), though it generally favours severely stressed and declining hosts over healthier trees.

*Sirex noctilio* is endemic to Europe, Asia and North Africa, where it is considered a secondary pest of various pine species (Spradbery and Kirk 1978, Chap. 5) and is of little economic or ecological concern. During the twentieth century, *S. noctilio* became established in several countries in the Southern Hemisphere including New Zealand (1900s), Tasmania (1952), mainland Australia (1961), Uruguay (1980), Argentina (1985), Brazil (1988) and South Africa (1994) (summarized by Ciesla 2003). In regions of this introduced range, the wasp has become a primary pest of some pine species (Rawlings 1948; Hurley et al. 2007). In some situations it has caused extensive mortality in these plantations of introduced pines, especially in those affected by stresses such as drought (Neumann and Minko 1981). In 2004, *S. noctilio* was first discovered in North America (Hoebeke et al. 2005). The extent to which this insect will be of economic concern in this region remains to be determined.

The woodwasp has a cryptic lifestyle (Fig. 2.1). Most of its life cycle is spent as a larva within the sapwood of its host (from which the name woodwasp derives) and this makes it difficult to detect. The development of *S. noctilio*, and thus its reproductive potential, is tied to the vigour of its basidiomycete fungal symbiont, *Amylostereum areolatum* (Fries) Boidin (e.g., Coutts and Dolezal 1965). Interactions among the two biota and a phytotoxin produced by the wasp allow the insect to breach the defences of its living host trees. Woodwasp populations are suppressed by a number of factors, including tree defence, environment and natural enemies. In this chapter, the life history, host preference and factors affecting population dynamics of *S. noctilio* are reviewed.

## 2.2 Insect-Fungus Complex

The *A. areolatum* symbiont of *S. noctilio* derives considerable benefit from its relationship with the woodwasp. It is protected in the wasp's mycangia before the insect drills through the protective bark of the tree and introduces the fungus directly into a suitable, relatively competition-free, host substrate. *Amylostereum areolatum* primarily spreads vegetatively and clonal lineages over wide geographic areas are demonstrated by a number of authors (e.g., Vasiliauskas et al. 1998; Thomsen and Koch 1999; Vasiliauskas and Stenlid 1999; Slippers et al. 2001). The close association of *A. areolatum* with its woodwasp symbiont is thought to be a reason that it rarely reproduces sexually in some areas of its native range, and is not yet known to fruit in its introduced range (Gilbertson 1984, Chaps. 5, 8).



**Fig. 2.1** The life-cycle of *Sirex noctilio* and its fungal mutualist, *Amylostereum areolatum*