Siricidae (Hymenoptera: Symphyta: Siricoidea) of the Western Hemisphere

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Abstract

Horntails (Siricidae) are important wood-boring insects with 10 extant genera and about 122 species worldwide. Adults and larvae of Siricidae are often intercepted at ports and are of concern as potential alien invasive species. The family consists of 7 genera and 33 species in the New World: *Eriotremex* with one species, *Sirex* with 14 species, *Sirotremex* with one species, *Teredon* with one species, *Tremex* with two species, *Urocerus* with seven species, and *Xeris* with seven species. Five of these species have been accidentally introduced from the Old World: *Eriotremex formosanus* (Matsumura, 1912) into southeastern United States, probably from Vietnam; *Sirex noctilio* Fabricius, 1793, an important pest of *Pinus* spp., into eastern North America, Argentina, Brazil, and Uruguay from central Europe; *Urocerus gigas* (Linnaeus, 1758) into Chile, probably from Europe; *Urocerus sah* (Mocsáry, 1881) into northeastern North America, probably from southern Europe or North Africa; and *Tremex fuscicornis* (Fabricius, 1783) into Chile, probably from China.

Six new species are described: *Sirex abietinus* Goulet, **n. sp.**; *S. hispaniola* Goulet**, n. sp.**; *S. mexicanus* Smith, **n. sp**.; *S. xerophilus* Schiff, **n. sp.**; *Xeris chiricahua* Smith, **n. sp.**; and *X. tropicalis* Goulet, **n. sp.** Five species are re-instated: *Urocerus caudatus* Cresson, 1865, **sp. rev.**; *U. nitidus* T. W. Harris, 1841, **sp. rev.**; *Sirex melancholicus* Westwood, 1874, **sp. rev.**; *S. obesus* Bradley, 1913, **sp. rev.**; and *S. torvus* M. Harris, 1779, **sp. rev.** Eleven new synonyms are proposed: *Neoxeris* Saini and Singh, 1987, **n. syn.** of *Xeris* Costa, 1894; *Sirex hirsutus* Kirby, 1882, **n. syn.** of *S. juvencus* (Linnaeus, 1758); *Urocerus zonatus* Norton, 1869, **n. syn.** of *S. nigricornis* Fabricius, 1781; *Urocerus edwardsii* Brullé, 1846, **n. syn.** of *S. nigricornis* Fabricius, 1781; *Sirex fulvocinctus* Westwood, 1874, **n. syn.** of *S. nigricornis* Fabricius, 1781; *Sirex abaddon* Westwood, 1874, **n. syn.** of *S. nigricornis* Fabricius, 1781; *Sirex hopkinsi* Ashmead, 1898, **n. syn.** of *S. nigricornis* Fabricius, 1781; *Sirex leseleuci* Tournier, 1890, **n. syn.** of *S. torvus* M. Harris, 1779; *Sirex duplex* Shuckard, 1837, **n. syn.** of *S. torvus* M. Harris, 1779; *Sirex latifasciata* Westwood, 1874, **n. syn.** of *Urocerus albicornis* (Fabricius, 1781); and *Xeris spectrum townesi* Maa, 1949, **n. syn.** of *X. indecisus* (MacGillivray, 1893). Five new lectotypes are designated for: *Paururus californicus* Ashmead, 1904; *P. pinicolus* Ashmead, 1898; *P. hopkinsi* Ashmead, 1904; *Sirex torvus* M. Harris; and *S. taxodii* Ashmead 1904. Three changes in rank from subspecies to species level are proposed: *Sirex californicus* (Ashmead), **n. stat.**, from *S. juvencus californicus*; *Urocerus flavicornis* (Fabricius), **n. stat.**, from *U. gigas flavicornis*; and *Xeris indecisus* (MacGillivray), **n. stat.**, from *X. morrisoni indecisus*. Two species are excluded from the New World Siricidae: *Sirex juvencus* (Linnaeus), and *Xeris spectrum* (Linnaeus); both species have been frequently intercepted in North America, but they are not established. One species is excluded from the Palaearctic Siricidae: *Sirex cyaneus* Fabricius. The European "*Sirex cyaneus*" is distinct from the American *Sirex cyaneus*; *Sirex torvus* M. Harris is the oldest name for this species.

We characterize the family based on all extant genera. The world genera are keyed and a reconstructed phylogeny is proposed. For genera not found in the New World, we provide a synonymic list, a description, and information about diversity with significant references. For genera in the New World, each genus includes the following (if available and/or

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pertinent): synonymic list, diagnostic combination, description for one or both sexes, taxonomic notes, biological notes, diversity and distribution, and references. Only New World Siricidae are treated at species level, each species includes the following (if available and/or pertinent): synonymic list, diagnosis, description of one or both sexes, geographical variation, taxonomic notes, origin of the specific epithet, biological notes, hosts and phenology (flight period data; a list of associated nematode and fungus species), and range.

DNA barcoding (cytochrome oxidase 1 – CO1) was shown to be a reliable identification tool for adults and larvae intercepted at ports. Larvae cannot be identified using classical morphological methods, but DNA barcoding can accurately distinguish larvae of all species tested to date. We include barcodes for 25 of the 33 New World species and consider in our taxonomic notes several Old World species as needed. DNA data has been most useful for confirming some morphologically similar species, associating specimens with two or three discrete color forms, and deciding the rank of some populations. The results have proved to be accurate and in agreement with species determined by classical morphological methods.

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A. General

1. Introduction

In 2004, specimens of *Sirex noctilio* Fabricius were discovered in New York State (Hoebeke *et al.* 2005). The species is known to cause major damage to pine plantations in South America, South Africa, Australia and New Zealand. The news of its establishment in North America was taken seriously by Canadian and American authorities and major surveys were started (and are ongoing). Hundreds of sampling sites in United States from Michigan to New Hampshire and in Canada from the eastern region of Lake Superior to New Brunswick were visited weekly and Siricidae extracted from cut logs placed in rearing containers.

With this sudden interest in horntail wasps, taxonomists got involved because adults of *S. noctilio* are not obviously distinguishable from those of some of the native species in eastern North America. It was known that species close to *S. noctilio* belong to two species complexes, the *cyaneus* and *californicus* complexes, but further work was needed to resolve the taxonomic problems. Therefore, more or less independently, the first three authors concluded that the North American species required revision. N. M. Schiff studied mitochondrial DNA (cytochrome oxidase 1 – CO1) of most North American and central European species, and provided information about ecology, sampling techniques and associated fungi; H. Goulet studied the species and higher classification based mainly on morphological information, wrote the identification keys and checked several type specimens; and D. R. Smith prepared parts of the introduction and a section on specimens intercepted in North America, refined nomenclatural information, studied many type specimens, prepared the reference section and was the main editor. C. Boudreault was responsible for statistics, illustrations, plate design, and HTML programming for the web version.

Because Siricidae are large, usually showy insects, most collections have specimens, but because standard collecting methods rarely work to capture adults only a few collections have large numbers of specimens, obtained mostly by rearing. Malaise traps catch a few adults; sweeping and the use of yellow pan traps do not catch any. Adults are most easily collected by rearing from trunks of dead or dying trees. Adults of some species go to the top of hills (Chapman 1954), and if the vegetation is low enough they can be sampled with a net; others are attracted to fire in fire-prone forests and may be hand collected on trunks and stumps.

The 3000–4000 adults of Siricidae in the Canadian National Collection of Insects, Ottawa were almost entirely obtained by Canadian Forest Service staff. Over 70% of the specimens had been reared. This gave us good series of reared specimens from known hosts which greatly helped to resolve taxonomic problems in the Nearctic region. As the work progressed we decided to treat all Western Hemisphere species and world genera. We could not treat the world fauna at species level because most of the species are centered in Asia, a region poorly represented in North American collections.

Viitasaari (1984, 1988) and Midtgaard and Viitasaari (1989) provided us with the main clue to solving species complexes using adult morphology. In their works, ovipositor features were covered systematically. Amazingly, the ovipositor pits (very likely of *S. noctilio* not *S. juvencus* as stated) were illustrated much earlier (Hartig 1837), and females of almost every species of *Sirex* in the New World appear to have a unique set of ovipositor features. The character has not been as significantly useful at species level in other genera but each had a unique combination of other features. Other characters such as larvae (Hartig 1837, Yuasa 1922 [excellent illustrations of the larva of *T. columba* and many other structures]), male genitalia (Crompton 1919, Chrystal 1928), fine structures of the last tarsomere (Holway 1935), adult spiracles (Tonapi 1958), fore wing cenchrus coupling (Cooley 1896), internal thoracic musculature (Daly 1963), and larval digestive system (Maxwell 1955) were not studied by us. Larvae were not identified by us using morphology; instead, they were more easily and accurately identified using DNA barcodes.

Linnaeus (1758) described the first Siricidae, *Sirex juvencus*, *Urocerus gigas* and *Xeris spectrum* (originally as *Ichneumon juvencus*, *I. gigas* and *I. spectrum*) from the Old World. *Sirex juvencus* has been intercepted many times at North American ports. In the New World, the first valid species described was *Tremex columba* (Linnaeus 1763) (originally as *Sirex columba*), the first of 56 names proposed for our 28 native species. We summarize in 25–year periods the species names proposed and treated as valid here. From 1758–1775, three names were proposed; only *T. columba* is still in use. 1776–1800, five names were proposed; four are still in use, *Sirex cyaneus* Fabricius, *S. nigricornis* Fabricius, *Urocerus albicornis* (Fabricius) and *U. flavicornis* (Fabricius). From 1801–1825, two species names were proposed; neither is in use today. From 1826–1850, five names were proposed; *Sirex nitidus* (T. W. Harris) is in use. From 1851–1875, 17 taxa were proposed; seven species names are in use here, *Sirex areolatus* (Cresson), *S. varipes* Walker, *Teredon cubensis* (Norton), *Urocerus californicus* Norton, *U. cressoni* Norton, *Xeris caudatus* (Cresson), and *X. melancholicus* (Westwood). Norton and Cresson had good collections at their disposal and together they contributed 38% of the names in use here. From 1876–1900, 13 names were proposed; four are in use here, *Sirex*

behrensii (Cresson), *Xeris indecisus* (MacGillivray), *X. morrisoni* (Cresson), and *X. tarsalis* (Cresson). From 1901–1925, eight species names were proposed; three are in use here, *Sirex californicus* (Ashmead), *S. obesus* Bradley, and *Urocerus taxodii* (Ashmead). By the end of this period, 90% of the named New World species were known. From 1926–1950, two names were proposed; one, *Sirex longicauda* Middlekauff, is in use here. From 1951–1975, no names were proposed. From 1976–2000, one name was proposed and is still in use; *Sirotremex flammeus* Smith.

In summary, Cresson proposed nine names, Westwood eight, Ashmead five, Fabricius four, and Kirby four. Of the names proposed by Cresson 67% are valid, by Westwood 12%, by Ashmead 40%, by Fabricius 100%, and by Kirby 0%. The best contributors of valid names are Linnaeus, Fabricius, Walker, Middlekauff, and Smith with 100% success, and Cresson and Norton with 67% success. These seven authors described 76% of the names in use today. Of the 56 species proposed, 22 are still in use in this paper. In this work we add six new species bringing the total number of native species to 28.

2. Material and Methods

Material for morphological Studies

We based this study on more than 12000 specimens. Most are preserved in collections, but many (over 3000 specimens) were part of surveys conducted in eastern Canada and south of the Great Lakes in the United States following the establishment of *Sirex noctilio* Fabricius. Most of these specimens were not retained. The following is a list of collections with their respective curators.

AEI American Entomological Institute, Gainesville, FL, USA. D. Wahl.

AMNH Department of Entomology Collection, American Museum of Natural History, New York, NY, USA. R. T. Schuh.

ANSP Academy of Natural Sciences, Philadelphia, PA, USA. J. Weintraub.

BDUC Biology Department, University of Calgary, Calgary, AB, Canada. R. Longair.

BMNH Department of Entomology, The Natural History Museum, London, England. C. Gillette.

BYUC Brigham Young University, Provo, UT, USA. S. M. Clark.

CASC Department of Entomology, California Academy of Sciences, San Francisco, CA, USA. W. J. Pulawski.

CASS Agriculture and Agri–Food Research Centre, Saskatoon, SK, Canada.

CFIA Canadian Food Inspection Agency, Ottawa, Ontario, Canada. H. Douglas.

CNC Canadian National Collection of Insects and Arachnids, Ottawa, ON, Canada. H. Goulet,

CUCC Clemson University Arthropod Collection, Clemson University, Clemson, SC, USA. J. C. Morse.

CUIC Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, NY, USA. E. R. Hoebeke.

DABH Department of Applied Biology, University of Helsinki, Helsinki, Finland. M. Viitasaari.

DEBU Department of Environmental Biology, University of Guelph, ON, Canada. S. A. Marshall & S. Paiero.

DENH University of New Hampshire Insect Collection, Department of Entomology, University of New Hampshire, Durham, NH, USA. D. S. Chandler.

EDUM Entomology Department, University of Manitoba, Winnipeg, MB, Canada. †R. E. Roughley.

EIHU Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

FRLC Atlantic Forestry Centre, Natural Resurces Canada, Fredericton NB, Canada. J. Sweeney.

FRNZ Scion – next generation biomaterials, Te Papa Tipu Innovation Park, Rotorua, New Zealand. S. Sopow.

FSCA Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, FL, USA. J. Wiley.

GLFC Great Lake Forest Centre, Natural Resources Canada, Sault Ste. Marie, ON, Canada. K. Nystrom.

HMUG Hunterian Museum, Department of Zoology, University of Glasgow, Glasgow, Scotland. G. Hancock.

HNHM Zoological Department, Hungarian Natural History Museum, Budapest, Hungary.

ICCM Section of Insects and Spiders, Carnegie Museum of Natural History, Pittsburgh, PA, USA. J. E. Rawlins.

IES Instituto de Ecología y Sistemática, La Habana, Cuba.

INHS Insect Collection, Illinois Natural History Survey, Champaign, IL, USA.

LECQ Laurentian Forestry Centre, Natural Resource Canada, Ste. Foy, QC, Canada. J. Klimaszewski.

LEMQ Lyman Entomological Museum and Research Laboratory, MacDonald College, McGill University, Ste. Anne de Bellevue, QC, Canada. T. A. Wheeler.

LSUK Linnean Society, Burlington House, Piccadilly, London, England.

MCZC Entomology Department, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. E. O. Wilson.

MHND Museo Nacional de Históoria Natural, Plaza de Cultura, Santo Domingo, Dominican Republic. C. Suriel.

MNHN Muséum National d'Histoire Naturelle, Paris, France. C. Villemant.

MRNQ Ministère des Ressources Naturelles, Direction de l'Environnement et de la Protection des Forêts, Service des Relevés et des Diagnostics, Québec, QC, Canada. C. Piché.

MTEC Department of Entomology, Montana State University, Bozeman, MT, U.S.A. M. A. Ivie.

NCSU North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, NC, USA.

NFRC Northern Forestry Centre, Natural Resource Canada, Northwest Region, Edmonton, AB, Canada. G. Pohl.

NFRN Atlantic Forestry Centre, Corner Brook, NL, Canada. P. Bruce.

NSMT Entomological Collection, National Science Museum (Natural History), Tokyo, Japan. A. Shinohara.

NZAC New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand. D. Ward.

OSAC Oregon State Arthropod Collection, Department of Zoology, Oregon State University, Corvallis, OR, USA. C. Marshall.

OXUM Hope Entomological Collections, University Museum, Oxford, England. J. E. Hogan.

PANZ Ministry of Agriculture and Forestry, Biosecurity New Zealand, Plant Health & Environment Laboratory, Auckland, New Zealand. O. Green.

PFRC Pacific Forestry Centre, Natural Resource Canada, Victoria, BC, Canada. L. Humble.

ROME Department of Entomology, Royal Ontario Museum, Toronto, ON, Canada. C. Darling.

SDEI Deutsches Entomologisches Institut, Senckenberg, Germany. A. Taeger and S. M. Blank.

UAIC Department of Entomology Collection, University of Arizona, Tucson, AZ, USA. D. Madison.

UAM University of Alaska Museum, Fairbanks, AK, USA. D. Sikes.

UAMC Universidad Autónoma de Morelos, Cuernavaca, Mexico.

UASM Department of Zoology, Strickland Entomological Museum, University of Alberta, Edmonton, AB, Canada. D. Shpeley.

ULQC Insect Collection, Department of Biology, Laval University, Quebec, QC, Canada. J. M. Perron.

UCRC University of California, Riverside, CA, USA. D. Yanega.

USBD Biology Department, University of Saskatchewan, Saskatoon, SK, Canada.

USFS–AK USDA Forest Service, State and Private Forestry, Forest Health Protection, Fairbanks Unit, Fairbanks, AK. J. J. Kruze.

USFS–GA USDA Forest Service, Southern Research Station, Athens GA, USA. D. Miller.

USFS–MS USDA Forest Service, Stoneville, MS, USA. N. M. Schiff.

USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. D.R. Smith.

ZMUC Department of Entomology, Zoological Museum, University of Copenhagen, Universitetsparken, Copenhagen, Denmark. L. Vilhelmsen.

Materials for DNA studies

Collection of samples: Woodwasps for the DNA analysis portion of this study were collected by numerous collaborators or the authors using 3 different methods. They were netted or hand-collected, especially at forest fires; reared from host material; or collected in Lindgren funnel or panel traps baited with terpenes and/or ethanol. The trapped specimens were mostly collected as by-products of bark beetle trapping programs. Specimens were frozen, preserved directly in 70%–95% ethanol or collected into diluted ethylene glycol or similar preservative and then transferred to 70%–95% ethanol. Specimens were accumulated at the USFS–MS, CNC, and PFRC for DNA analysis.

Methods for morphological studies

Most specimens were studied and images taken with a MZ16 Leica binocular microscope and an attached

Leica DFC420 digital camera. Some specimens were photographed using a DSLR Canon Rebel Xti camera with a 100 mm macro lens. Multiple images through the focal plane were taken of a structure and these combined using Combine ZM or ZP designed by Alan Hadley to produce a single, focused image. Specimens were illuminated with a 13 watt daylight fluorescent lamp.

Methods for DNA studies

DNA Isolation. DNA was isolated amplified and sequenced both in Guelph and Stoneville, MS. DNA from specimens from Ottawa and Victoria were sequenced in the Biodiversity Institute of Ontario, Guelph, ON, according to standard protocols (as detailed in Fernandez-Triana *et al.* 2011). Protocols used in Stoneville were as follows. Tissue for extraction was collected from the thorax either by pulling off a hind leg and collecting the muscle tissue still attached to the coxa or by digging tissue directly from the thorax with a pair of forceps. Genomic DNA was isolated from the tissue using either a slightly modified Quiagen DNeasy spin-column protocol for animal tissues or the Masterpure ™ Yeast DNA Purification kit by Epicentre (Madison, WI). We modified the DNeasy spin–column protocol by changing the conditions of the proteinase K incubation from 1–3 hrs at 56° C to 1 hr at 70° C and by changing the final elution solution from 200µl Buffer AE to 50µl Buffer AE plus 200µl Ambion nuclease free water. In all extractions, care was taken to avoid digestive tract tissue and eggs which might contain microbial contaminants such as *Wohlbachia* sp. Early in the study, a *Wohlbachia* species was sequenced from a woodwasp but not from a species used in this study. We have sequenced more than 1000 woodwasps (leg or thorax tissue) since then with no further discovery of *Wohlbachia*.

Amplification and clean up. Over the course of the study several PCR reaction amplification protocols were used successfully. The most evolved and preferred protocol is very similar to that used by Roe *et al.* (2006). PCR reactions containing 10µl of DNA template, 9µl of Ambion nuclease free water, 2.5 µl Advantage 2 10X buffer (Clontech, Mountain View, CA), 2 µl of each oligo (each at 10mM), 1.5 µl of dNTP mix (each at 10mM) and 0.4 µl of Advantage 2 Taq, were amplified in a PTC-100 Programmable Thermal Controller (M. J. Research Inc.) as follows: an initial denaturation step at 94°C for 2 minutes followed by 35 cycles of 94°C for 30 seconds, 45°C for 30 seconds and 68°C for 2 minutes, followed by a final extension at 68°C for 10 minutes. The extension steps were at 68°C rather than 72°C because Advantage 2 Taq is more efficient at the lower temperature (Manufacturer's instructions). The oligos used were LCO1490: 5'ggtcaacaaatcataaagatattgg-3'and HCO2198: 5'-taaacttcagggtgaccaaaaaatca-3'of Folmer *et al.* (1994) where the numbers refer to the position of the *Drosophila yakuba* 5' nucleotide. PCR Products were visualized on 30% acrylamide/bis gels (mini Protean II electrophoresis cell by BioRad) stained with either ethidium bromide or preferably EZ-Vision 2 (N650-Kit by Amresco Inc.). PCR products were cleaned using an Exo-SAP protocol. Up to 20 µl of PCR product was mixed with 8µl of Exo-SAP (2µl Exonuclease I at 10U/µl, USB product no. 70073Z, Cleveland, OH; 20 µl Shrimp Alkaline Phosphatase at 1U/µl USB product no. 70092Z, Cleveland, OH); 78 µl ddH_2O) and heated to 37 °C for one hour followed by 15 minutes at 80°C.

Sequencing. Double stranded PCR products (at least 20ng/µl) were sequenced on an ABI 3730xl sequencer (Applied Biosystems, Foster City, CA) using BigDye 3.1 in 10µl reactions (1.75µl 5X sequencing buffer, 0.5 µl BigDye 3.1, 0.8 µl 10 µM primer, at least 20 ng DNA template and water up to 10 µl). DNA template was quantified by comparison to Low DNA Mass Ladder (Invitrogen cat. No. 10068-013, Carlsbad, CA), at least 1 µl of template was used even if the concentration of DNA appeared to be significantly greater than 20 ng/µl. The cycle sequencing reaction was 2 minutes at 96 °C followed by 25 cycles of 96°C for 30 seconds, 50 °C for one minute and 60°C for 4 minutes. The sequencing reaction (10µl) was stopped by addition of 2.5 µl 0.125 M EDTA (pH 8.0) followed by centrifugation at 4000 rpm for one minute. The products were precipitated for 30 minutes in the dark by addition of 30µl of 100% ethanol followed by centrifugation at 4000 rpm for 30 min at 4°C. The samples were washed with 100µl of 70% ethanol spun for 15 minutes at 1650 rpm for 15 minutes and then air-dried in the dark for 15 minutes. Dried products were stored at -20°C until injection. Products were re-upped in 100µl of deionized water, centrifuged at 4000 rpm for 2 minutes and injected immediately into the sequencer using the ABI default injection module appropriate for the installed capillary array, but decreasing the injection time to 2 sec.

Data Manipulation. Sequences were captured using Data Collection Software v3.0 with Dye set Z_BigDyeV3 from Applied Biosystems which gave us ab1. sequence trace files and seq. sequence text files. Templates were sequenced in both directions and the corresponding sequences were paired into individual specimen contigs using Lasergene Seqman by DNAStar. To obtain full length sequences it was sometimes necessary to sequence individual specimens several times and combine the partial sequences to form the final sequence used for analysis. Individual specimen contigs were aligned using

Clustal V, and built into trees (Neighbor Joining) (Saitou and Nei 1987) using Megalign also by DNAStar.

Exclusion of Numts and Heteroplasmy. Two of the potential pitfalls of using mitochondrial sequences for identification include mistakenly sequencing nuclear pseudogenes of mitochondrial origin (NUMTs), or obtaining multiple sequences from heteroplasmic individuals. To reduce the risk of NUMTs we were careful to select only muscle (mitochondrial rich) tissue from specimens and all sequences were translated and inspected for stop codons and insertions and deletions (characteristics of pseudogenes). To date, all siricid sequences have been free of stop codons, insertions and deletions. Heteroplasmy is when an individual has more than one mitochondrial haplotype (sequence). To reduce possible variation due to heteroplasmy we sequenced double stranded PCR products directly rather than sequencing clones. If there were rare alternate haplotypes they would be masked by the most common haplotype. We further sequenced many individuals multiple times with no variation (data not shown).

Methods for active collecting, trapping and rearing Siricidae

Although siricids are large and colorful insects, they are not commonly encountered in general collecting in forests and more specialized techniques are often used to obtain them. These methods fall into three general categories: collecting in specific habitats based on knowledge of siricid behavior, trapping using a variety of different traps, and rearing from infested wood. With the recent discovery of *Sirex noctilio* in North America (Hoebeke *et al.* 2005, deGroot *et al.* 2006) there has been increased interest in surveys for *S. noctilio* and other siricids and the techniques below are evaluated in light of their utility for survey work.

Active collecting. Like many wood-boring insects, *S. noctilio* and presumably other siricids are attracted to the volatiles produced by wounded, stressed or dying trees (Madden 1971, Newmann *et al.* 1982). In some circumstances a single, cut tree can be attractive. NMS and Paul Lago collected more than 100 specimens of *S. nigricornis* and many other wood borers and parasitoids over a 3-day period in October, 2001, on a single loblolly pine (DBH approximately 30 cm) that was cut into approximately 50 cm bolts at a semi rural-setting in Oxford, Mississippi. Unfortunately, this was a rare occurrence; NMS has attended many freshly cut trees that were not visited by siricids. Presumably, in Oxford, there was a local population of recently emerged *S. nigricornis* and the cut loblolly pine was the only local source of volatiles.

Most often, siricids are attracted to areas where there are many wounded trees. In Western North America, siricids are commonly found at forest fires. Males form mating aggregations high up on unburned trees at the edge of forest fires and females can be found ovipositing into freshly burned stumps or trees (Middlekauf 1960, Middlekauf 1962, Westcott 1971, Schiff unpublished data). Larvae can develop in the fire-killed trees and adults sometimes emerge from houses built with salvaged lumber (Middlekauf 1962, Lynn Kimsey personal communication). Siricids are also found at logging decks and at mills where the cut trees presumably release attractive volatiles (Wickman 1964, Wood Johnson personal communication). Siricids can be surveyed at fires and mills but these are not always located in the study area of interest.

Siricids are also known to "hill-top". Males and females of many widely dispersed insect species find mates at prominent landscape features like the tops of hills. Typically, there are more males than females and the host plants do need to be present as the females can fly to the host after mating. "Hilltopping" is probably much more common than has been reported because it is unusual to find a hill top with short vegetation where it can be observed (for general information, see Skevington (2008)). Similar behaviour has also been noted on fire towers. Specimens of *Urocerus sah* and *Xeris melancholicus* were collected over several years at the top of Mount Rigaud in eastern Canada (Fig. A2.1). At the same site, males of many species of Diptera, Lepidoptera, other Hymenoptera and Coleoptera were observed in similar aggregations. Among Hymenoptera, males of *Xiphydria* spp., *Trichiosoma triangulum* Kirby and *Cimbex americana* Leach were commonly collected with only occasional females being collected. This phenomenon is widespread. J. O'Hara, a dipterist, collected many males of *Sirex obesus* Bradley on hill tops in Arizona and New Mexico, Chapman (1954) recorded numerous males of *Urocerus flavicornis* on a mountain top in western Montana, and Jennings and Austin collected or recorded nine males of *Austrocyrta fasciculata* Jennings and Austin (Xiphydriidae) aggregating on top of Mount Moffatt and Mount Rugged in Queensland, Australia (Jennings *et al*. 2009).

Trapping. Siricids are most commonly collected by three trapping methods: 1) flight intercept trapping, 2) using artificial tree-mimicking traps baited with a chemical lure and 3) using trap or lure trees.

1) The most commonly used flight intercept trap is the Townes style Malaise trap (Townes 1972). Although Malaise style traps were designed to catch Hymenoptera, including Symphyta, they only occasionally catch siricids (Smith and Schiff 2002) and are generally considered to be too expensive to use for siricid surveys.

2) The use of artificial tree-mimicking traps with lures for siricids is largely a byproduct of bark beetle trapping programs. In fact, the discovery of *S. noctilio* in the United States resulted from the identification of a siricid caught in an exotic bark beetle survey funnel trap (Hoebeke *et al.* 2005). Almost all the survey work since the discovery of *S. noctilio* in North America has used artificial traps. The traps most commonly used are the Lindgren multiple-funnel trap and the cheaper cross-vane trap (Figs, A2.2 and A2.3). In silhouette, the traps mimic tree trunks and both use liquid filled collecting vessels. Typically the traps are baited with lures that mimic host volatiles of a wounded tree, namely a combination of monoterpenes and/or ethanol. These traps are relatively cheap and easy to assemble and service but like the Malaise trap they are not particularly efficient. In a 1999 study of five types of traps, 1661 siricids were collected over 5300 trap days for a trapping rate of approximately one siricid every three days. Presumably these are optimal results because the traps were located around a mill considered to be a wood-borer rich environment (McIntosh *et al.* 2001). The relatively low efficiency of these traps may be a function of the type of lure. These baited traps likely compete with all the stressed or damaged trees in the area, which reduces their effectiveness. Presumably trapping would be more efficient if the traps were baited with specific sex pheromone lures but none have been identified for Siricidae to date although components of contact sex pheromones for *S. noctilio* have recently been reported (Böröczky *et al.* 2009). An anomaly of artificial traps is that they seldom catch male siricids. We believe this is because traps are normally positioned with the top approximately two meters from the ground to facilitate collecting samples and male siricids spend most of their time in tree tops.

3) Originally, "trap" trees were used as a means to detect the presence of *S. noctilio* in Southern Hemisphere *Pinus radiata* plantations. Selected trees that were mechanically wounded were found to be attractive to *S. noctilio*, depending on the season and degree of wounding. Felled trees were attractive immediately but only susceptible to attack for about 2 weeks whereas girdled trees were not attractive for 9–12 days but remained attractive for a season or more (Madden 1971, Madden and Irvine 1971). The method was later refined by switching to use of a chemical herbicide instead of mechanical wounding (Morgan and Stewart 1972, Minko 1981, Newmann *et al.* 1982) and the trap trees evolved into a delivery system for parasitic nematodes as well as a means of detecting *S. noctilio*. Once the wounded trap tree was infested with *S. noctilio*, it would be felled and inoculated with nematodes. The nematodes would attack the larvae and be distributed when the adult woodwasps emerged. In the northern United States, the suitability and attractiveness of trap trees for *S. noctilio* is dependent on timing of herbicide injection and host tree species (Zylstra *et al.* 2010). Although this is the preferred method for detecting *S. noctilio* and delivering the parasitic nematode to control infestations in the Southern Hemisphere, it is labor intensive for survey work and requires landowner consent to wound trees. As far as we know trap tree methods have not been developed for any native species.

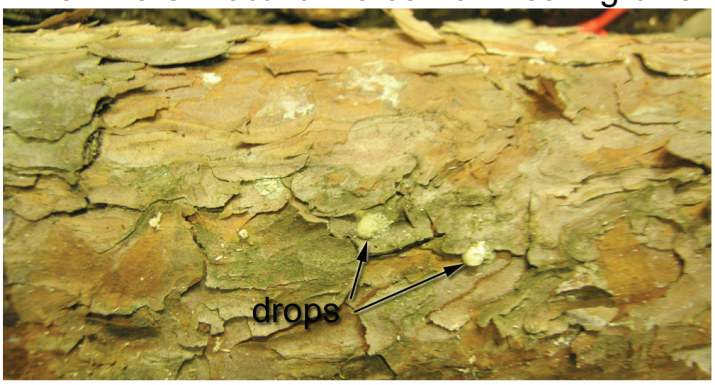
Rearing. Perhaps the best way to collect siricids is by rearing them from infested logs. The advantages of this method are that males are often reared along with females, the host tree can often be positively identified, and living specimens can be obtained for biological studies. This method can also be proactive. Specimens of *Urocerus taxodii* for this study were reared by wounding three bald cypress trees in the Delta National Forest, Sharkey Co., Mississippi, waiting for them to be attacked and later caging 1.5 meter bolts from the trees at the USFS–MS. Many other specimens in this study were also reared from wounded trees as part of a decade long Canadian Forest Service wood borer survey (as in Figs. A2.4, A2.5 and A2.6). Disadvantages include difficulty finding suitably infested trees and the space and time required for rearing. NMS has found siricid-infested trees by following siricid specific parasitoids like the giant ichneumonid wasps *Megarhyssa* spp., and looking for siricid damage such as perfectly round emergence holes. In some cases, after multiple drillings, female siricids and/or *Megarhyssa* can no longer withdraw their ovipositors and they become stuck and die. Ants or birds dispose of the bodies but the ovipositors sometimes remain protruding from the wood, indicating siricid infested trees (Spradberry and Kirk 1978, Schiff, unpublished data). Another clue is to look for the characteristic brown staining in cut timber resulting from the symbiotic fungus, *Amylostereum* sp. (Spradberry and Kirk 1978, Tabata and Abe 1997).

A2.2 D. Hauggen showing a vane trap

A2.3 K. Zylstra holding a Lindgren trap

A2.4 Rearing bins with boles

A2.5 Live *S. noctilio* males from rearing bins



A2.6 Pine pitch drops at oviposition sites

A2.1: Top of Mount Rigaud (about 200m above valley) - vegetation <3 m

3. Morphology

Structural terms. The following is intended as an overview of adult siricid structure wherein terms used in this work are defined and illustrated. Terms for structures mostly follow Huber and Sharkey (1993), but a few terms are specific to sawflies and Siricidae. English terms are used for the female genitalia for which the numerous figures in Ross (1937) were consulted. The terms used by Wong (1963) are also given in parenthesis.

The body consists of three distinct sections: the **head**, **thorax** and **abdomen** (lateral habitus of female Fig. A3.1 and lateral habitus of male Fig. A3.2).

The head consists of the **head capsule**, **eye**, **antenna**, and **mouthparts**) (Fig. A3.1).

Head capsule. The head capsule is divided into several regions that usually have indistinct boundaries. In frontal view the **clypeus** is the region below and between the antennal sockets (Fig. A3.4). The **face** is the region lateral to the clypeus ventral to the antennal sockets which is mostly composed of the **antennal scrobe** (Fig. A3.4), a depression that receives the antennal scape when it is appressed to the head. The **frons** is the region between the inner edges of the eyes between the ventral edges of the antennal sockets and **median ocellus** (Fig. A3.4). The **vertex** is the region between the ventral margin of the median ocellus and highest part of the head capsule, which above the eyes in dorsal view extends laterally to about outer margin of each eye (Figs. A3.4, A3.6). The vertex has three ocelli, the **median ocellus**, and two **lateral ocelli**, but most Siricidae lack the clearly differentiated postocellar furrow behind each lateral ocellus that is more apparent in most other sawflies. The **gena** (often referred to as the temple) is the surface posterior to the eye in lateral view, including the surface below the eye (Fig. A3.5). Although the **occiput** is not clearly differentiated from the gena and vertex it is considered as the posterior surface of the head capsule (Figs. A3.5, A3.6). The occiput surrounds the foramen magnum (an opening between the head and the thorax) and meets ventrally along the occipital junction.

Mouth parts. The **labrum** is a very small, finger-like structure that is normally concealed under the clypeus between the **mandibles**. The **labial palp** (Fig. A3.5), though very short, consists of two or three palpomeres that are clearly visible below the mandible. The **maxillary palp** consists of a single palpomere that is hidden under other mouth parts.

Antenna. The antenna is divided into three principal sections, the **scape**, **pedicel** and **flagellum**. Little is described in this work for the first two sections but various character states of the flagellum are described. The flagellum consists of 4 to about 30 **flagellomeres**

that are numbered consecutively following the pedicel (Fig. A3.11).

The thorax consists of three major sections, the **prothorax**, **mesothorax** and **metathorax**, including the **wings** and the **legs**.

Prothorax (Figs. A3.1, A3.3). The prothorax is the anterior segment of the thorax. It consists of a dorsal, transverse sclerite, the **pronotum**, that laterally extends ventrally toward the procoxae. On either side ventral to the pronotum is the **propleuron**. The prothorax lacks wings but bears a pair of **fore legs**.

Mesothorax (Figs. A3.1, A3.3). The mesothorax is the middle segment of the thorax. The dorsal sclerite, the **mesonotum** is divided by the transscutal fissure (we are not certain that the broad furrow is really this structure seen in later Hymenoptera lineages, but its starting and ending point match) into an anterior mesoscutum and posterior axilla and mesoscutellum. The lateral surface of the mesothorax is the **mesopleuron**, which is differentiated into an anterior **mesepisternum** and posterior **mesepimeron**. The mesothorax has a pair of **fore wings** and a pair of **middle legs**.

Metathorax (Figs. A3.1, A3.3). The metathorax is the posterior segment of the thorax. The dorsal sclerite of the metathorax, the **metanotum**, bears a pad, the **cenchrus**, anterolaterally (Fig. A3.3). The lateral surface of the metathorax, the **metepisternum** and **metepimeron**, are not referred to in this work except for color patterns. The metathorax has a pair of **hind wings**, and a pair of **hind legs**.

Wings. The characteristic wing cells and veins of the fore and hind wings are illustrated in Figs. A3.29 & A3.30. One of the most striking features of Siricidae is what appears to be incredible variation in wing venation, including the appearance or the disappearance of veins symmetrically or asymmetrically on either wing. Such variation is very rarely seen in other Hymenoptera, a group where wing veins are important for classification. Habitus images in Schiff *et al.* (2006) provide many examples of variation in siricid wing venation and although this was not their intended goal, it is easy to observe the venation anomalies among the nicely spread specimens.

Some veins of Siricidae are considered as part of the ground plan of the Hymenoptera such as the basal portion of vein 2A and the presence of fore wing vein cu1. The tendency for veins to appear or disappear in Siricidae might suggest atavisms, i.e., reactivation of long lost character states or a reversal to an ancestral state but we are more tempted to view the feature as newly created within the Siricidae. For example, we have seen specimens with a partial cross vein found basal to vein cu1, for which there is no equivalent in other Hymenoptera. Despite the exceptional variation in veins of Siricidae, we have used wing venation in keys to subfamily and genera. However, where possible we supplement these wing characters with others features not associated with wings.

Legs (Figs. A31 and A3.2). Each leg consists of five sections, the **coxa**, **trochanter**, **femur**, **tibia** and **tarsus**. This last section, the tarsus, consists of five tarsomeres that are numbered consecutively from the tibia. The prefixes "pro", "meso" or "meta" are used to indicate to which thoracic segment each leg belongs (see hind leg in Fig. A3.2). The tarsal pads (pulvillus/pulvilli), also known as plantulae (Schulmeister 2003), are membranous surfaces ventrally on tarsomeres 1–4 (Figs. A3.27 & A3.28) that are white and convex, and extend very slightly anterior to the apical margin of the tarsomeres (Schulmeister, 2003). In some species, the tarsal pads are relatively short (Fig. A3.28). The tarsal pads can best be observed on metatarsomere 2 because the tarsi of the fore and middle legs are often folded close to the body and the tarsal pads are then hidden. Observation of the tarsal pads is important for identification and is usually easy unless the specimen is covered with oil. A fine paint brush moistened with 95% ethanol can be used to help remove oil.

The abdomen consists of several segments that are numbered consecutively following the thorax. Tergum 1 (first abdominal tergum, Fig. A3.3) has a deep longitudinal cleft medially, it is not fused to the metapleuron laterally and although it is fused dorsally to the thorax it is separated from it by a deep furrow along its anterior edge. Structure of the abdomen of males and females otherwise differs and for this reason they are discussed separately below.

Female abdomen. The female abdomen has ten terga (singular: **tergum**) dorsally and seven sterna (singular: **sternum**) ventrally (Fig. A3.7), of which terga 8–10 are conspicuously modified. Tergum 8 is greatly enlarged and is extended posteriorly. Tergum 9 is the largest tergum and has a deeply impressed dorsomedian impression, the **median basin** (Fig. A3.3), also known as the precornal basin. The lateral edges of the median basin are sharply outlined only near its base to almost to the posterior edge of tergum 9 (Fig. A3.12). The anterior edge of the basin, when visible, is ridge-like and its lateral limits are outlined by two slightly convergent furrows. The maximum width of the basin at its base is measured between the outer furrows, which are usually outlined in black. The posterior edge of the basin is a furrow between terga 9 and 10, which is often interrupted medially in specimens of *Sirex*. Tergum 10 is modified as a sharp horn-like projection, the **cornus**. The cornus varies in shape, but its apex forms a short tube (Fig. A3.9) that probably assists adult movement in their larval host

tunnels.

The abdomen posterior to sternum 7 has an **ovipositor** that is covered by two **sheaths** when not in use. Each sheath consists of three parts: a basal small sclerite dorsobasally (valvifer 1), a long basoventral sclerite (valvifer 2), and an apical sclerite (valvula 3). In this work only the last two sclerites are referred to, as **basal section** and **apical section** of the sheath (Fig. A3.26). The length of these two sections is compared to one another and to the fore wing length.

The ovipositor consists of a fused pair of dorsal **lances** (valvula 2) and a pair of ventral **lancets** (valvula 1) (Figs. A3.16 & A3.17). The lance and lancet slide along each other and help move the egg along the ovipositor as well as drilling in wood and removing the resulting sawdust for egg deposition. The part described in this work is the lancet, which is divided in numerous sections that we called annuli. Lancet annuli usually are outlined by vertical to slanted ridges (Fig. A3.17). The annuli are usually present to the base of the lancet, but in some species several basal annuli are difficult to distinguish because each annulus is barely outlined dorsally near the lance. The number of annuli varies within species and between species. The apex of the lancet consists of four annuli each with a large tooth (Fig. A3.17). Some or all of the annuli, anterior these four apical annuli, have a pit adjacent to the line or ridge of the annulus (Fig. A3.17). The size of the pit varies from 0.1–0.7 times the length of the annulus (Figs. A3.18 – A3.21), but regardless of whether small or large the pits may gradually become markedly smaller anteriorly or even disappear suddenly or gradually toward the base. The pits may also be wide to narrow, from 2.5–1.0 times as long as high (Figs. A3.18 to A3.21). To photograph the lancet for the best range of tonalities, we oriented it toward the light. Therefore contrary to normal, we present images of the ovipositor in lateral view but with the lancet at the top rather than at the bottom of the image. This view is most similar to what will be seen by users when viewing a female abdomen in lateral view with the ventral surface facing away from the user (toward the top of the page in most of our images).

Male abdomen. The male abdomen has eight terga dorsally and nine sterna ventrally (Fig. A3.8). Tergum 8 is slightly longer than the preceding segments. The posterior edge of sternum 8 is narrowly or widely concave and sternum 9 is extended posteriorly as a horn or cornus. The lateral portion of the genitalia (the harpes) is usually visible between tergum 8 and sternum 9, but this was not studied here.

In addition to structural terms for body parts, some terms designate surface features, such as ridges (plural carinae, singular carina), furrows (plural sulci, singular sulcus), pits (punctures) and microsculpture. The meaning of ridges and furrows are clear but pits and microsculpture require more discussion.

Pits are concave impressions consisting of multiple cells. Each pit is usually associated with a sensory cell, which in most pits of Siricidae is a seta or seta-like mechanoreceptor. We use the word "pit" rather than the more common expression "puncture" because it refers to a concave impression not a hole through the cuticle. Pit sizes are compared to the maximum diameter of a lateral ocellus (e.g., for a small pit, the diameter may be 0.1 times the diameter of a lateral ocellus whereas for a large pit it may be 0.5 times the lateral ocellus diameter), and the density is expressed as the number of typical pit diameters between pits (Figs. A3.22 & A3.23). Pits in Siricidae are usually simple concave and round impressions, but those on the mesoscutum and mesoscutellum may be very dense and polygonal with their edges becoming ridges of various heights so as to look like irregular craters or a fish net (Fig. A3.24). An unusual type of pit in Siricidae is the "pegged pit", which is found on at least the ventral surface of most flagellomeres (Fig. A3.25). Each pegged pit has a sensory cell.

Microsculpture consists of small cellular imprints on the cuticle within which there is no sensory cell. Typical microsculpture of insects is roughly hexagonal. The edge of a cellular imprint is almost always outlined by sharp furrows that forms a net- or mesh-like pattern resembling a fishing net. The surface area delimited by the furrows or meshes is called a "sculpticell" (Allen and Ball, 1980). A sculpticell surface may be flat, concave or pit-like (Fig. A3.13), convex, scale-like (i.e., surface is raised along the posterior or apical edge) (Fig. A3.14), or even seta-like. Each sculpticell is normally completely outlined by meshes but sometimes one or more sculpticells can be fused (Fig. A3.15). Sculpticells can also be stretched laterally (e.g., transverse meshes may be 2–4 times as wide as long), or longitudinally (an uncommon feature).

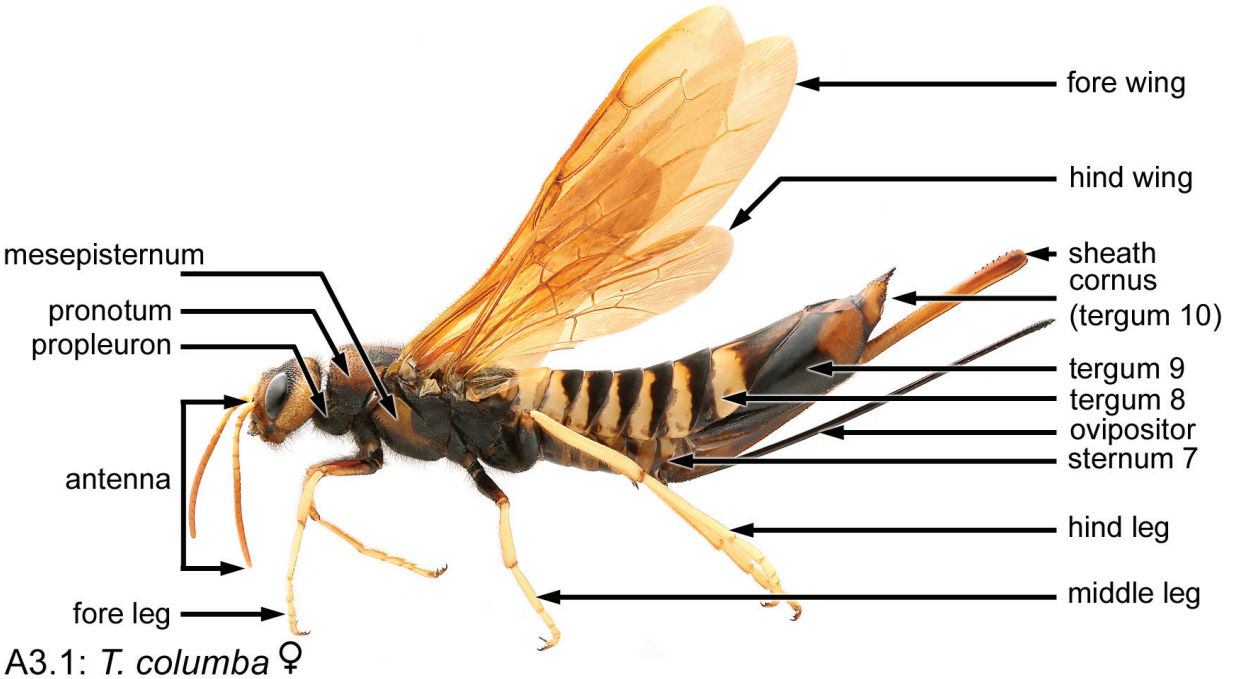
Microsculpture is best observed at magnifications above 50 times under diffuse light. To reduce glare a translucent piece of plastic (e.g., tracing acetate) should be positioned between the light source and specimen about 20 mm from the specimen. A 13–watt daylight fluorescent light source also gives very good results.

Size is one variable that affects all structures of a specimen, but which normally is not analyzed or discussed in detail. Size range within well sampled siricid species is great. For example, both sexes of *S. noctilio* may range between 8 and 36 mm and similar size variation is true for many other species studied. One effect of body size is pit size. Because the taxonomically most significant pits are on the head, the size of pits is stated in relation to a nearby reference point, the diameter of a lateral ocellus. Pit density is also affected by specimen size,

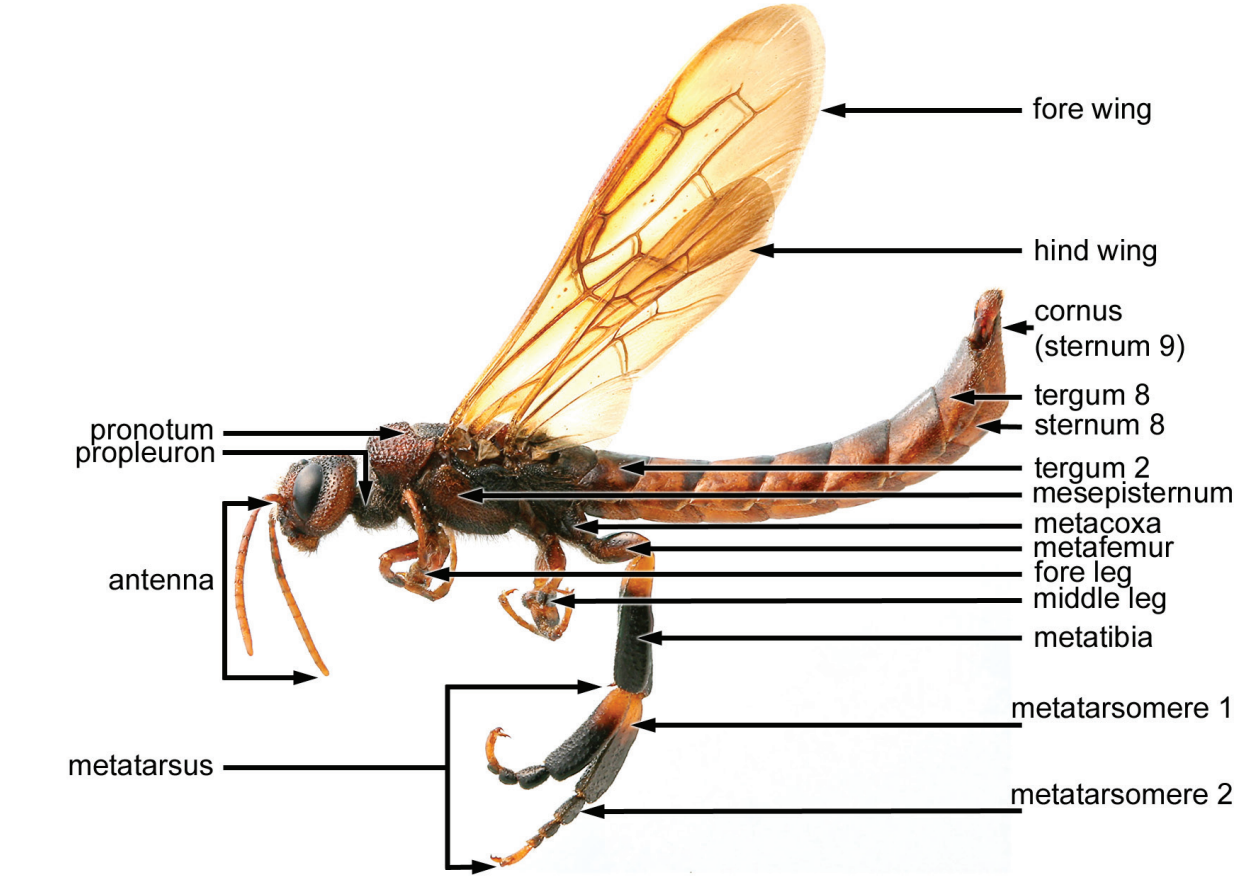
often being denser in larger than in smaller specimens of a species. Although the shape of the female cornus does not vary with size for most species (e.g., in *S. nigricornis*, it remains angular in lateral view for all sizes) in *S. californicus* the edge of the cornus is convex in the largest females, whereas it is straight in medium size females, and angular in small females.

Measurements. When possible, 30 specimens of each sex were measured. Means and standard deviations were calculated using Microsoft Excel software. The main measurements are the length of the basal and apical sections of the ovipositor sheath and the maximum length of the fore wing. Because a limited number of ovipositors were studied for each species, a range in the observed variation (e.g., for the ovipositor: relative size of pits at base and middle, relative height of pits, shape of pits, total number of annuli, annulus numbers between basal and apical sections of sheath, ridge development on apical pits and on ventral surface of lancet on annuli before the teeth annuli.). For a few species, distances between pits 1 and 2, 4 and 5, and 9 and 10 of the ovipositor relative to the ovipositor diameter (including lance and lancet) between these pairs of pits is given. Other measurements were recorded as required. Measurements considered useful are given in Tables 1–5 in the "Appendix 1: statistical data". Range of a measurement is given in the identification keys based on the calculation of two standard deviations. If a measurement falls within the overlap between values of the calculated two standard deviations, the character was rejected in favor of other characters, but if it is outside the range of the overlap portion, it is considered as a useful key character with a 1% chance of error.

Barcode information. For each specimen the following is recorded: country, year, state/province, specimen code, and number of base pairs.



A3.1: *T. columba* ♀



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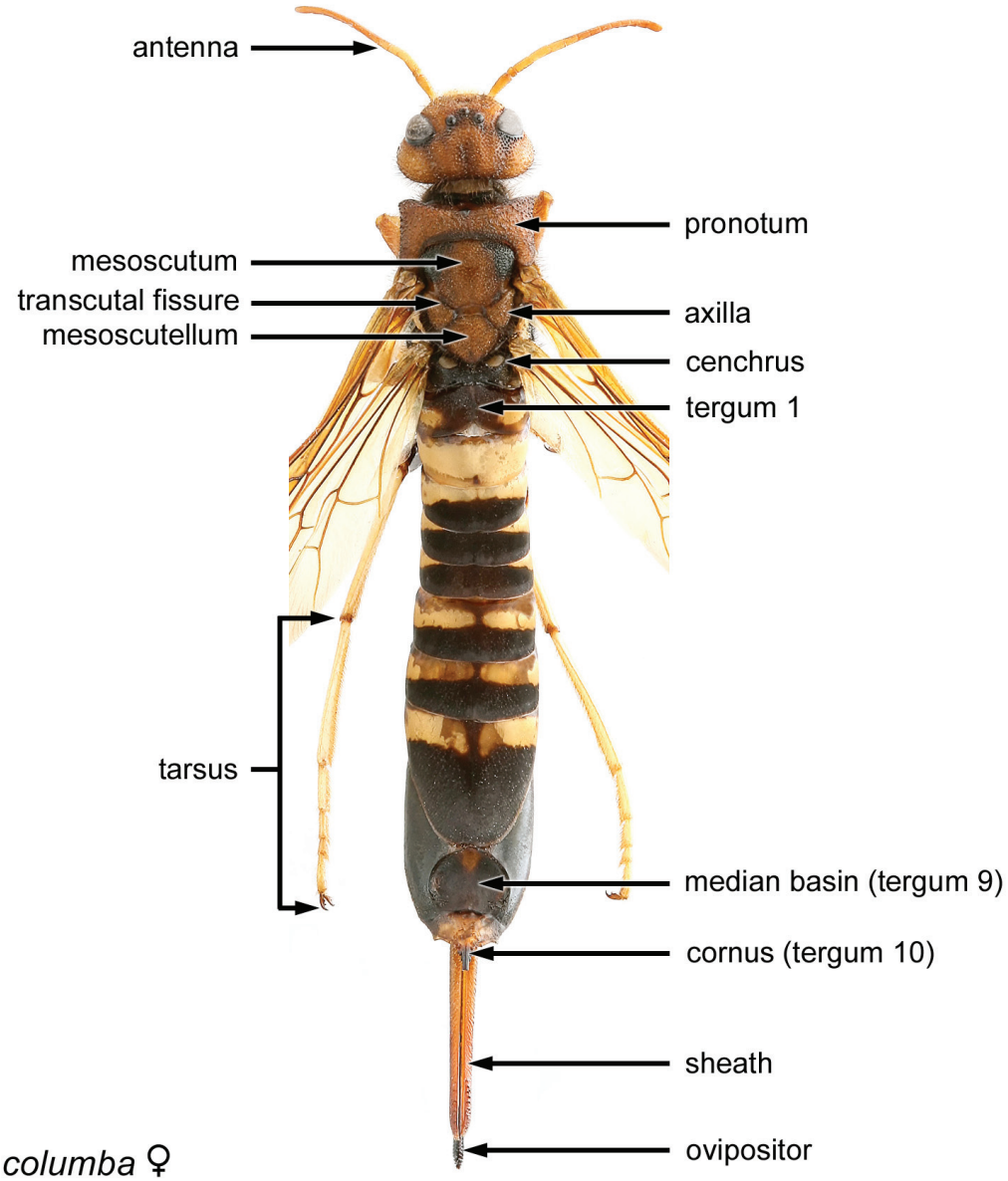

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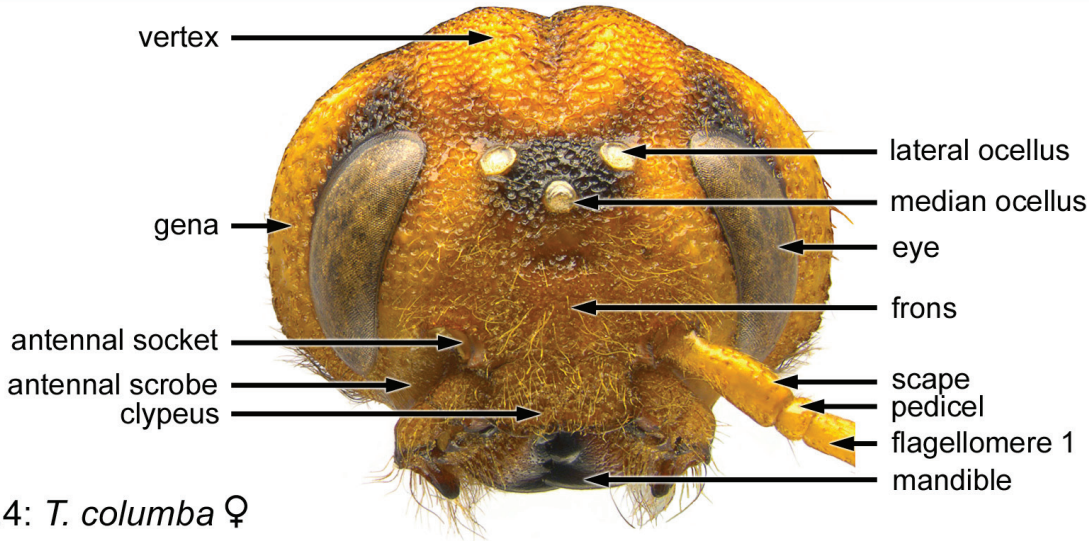

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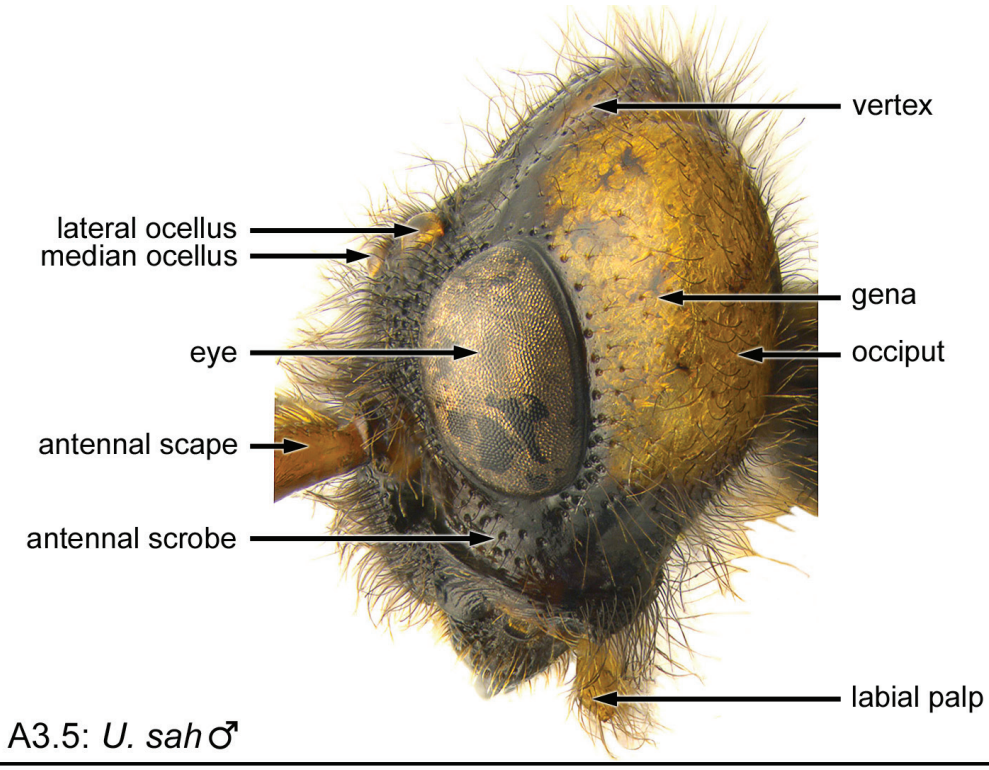
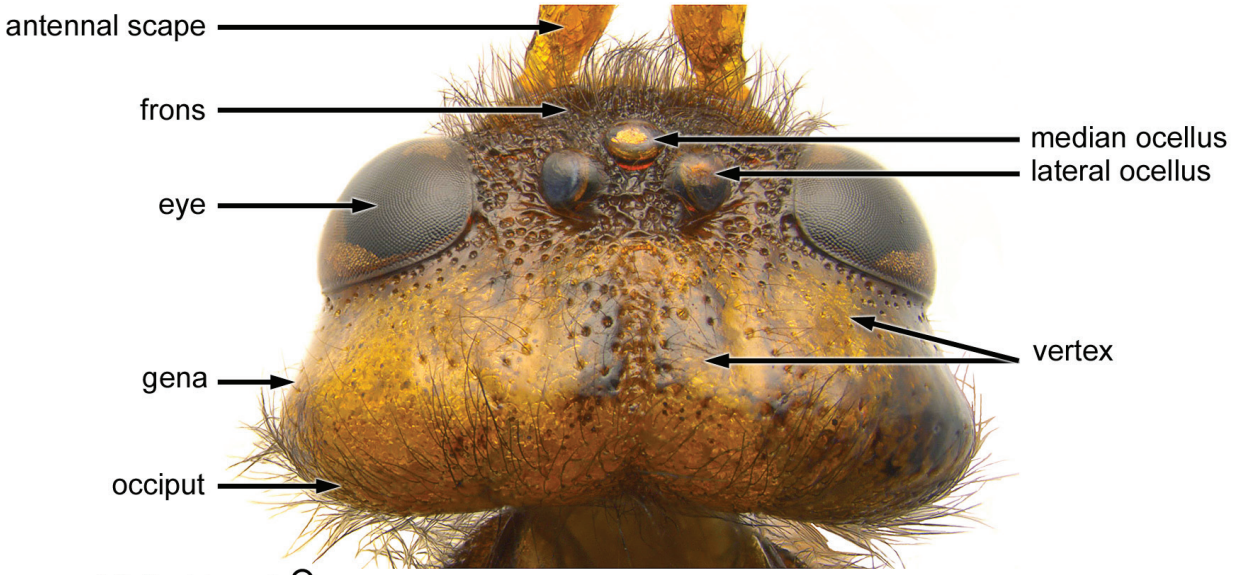
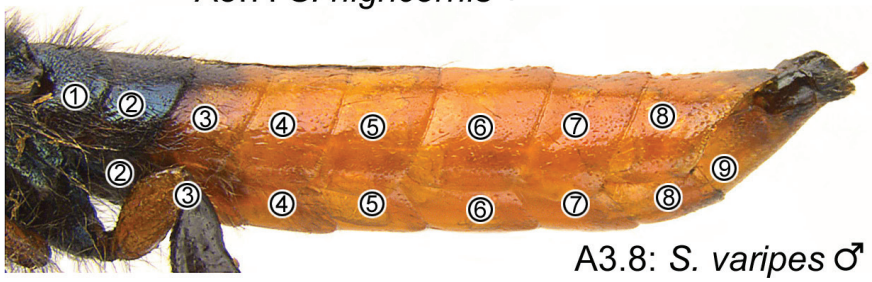


A3.5: *U. sah*♂

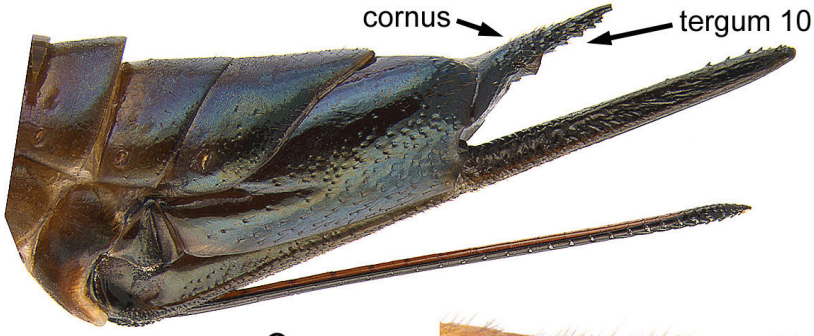


A3.6: *U. sah*♀

A3.7: *S. nigricornis* ♀

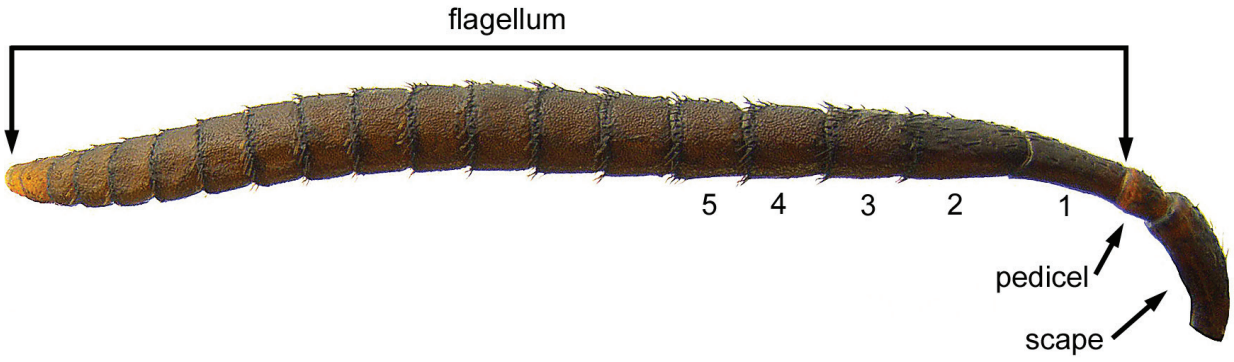


A3.8: *S. varipes* ♂

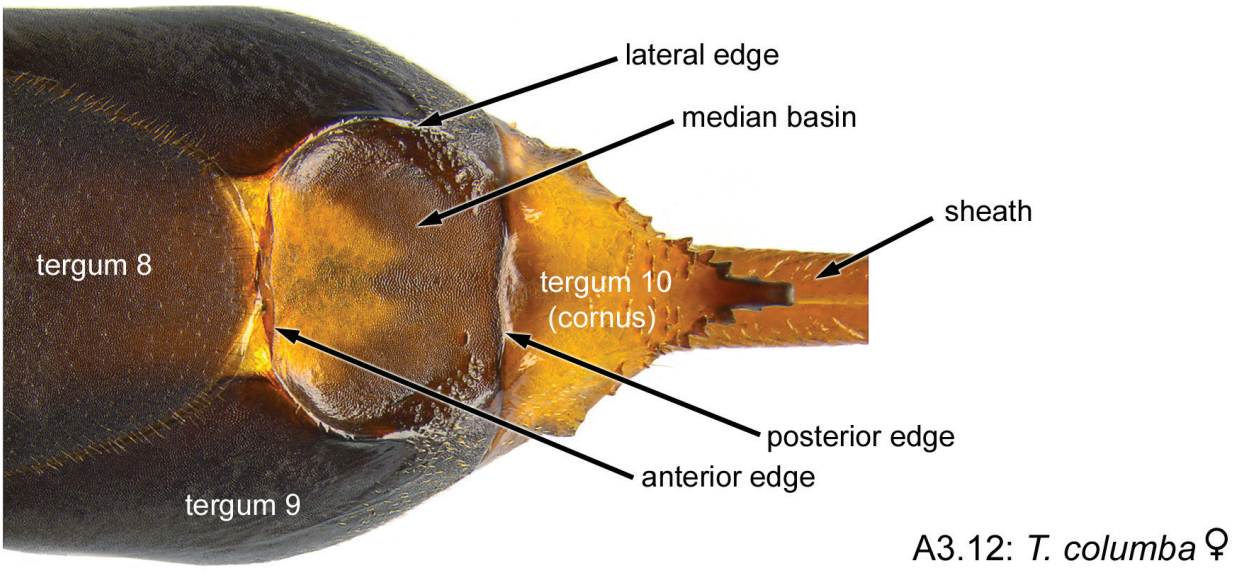


A3.9: *S. nitidus* ♀

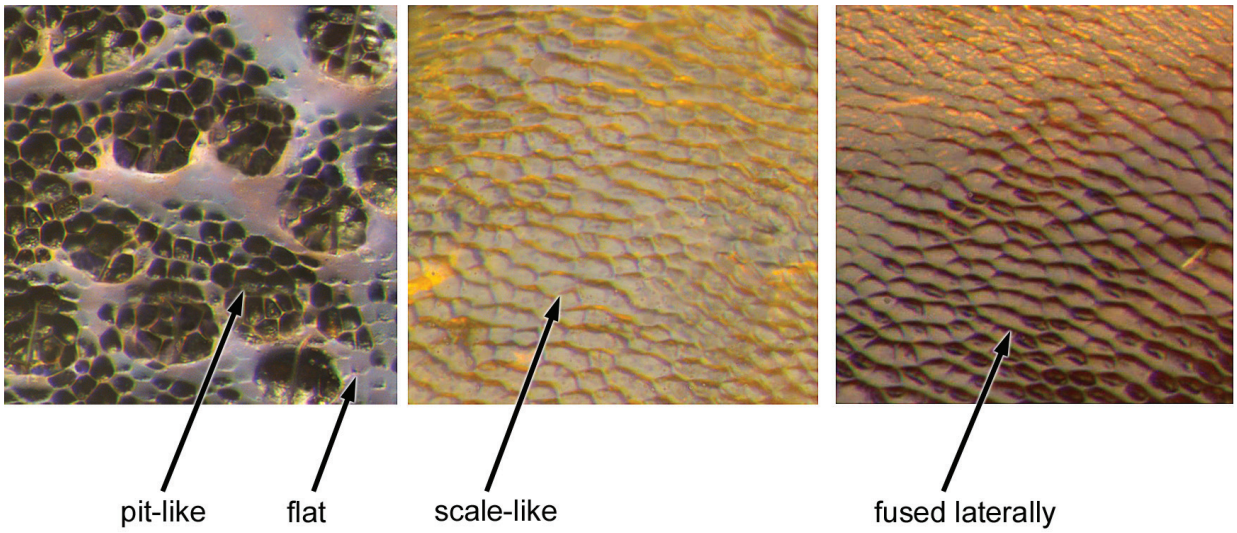
A3.10: *S. nitidus* ♂



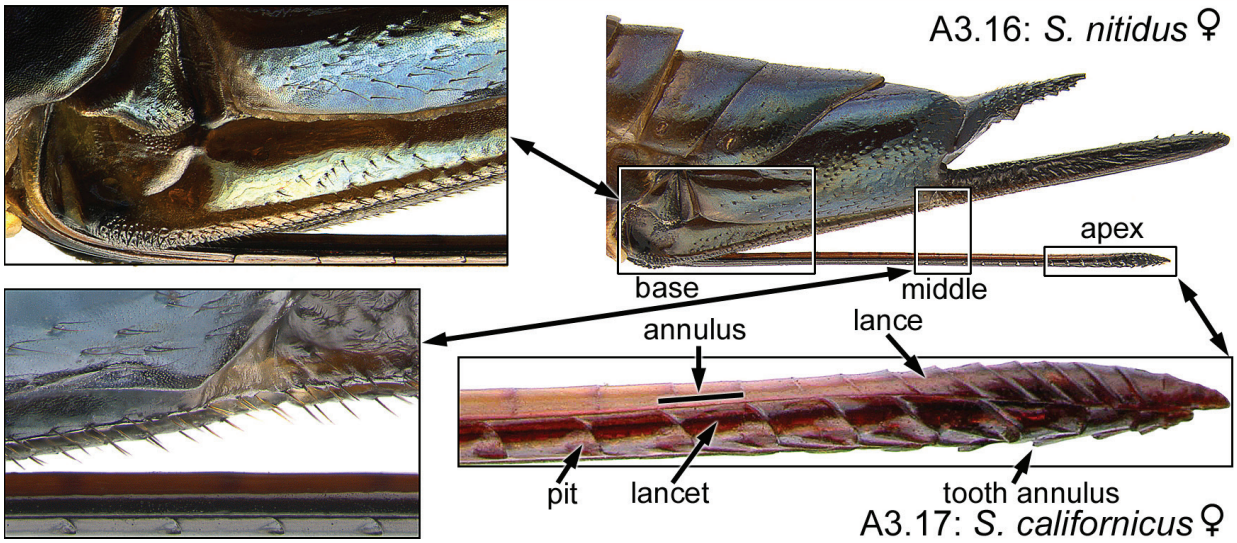
A3.11: *E. formosanus* ♀



A3.12: *T. columba* ♀

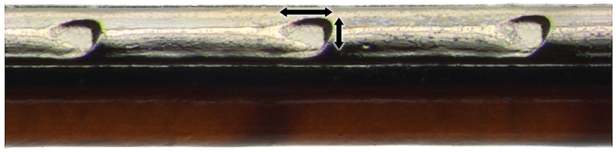


A3.13: *A. hyalinatus* ♀ A3.14: *U. cressoni* ♀ A3.15: *U. albicornis* ♀

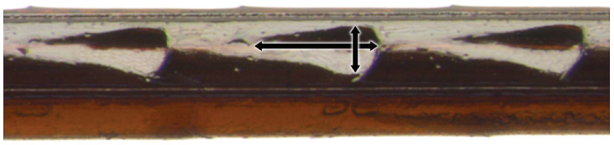


A3.16: *S. nitidus* ♀

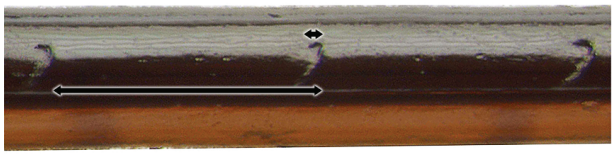
A3.17: *S. californicus* ♀



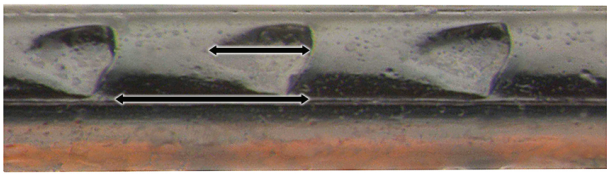
A3.18: *S. nitidus* ♀ small



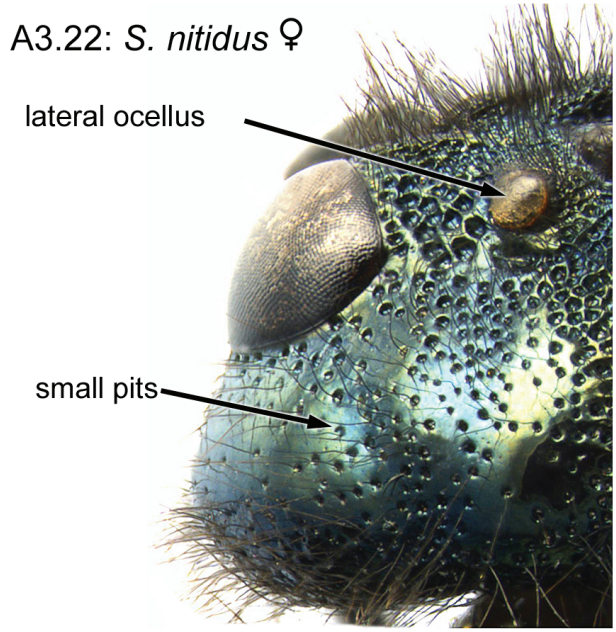
A3.19: *S. xerophilus* ♀ large



A3.20: *S. cyaneus* ♀ short

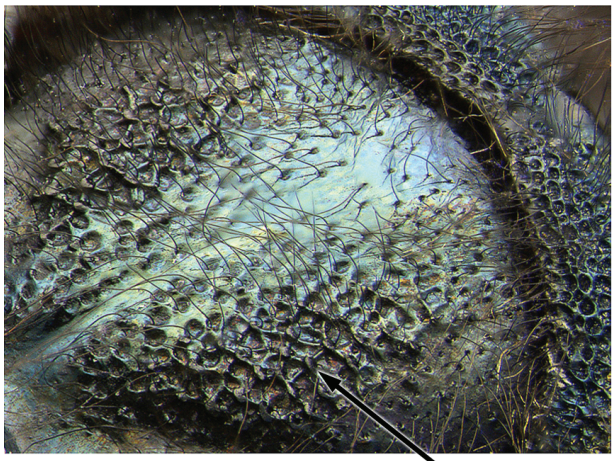


A3.21: *S. noctilio* ♀ long

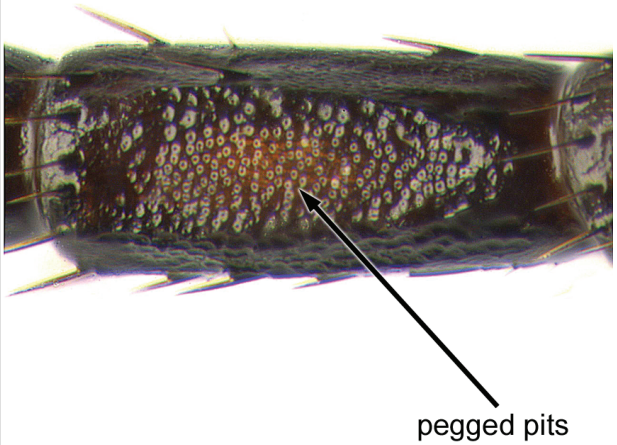


A3.22: *S. nitidus* ♀

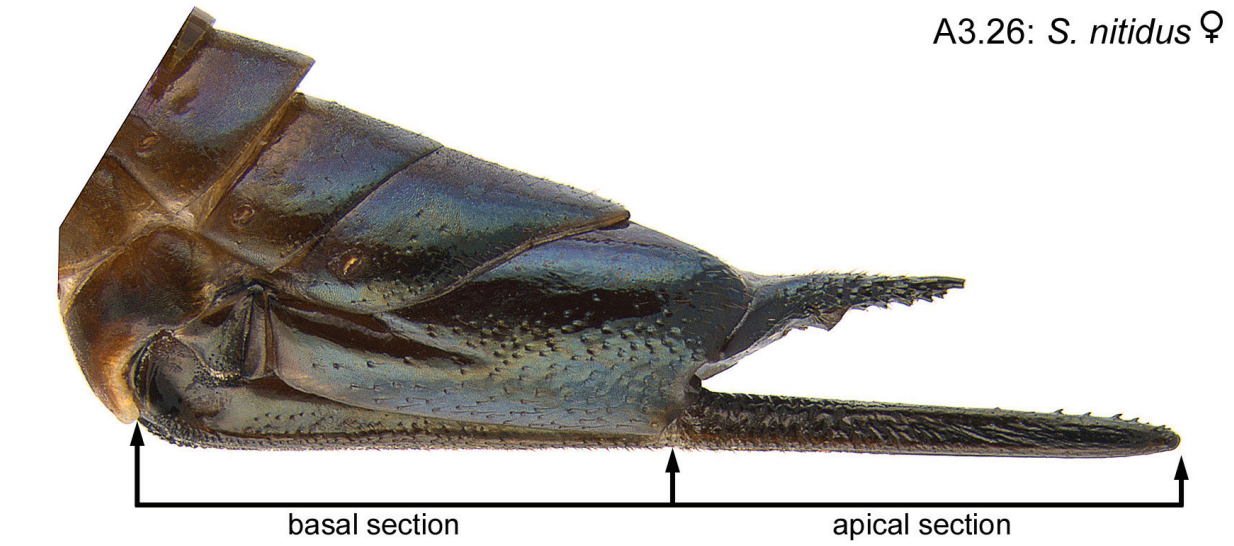
A3.23: *S. mexicanus* ♂

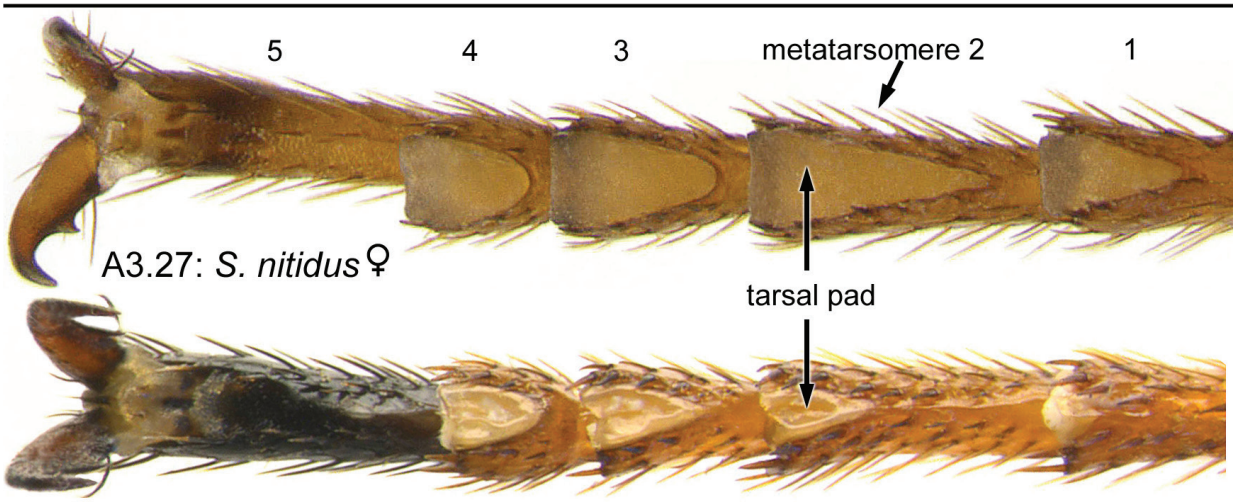


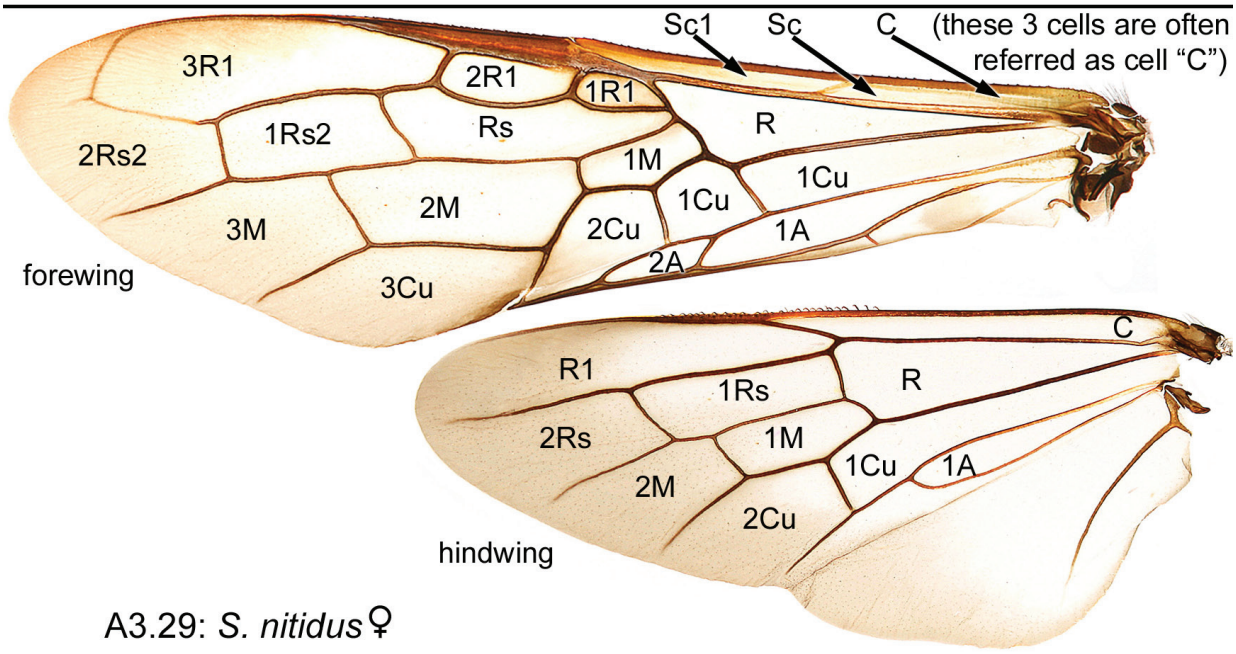
A3.24: *S. nitidus* ♀

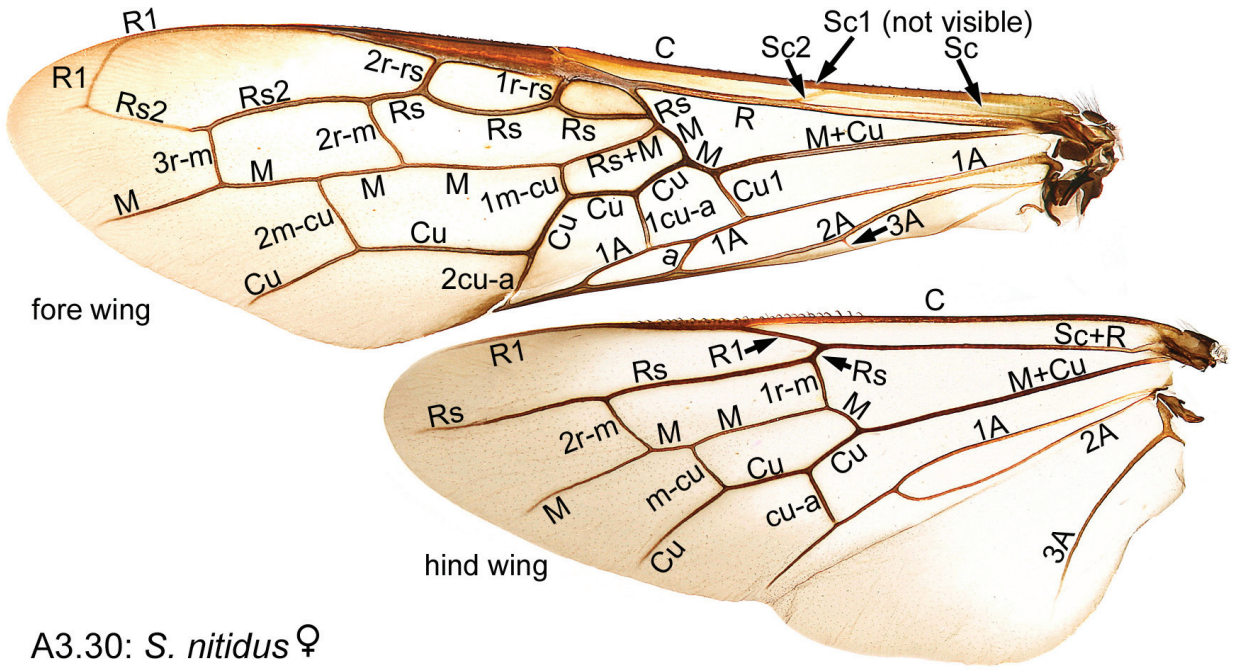


A3.25: *S. cyaneus* ♀


A3.26: *S. nitidus* ♀
basal section
apical section


5
4
3
metatarsomere 2
1
A3.27: *S. nitidus* ♀
tarsal pad
A3.28: *S. noctilio* ♀


Sc1
Sc
C
(these 3 cells are often referred as cell "C")
3R1
2R1
1R1
R
Rs
1Rs2
2Rs2
1M
1Cu
1Cu
2M
3M
2Cu
1A
2A
3Cu
forewing
C
R1
1Rs
R
2Rs
1M
1Cu
1A
2M
2Cu
hindwing
A3.29: *S. nitidus* ♀



A3.30: *S. nitidus* ♀

4. Biology

Our knowledge of the biology of Siricidae is uneven. We know very little about most genera and species except for *Sirex noctilio*, which, as the major pest of pines in the Southern Hemisphere, was the focus of an intense and successful classical biological control program in the 1960s, 70s and 80s (Haugen and Underdown 1990, Haugen *et al.* 1990). Much of what we know about the biology of *S. noctilio* has been summarized in review papers by Morgan (1968) and Talbot (1977) and most recently in several chapters of the book *The Sirex Woodwasp and its Fungal Symbiont* (Slippers *et al.* 2011). We do not attempt to match the details of these works here but instead present a generalized version of siricid biology, leaning heavily on our knowledge of *S. noctilio*. Although we use it as our model species, it is important to recognize that *S. noctilio* differs fundamentally from most other species in that, where it is adventive, it attacks and kills stressed but relatively healthy trees. In its native range, like most other siricids, it is relatively benign.

The central paradigm of siricid woodwasp biology is that they live in symbiotic relationships with basidiomycete wood decay fungi (Buchner 1928, Cartwright 1929, 1938, Clark 1933, Francke-Grossman 1939, Stillwell 1960, 1962, 1964, 1965, 1966, 1967 and Gaut 1969, 1970, Slippers *et al.* 2003, among others). Female woodwasps carry fungal arthrospores, oidia or hyphal fragments in paired abdominal glands (intersegmental pouches) called mycangia and inoculate their tree host with fungus at oviposition. The fungus grows through the tree and larvae feed on the fungus as they bore through the wood. This relationship is mutualistic and obligate as far as we know for all genera and species except the genus *Xeris*. Adult females of *Xeris* species have significantly reduced glands that do not contain a wood decay fungus. They oviposit exclusively into trees that have already been attacked by another genus of woodwasp and infested with an appropriate wood decay fungus (Franke-Grossman 1939, Stillwell 1966, Spradberry 1976, Fukuda and Hijii 1997).

Early literature attempting to associate siricid species with specific symbionts was confusing because it was difficult to identify the fungi using classical methods and the Siricidae were in need of revision (Morgan 1968, Talbot 1977). With the development of molecular identification methods and taxonomic revisions, associating each siricid woodwasp with its specific symbiont has become less problematic. To date, four species of basidiomycete wood decay fungi are associated with Siricidae. *Tremex columba* (Stillwell 1964), *T. fuscicornis* in Poland (Pažoutova and Šrůtka 2007), *T. longicollis* in Japan (Tabata and Abe 1995), and *Eriotremex formosanus* (Schiff unpublished data from North America) use *Cerrena unicolor* whereas *Sirex noctilio, S. nitobei* from Asia and *S. juvencus* from Europe use *Amylostereum areolatum* (Gaut 1969, 1970); *Urocerus japonicus* and *U. antennatus* both from Japan use *Amylostereum laevigatum* (Tabata and Abe 1997, 1999) and all other siricids examined (including *Sirex cyaneus*, *S. imperialis S. areolatus, S. californicus,*

S. nigricornis, S. varipes, Urocerus californicus, U. flavicornis, U. gigas, U. augur and U. sah (Stillwell 1966, Gaut 1970, Schiff unpublished data) use *Amylostereum chailletii*. Although woodwasp/fungus specificity is generally accepted, a recent exception was the isolation of *Amylostereum areolatum* from two specimens of *Sirex nigricornis* (formerly *edwardsii*) that were reared from logs also infested with *S. noctilio*. Presumably, the *S. nigricornis* acquired *A. areolatum* when they fed on parts of the tree already infested by the symbiont from *S. noctilio* (Nielsen *et al.* 2009).

In the *Sirex noctilio /Pinus radiata* association, the symbiotic fungus has two basic functions; it provides food for developing woodwasp larvae and, in conjunction with phytotoxic mucus, it kills the tree, rendering it more suitable for fungal growth. Like most wood boring insects, siricids do not make the complex of cellulases necessary to digest wood and must either obtain them from symbionts or eat something that digests cellulose for them (Chapman1982), in this case the symbiont itself (mycophagy). Indirect evidence suggests they do both. *Sirex cyaneus* larvae have been observed to live and grow for three months on pure culture of their symbiont (Cartwright 1929) and Kukor and Martin (1983) demonstrated that *S. cyaneus* acquired digestive enzymes from its fungal symbiont, *Amylostereum chailletii.* Fungal mediated nutrition is very important to *Sirex noctilio* and fungal growth is positively correlated with adult size and thus fecundity, and dispersal ability (Madden 1981).

The ability to kill the host tree with fungus and mucus distinguishes *Sirex noctilio* from most other siricids and is the reason why *S. noctilio* is a major pest of some hosts whereas most other woodwasps are not. Oviposition behavior of *S. noctilio* has been well studied. Females drill into stressed trees and depending on the tree's response either deposit eggs followed by a dose of fungus and mucus in a separate shaft (Coutts and Dolezal 1969, Madden 1981), or they deposit only the fungus and mucus. In the latter case, injecting only fungus and mucus is adaptive because the tree is rendered more suitable for future oviposition. There are generic level differences in drilling behavior. *Sirex* species make from 1–4 drills per insertion of the ovipositor through the bark, only some of which contain eggs and/or fungus; *Urocerus* species make a single long drill with many eggs alternating with masses of fungus; *Xeris* species make from 1–5 long drills per insertion with a few eggs in each drill but no fungus (Spradbery 1977) and *Tremex columba* either leaves unfertilized eggs in the adult female emergence tunnel or up to 7 presumably fertilized eggs in each oviposition tunnel (Stillwell 1967). Siricids like other Hymenoptera are haplodiploid with unfertilized eggs becoming males and fertilized eggs developing into females. It is important to note that neither fungus nor mucus alone kills the tree — only in combination are they toxic (Coutts 1969a and b). The mucus, produced by glands in the female abdomen and stored in a median reservoir, weakens the tree's immune response allowing the phytotoxic fungus to kill the tree. Woodwasps other than *Sirex noctilio* all have mycangia and mucus reservoirs but their function has not been well studied. Spradberry (1973) determined the effects of various combinations of mucus and fungus from three genera of woodwasps, *Sirex, Urocerus* and *Xeris*, on live trees or fresh branches of several coniferous hosts and found that *Amylostereum areolatum* and the mucus from *Sirex noctilio* on *Pinus radiata* was the most phytotoxic combination. This explains why *S. noctilio* has been such a great pest of *P. radiata* plantations in the Southern Hemisphere but does not explain the presence of mucus glands in non toxic species. Presumably, in other woodwasps the mucus helps condition the tree in a more subtle way to improve growth of the fungus. Recently, *Tremex fuscicornis,* adventive in Chile, has been reported to kill weakened hardwoods and even vigorous *Acer negundo* and *Populus* sp. (Baldini 2002, Ciesla 2003). Presumably, the combination of fungus and mucus from *Tremex fuscicornis* can kill selected hardwoods just as *Sirex noctilio* kills some pines. Perhaps comprehensive studies of the effects of fungus and mucus from different siricid species on a wide variety of exotic hosts may predict which species will become pests in adventive situations.

Adult behavior of Siricidae is poorly known except for *Sirex noctilio*. In general, males emerge from the tree earlier than females and fly to the tops of trees to form swarms (Madden 1982, Schiff unpublished data). Individual females are mated when they fly into the swarm; they then proceed to oviposit in weakened trees. Studies of *S. noctilio* indicate that females select the height of oviposition sites based on moisture content (Coutts and Dolezal 1965) and localized turgor pressure within the host (Madden 1968, 1981). Western North American *Sirex* and *Urocerus* species have been observed ovipositing in the base of burned trees where presumably the turgor pressure and moisture content are appropriate (Schiff unpublished data). At least in *Sirex noctilio* (Madden 1981), and presumably in other species, there is selection for host condition that is most favorable for growth of the fungal symbiont.

The life cycle of siricid woodwasps is quite varied. Some species develop in a single year others may take 2–3 years (Stillwell 1966, 1967) and some like *Sirex noctilio* and *Tremex columba* can rush part of the population through in less than one year while other individuals take a full year or more. Depending on the availability and quality of the fungus, there are from 6–12 larval instars (Stillwell 1928, 1967, Madden 1981) that can mine 5–20 cm for *Sirex* and *Urocerus* spp. and up to 3 m for *Tremex*

columba up and down in the trunk of the host (Solomon 1995). Larvae are cylindrical and have a characteristic "S" shape with a cornus (spike) on the last segment. The cornus is thought to help the larvae pack the frass in the tunnel. When the larvae finish feeding they turn sharply to the outside of the tree leaving a characteristic "J" shaped end of the mine. As the exit mines are perpendicular to the surface of the tree, emergence holes are perfectly round. Female woodwasp larvae have paired hypopleural organs in the fold between the first and second abdominal segments (Parkin 1941, 1942, Stillwell 1965). These organs are believed to be involved with transfer of the symbiont to the adult (see Morgan 1968 and Talbot 1977 for discussion).

Most of our knowledge of the natural enemies of siricids comes from efforts to control *Sirex noctilio* in Australia. The primary effort was to search for natural enemies that controlled siricids in their native lands and determine if they could be used to control populations of *S. noctilio* adventive in Australia. Starting in the early 1960s a massive effort was made to search for and rear parasitic wasps (parasitoids of each siricid species are listed in a separate section of this publication). Many species were collected, reared, released and became established in Australia (Kirk 1974 and 1975, Spradberry and Kirk 1978, Taylor 1967a and 1967b, and others) but the parasitoid wasp complex (including ichneumonids, ibaliids and stephanids) seldom killed more than 40% of the *Sirex noctilio* population and was not effective in preventing population outbreaks (Haugen *et al.* 1990). However, in 1962 nematode parasites were discovered in *S. noctilio* in New Zealand (Zondag 1962) and their biology was described a few years later (Bedding 1967, modified in 1972). The biology of the nematodes is intimately entwined with the biology of siricids and their fungal symbionts and is summarized briefly here. The nematode *Beddingia (Deladenus) siricidicola* has two alternate life cycles each with a different female morphology. The two forms, one mycetophagous and the other parasitic on siricids, are morphologically distinct and were originally thought to be representatives of two different nematode families, Neotylenchidae and Allantonematidae, respectively. The mycetophagous form feeds on fungal mycelium and will feed continuously for many generations as long as the fungus quality is maintained. If environmental conditions change or the nematode encounters a siricid larva, the alternate cycle begins. Juvenile nematodes develop into the alternate (parasitic) morphology and penetrate the cuticle of the siricid larva leaving a small dark mark at the entry site. In the haemocoel of the siricid larva, the nematode increases greatly in size, waiting to reproduce ovoviviparously when the woodwasp pupates. At the end of pupation juvenile nematodes emerge from their mother and migrate to the gonads of the adult woodwasp where they begin to feed on the eggs in the female or the testes in the male, respectively. The nematodes do not appear to affect the development or behavior of the adult wasp and when the female woodwasp emerges from the host she mates and oviposits in new trees. However, instead of depositing a new generation of woodwasps she deposits eggs filled with parasitic nematodes. As many woodwasps often oviposit into a single tree, the nematodes are quickly spread through the population, effecting control in as little as three years (Haugen and Underdown 1990). Male woodwasps infested with nematodes mate but do not transfer nematodes to females and are thus a dead end for the nematode. The use of nematodes to control woodwasps has been improved by development of techniques to handle nematodes and by selection of optimal strains (Bedding and Akhurst 1974, Bedding and Iede 2005, Bedding 2009). Seven species of nematodes parasitic on 31 host species (siricids or their parasitoids) have been described from around the world (Bedding and Akhurst 1978) and there are more awaiting description (Bedding, personal communication, Schiff, unpublished data). They can be divided into three groups based on their fungal associations. The mycetophagous form of *Beddingia siricidicola* feeds only on *Amylostereum areolatum*. The mycetophagous form of *Beddingia rudyi*, *B. imperialis*, *B. nevexii*, *B. canii*, *B. proximus* and an undescribed species feed only on *Amylostereum chailletii* and the mycetophagous form of *Beddingia wilsoni* feeds on both. Even though they do not carry a fungal symbiont of their own, *Xeris* species, like many of the wasps parasitic on siricids, can be parasitized by *Beddingia* species (Bedding and Ackhurst 1978, see table 2). This information is presented in a table in Bedding and Akhurst (1978) with the siricid hosts. Taxonomic revisions of the Siricidae and easier methods to identify fungal symbionts may change this information slightly; for example, *Urocerus japonicus* and *U. antennatus* are listed as using *Amylostereum chailletii* instead of *A. laevigatum* as their symbiont.

Although they cannot be easily manipulated to target a particular infestation, birds are also natural enemies of both adult and larval siricids. In Tasmania, the dusky wood swallow, the forest raven, and the spine-tailed swift, attacked mating swarms of *Sirex noctilio* in the tops of trees to such an extent that they altered sex ratios in the next year's population (Madden 1982), and Spradberry (1990) found an overall larval predation rate of 28.8% by woodpeckers in a European study.

Hosts

Hosts of New World species of Siricidae are summarized from Cameron (1965), Middlekauff (1960), Ries (1951), Smith (1979) and specimens studied in collections. In the list below we have rearing records of New World Siricidae from 13 plant families and 76 plant species. The host cited is the plant on which the larvae actually fed or the female was found ovipositing, plant species on which adults were found resting are not included. For accidentally introduced siricid species, we consider only host plant records with plant species native or introduced to North America, and host plant genus records from the Palaearctic found also in North America as native or ornamental plant genera. In the "Hosts" section under each species of siricid species treated, we list the plant species attacked and, when possible, we add in parenthesis the number of specimens we have recorded from a given host. We also include published records if we are confident about the accuracy of the published siricid name.

HOST SPECIES	SIRICID SPECIES	COMMENTS
CUPRESSACEAE		
Chamaecyparis sp.	*Urocerus gigas* (Linnaeus)	Introduced into Argentina, Brazil, Chile
Cupressus macrocarpa	*Sirex areolatus* (Cresson)	
	Sirex behrensii (Cresson)	
	Sirex californicus (Ashmead)	
	Xeris tarsalis (Cresson)	
Juniperus occidentalis	*Sirex areolatus* (Cresson)	
	Xeris tarsalis (Cresson)	
Juniperus scopulorum	*Sirex areolatus* (Cresson)	
Calocedrus decurrens	*Sirex areolatus* (Cresson)	
	Urocerus californicus Norton	
	Xeris indecisus (MacGillivray)	
	Xeris tarsalis (Cresson)	
Sequoia sempervirens	*Sirex areolatus* (Cresson)	
Thuja sp.	*Sirex areolatus* (Cresson)	
Thuja occidentalis	*Urocerus flavicornis* (Fabricius)	
Thuja plicata	*Sirex nitidus* (T. W. Harris)	Suspect or rare occurrence
	Urocerus albicornis (Fabricius)	
	Xeris tarsalis (Cresson)	
Taxodium distichum	*Sirex areolatus* (Cresson)	
	Urocerus taxodii (Ashmead)	
PINACEAE		
Abies sp.	*Sirex cyaneus* Fabricius	
	Sirex longicauda Middlekauff	
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Urocerus sah (Mocsáry)	Introduced into eastern North America
	Xeris indecisus (MacGillivray)	
Abies amabilis	*Sirex abietinus* Goulet, n. sp.	
	Sirex varipes Walker	
	Urocerus albicornis (Fabricius)	
Abies balsamea	*Sirex cyaneus* Fabricius	
	Sirex longicauda Middlekauff	
	Sirex nitidus (T. W. Harris)	Rare occurrence
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus cressoni Norton	
	Xeris caudatus (Cresson)	
	Xeris melancholicus (Westwood)	

HOST SPECIES	SIRICID SPECIES	COMMENTS
Abies concolor	*Sirex longicauda* Middlekauff	
	Sirex abietinus Goulet, n. sp.	
	Urocerus californicus Norton	
	Urocerus flavicornis Fabricius	
	Xeris caudatus (Cresson)	
	Xeris indecisus (MacGillivray)	
	Xeris morrisoni (Cresson)	
Abies fraseri	*Sirex cyaneus* Fabricius	
	Urocerus albicornis (Fabricius)	
	Urocerus cressoni Norton	
Abies grandis	*Sirex cyaneus* Fabricius	Probably *Sirex abietinus* Goulet, n. sp.
	Xeris indecisus (MacGillivray)	
Abies lasiocarpa	*Sirex abietinus* Goulet, n. sp.	
	Sirex nitidus (T. W. Harris)	Rare occurrence
	Sirex varipes Walker	
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus flavicornis (Fabricius)	
	Xeris caudatus (Cresson)	
	Xeris indecisus (MacGillivray)	
Abies magnifica	*Sirex cyaneus* Fabricius	Probably *Sirex abietinus* Goulet, n. sp.
	Sirex longicauda Middlekauff	
	Sirex varipes Walker	
	Urocerus californicus Norton	
Abies nobilis	*Urocerus californicus* Norton	
Cedrus **sp**.	*Urocerus gigas* (Linnaeus)	Introduced into Argentina, Brazil, Chile
Larix **sp**.	*Sirex cyaneus* Fabricius	
	Sirex noctilio Fabricius	May be misidentified or rare occurrence
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
Larix laricina	*Sirex nitidus* (T. W. Harris)	
	Urocerus albicornis (Fabricius)	
Larix occidentalis	*Sirex californicus* (Ashmead)	
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus cressoni Norton	
	Urocerus flavicornis (Fabricius)	
	Xeris caudatus (Cresson)	
	Xeris indecisus (MacGillivray)	
Picea sp.	*Sirex nigricornis* Fabricius	Suspect or rare occurrence
	Sirex nitidus (T. W. Harris)	
	Sirex noctilio Fabricius	May be misidentified
	Urocerus cressoni Norton	
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Urocerus sah (Mocsáry)	Introduced into eastern North America
Picea abies	*Sirex juvencus* (Linnaeus)	Intercepted specimens, not established
	Sirex nigricornis Fabricius	
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Xeris indecisus (MacGillivray)	

HOST SPECIES	SIRICID SPECIES	COMMENTS
Picea engelmannii	*Sirex abietinus* Goulet, n. sp.	
	Sirex nitidus (T. W. Harris)	
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus flavicornis (Fabricius)	
	Xeris caudatus (Cresson)	
Picea glauca	*Sirex cyaneus* Fabricius	
	Sirex abietinus Goulet, n. sp.	
	Sirex nitidus (T. W. Harris)	
	Urocerus albicornis (Fabricius)	
	Urocerus flavicornis (Fabricius)	
	Xeris caudatus (Cresson)	
	Xeris melancholicus (Westwood)	
Picea mariana	*Sirex cyaneus* Fabricius	Occasional
	Sirex nitidus (T. W. Harris)	
	Urocerus albicornis (Fabricius)	
Picea pungens	*Xeris caudatus* (Cresson)	
	Xeris morrisoni (Cresson)	
Picea rubens	*Sirex nitidus* (T. W. Harris)	
Picea sitchensis	*Sirex abietinus*, Goulet, n. sp.	
	Sirex varipes Walker	May not been reared
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus cressoni Norton	
	Urocerus flavicornis (Fabricius)	Introduced into Argentina, Brazil, Chile
	Urocerus gigas (Linnaeus)	
	Xeris indecisus (MacGillivray)	
Pinus sp.	*Sirex longicauda* Middlekauff	
	Sirex nigricornis Fabricius	
	Sirex mexicanus Smith, n. sp.	Likely host
	Sirex obesus Bradley	
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Urocerus sah (Mocsáry)	Introduced into eastern North America
Pinus banksiana	*Sirex nigricornis* Fabricius	
	Urocerus albicornis (Fabricius)	
	Urocerus flavicornis (Fabricius)	
	Xeris melancholicus (Westwood)	
Pinus clausa	*Sirex nigricornis* Fabricius	
Pinus contorta	*Sirex areolatus* (Cresson)	
	Sirex californicus (Ashmead)	
	Sirex nitidus (T. W. Harris)	Unexpected occurrence
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus cressoni Norton	
	Urocerus flavicornis (Fabricius)	
	Xeris caudatus (Cresson)	
	Xeris indecisus (MacGillivray)	
Pinus coulteri	*Sirex californicus* (Ashmead)	

HOST SPECIES	SIRICID SPECIES	COMMENTS
Pinus echinata	*Sirex nigricornis* Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
Pinus elliottii	*Eriotremex formosanus* (Mat.)	Introduced in southeastern United States
	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
Pinus jeffreyi	*Sirex areolatus* (Cresson)	
	Sirex behrensii (Cresson)	
	Sirex californicus (Ashmead)	
Pinus lambertiana	*Sirex areolatus* (Cresson)	
	Sirex behrensii (Cresson)	
	Urocerus californicus Norton	
Pinus monticola	*Sirex californicus* (Ashmead)	
Pinus palustris	*Eriotremex formosanus* (Mat.)	Introduced into southeastern North America
	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
Pinus ponderosa	*Sirex behrensii* (Cresson)	
	Sirex californicus (Ashmead)	
	Sirex longicauda Middlekauff	
	Sirex xerophilus Schiff, n. sp.	
	Sirex obesus Bradley	
	Sirex varipes Walker	
	Urocerus californicus Norton	
	Xeris caudatus Cresson)	
	Xeris indecisus (MacGillivray)	
Pinus radiata	*Sirex areolatus* (Cresson)	
	Sirex behrensii (Cresson)	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
Pinus resinosa	*Sirex nigricornis* Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus albicornis (Fabricius)	
Pinus rigida	*Sirex nigricornis* Fabricius	
	Urocerus cressoni Norton	
Pinus strobus	*Sirex cyaneus* Fabricius	Suspect or rare occurrence
	Sirex longicauda Middlekauff	
	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus albicornis (Fabricius)	
	Urocerus flavicornis (Fabricius)	
Pinus sylvestris	*Sirex californicus* (Ashmead)	
	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile

HOST SPECIES	SIRICID SPECIES	COMMENTS
Pinus taeda	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus cressoni Norton	
Pinus virginiana	*Sirex nigricornis* Fabricius	
	Urocerus cressoni Norton	
Pseudotsuga menziesii	*Sirex areolatus* (Cresson)	
	Sirex californicus (Ashmead)	
	Sirex longicauda Middlekauff	
	Sirex nitidus (T. W. Harris)	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa, Uruguay and eastern North America
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Urocerus cressoni Norton	
	Urocerus flavicornis (Fabricius)	
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Xeris caudatus (Cresson)	
	Xeris indecisus (MacGillivray)	
	Xeris morrisoni (Cresson)	
Tsuga heterophylla	*Sirex abietinus* Goulet, n. sp.	
	Sirex nitidus (T. W. Harris)	Suspect record or rare occurrence
	Sirex varipes Walker	
	Urocerus albicornis (Fabricius)	
	Urocerus californicus Norton	
	Xeris indecisus (MacGillivray)	
ACERACEAE		
Acer sp.	*Tremex columba* (Linnaeus)	
Acer rubrum	*Tremex columba* (Linnaeus)	
Acer negundo	*Tremex columba* (Linnaeus)	
	Tremex fuscicornis (Fabricius)	Introduced into Chile
Acer saccharum	*Tremex columba* (Linnaeus)	
BETULACEAE		
Carpinus sp.	*Tremex columba* (Linnaeus)	
FABACEAE		
Robinia sp.	*Tremex columba* (Linnaeus)	
Robinia pseudoacacia	*Tremex fuscicornis* (Fabricius)	
FAGACEAE		
Castanea dentata	*Tremex columba* (Linnaeus)	
Fagus sp.	*Tremex columba* (Linnaeus)	
Fagus grandifolia	*Tremex columba* (Linnaeus)	
Quercus sp.	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
	Tremex columba (Linnaeus)	
Quercus alba	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
Quercus laurifolia	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
Quercus nigra	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
Quercus phellos	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
HAMAMELIDACEAE		
Liquidambar styraciflua	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
JUGLANDACEAE		
Carya sp.	*Eriotremex formosanus* (Mat.)	Introduced into southeastern United States
	Tremex columba (Linnaeus)	

HOST SPECIES	SIRICID SPECIES	COMMENTS
Carya illinoensis	*Tremex columba* (Linnaeus)	
Juglans cinerea	*Tremex columba* (Linnaeus)	
NYSSACEAE		
Nyssa sylvatica	*Tremex columba* (Linnaeus)	
OLEACEAE		
Fraxinus sp.	*Tremex columba* (Linnaeus)	
PLATANACEAE		
Platanus occidentalis	*Tremex columba* (Linnaeus)	
ROSACEAE		
Malus sp.	*Tremex columba* (Linnaeus)	Collected or reared
Pyrus sp.	*Tremex columba* (Linnaeus)	Collected or reared
SALICACEAE		
Populus sp.	*Tremex columba* (Linnaeus)	
Populus nigra	*Tremex fuscicornis* (Fabricius)	Introduced into Chile
Salix **sp.**	*Tremex columba* (Linnaeus)	
ULMACEAE		
Celtis sp.	*Tremex columba* (Linnaeus)	
Celtis laevigata	*Tremex columba* (Linnaeus)	
Celtis occidentalis	*Tremex columba* (Linnaeus)	
Ulmus sp.	*Tremex columba* (Linnaeus)	
Ulmus americanus	*Tremex columba* (Linnaeus)	
Ulmus glabra	*Tremex columba* (Linnaeus)	

Parasitoids

Parasitoids of Siricidae are not very diverse, but they are striking for their large size. Not all parasitoid species have large specimens, but most have specimens ranging from small to very large depending on size of the host specimen. They are all easily recognized at family and generic level, and in many instances at species level. The North American parasitoids of Siricidae are keyed for *Megarhyssa*, *Pseudorhyssa*, and *Rhyssa* (Ichneumonidae) (Townes and Townes 1960), for *Ibalia* (Ibaliidae) (Liu and Nordlander 1992, 1994), and for *Schlettererius* (Stephanidae) (Townes 1949, Aguiar and Johnson 2003). Adults of most species fly before the main flight period of their siricid host. Even when the host adults are flying commonly, some parasitoids can still be found. Oviposition may easily be observed when it occurs on the lower portion of a tree trunk. We observed a female of *Megarhyssa macrura* (Linnaeus) ovipositing for 15 minutes (Fig. A4.1). Miller and Clark (1935: 155) observed and illustrated the oviposition stages in *Rhyssa persuasoria* (Linnaeus). For more information on the biology of parasitoids and their host trees see Champlain (1922), Chrystal and Myers (1928a, 1928b), Chrystal (1930), Hanson (1939), Cameron (1965), Taylor (1977) and Kirk (1974, 1975). An unusual behaviour of *Megarhyssa* is described by Fattig (1949). Males were observed inserting their abdomen for some time into the emergence hole of a female. Then, they waited for the female to emerge, and mated several times. A female parasitoid may visit the same tree several times in search of hosts.

New World species of parasitoids associated with Siricidae are listed below. Because it is often difficult to associate a parasitoid with a siricid host we also provide a list of named tree species as a clue. The flight period and range for each parasitoid species is then given.

PARASITOID SPECIES	SIRICID SPECIES	TREE HOST & NOTES
IBALIIDAE		
Ibalia anceps Say (Fig. A4.2)	*Tremex columba* (Linnaeus)	See host trees under *T. columba*
Ibalia arizonica Liu & Nordlander	**C**onifer Siricidae	
Ibalia kirki Liu & Nordlander	Perhaps *Sirex nitidus* (T. W. Harris)	*Picea engelmannii*

PARASITOID SPECIES	SIRICID SPECIES	TREE HOST & NOTES
Ibalia leucospoides (Hochenwarth) (Fig. A4.3)	*Sirex* sp. *S. behrensii* (Cresson) *Sirex noctilio* Fabricius *S. cyaneus* Fabricius *S. areolatus (*Cresson) *S. nigricornis* Fabricius *Urocerus* sp. *U. albicornis* (Fabricius) *Xeris* sp.	Various conifers genera; common in *Pinus resinosa*
Ibalia montana Cresson	Probably conifer Siricidae	
Ibalia ruficollis Cameron	Probably conifer Siricidae	
Ibalia rufipes Cresson	*Sirex cyaneus* Fabricius or *S. nitidus* (T. W. Harris)	Various conifers genera
ICHNEUMONIDAE		
Megarhyssa atrata (Fabricius) (Fig. A4.4)	*Tremex columba* (Linnaeus) *Urocerus* sp.	See host trees under *T. columba* Unlikely host
Megarhyssa greeni Viereck	*Tremex columba* (Linnaeus)	See host trees under *T. columba*
Megarhyssa macrura (Linnaeus) (Fig. A4.5)	*Tremex columba* (Linnaeus)	See host trees under *T. columba*
Megarhyssa nortoni (Cresson)	*Sirex noctilio* Fabricius *Urocerus albicornis* (Fabricius) *Xeris morrisoni* (Cresson)	*Abies concolor*, *A. grandis*, *A. lasiocarpa*, *A. magnifica*, *Picea sitchensis*, *Pinus contorta*, *P. jeffreyi*, *Pseudotsuga menziesii, Tsuga canadensis*
Rhyssa alaskensis Ashmead	Siricidae on conifers	*Abies lasiocarpa, Picea englemannii, P. sitchensis, Pinus contorta, Tsuga heterophylla*
Rhyssa crevieri (Provancher)	*Sirex noctilio* Fabricius *Urocerus albicornis* (Fabricius)	*Abies balsamea*
Rhyssa hoferi Rohwer	Siricidae on conifers	*Juniperus* sp., *Pinus edulis, P. ponderosa*
Rhyssa howdenorum Townes & Townes	*Sirex cyaneus* Fabricius *S. nigricornis* Fabricius	*Pinus virginiana*
Rhyssa lineola (Kirby) (Fig. A4.6)	*Sirex* sp. *Sirex nigricornis* Fabricius S. *cyaneus* Fabricius or *S. nitidus* (T. W. Harris) *S. noctilio* Fabricius *Urocerus albicornis* (Fabricius) *U. flavicornis* (Fabricius)	*Abies balsamea, A. fraseri, A. lasiocarpa, Picea sitchensis, Pinus radiata, P. rigida, Tsuga canadensis*
Rhyssa persuasoria (Linnaeus) (Fig. A4.7)	*Sirex areolatus* (Cresson) *S. cyaneus* Fabricius *S. noctilio* Fabricius *Xeris* sp.	*Abies balsamea*, *A. concolor*, *A. lasiocarpa*, *Juniperus scopulorum*, *Larix decidua*, *Picea engelmannii*, *Pinus edulis*, *P. ponderosa*, *P. virginiana*
Rhyssa ponderosae Townes & Townes	*Sirex areolatus* (Cresson)	*Pinus ponderosa*
Pseudorhyssa nigricornis (Ratzeburg) (Fig. A4.8)	Cleptoparasite on *Rhyssa* spp.	*Abies balsamea, A. concolor, Picea engelmannii, P. mariana, Pinus ponderosa, Larix laricina*
STEPHANIDAE		
Schlettererius cinctipes (Cresson) (Fig. A4.9)	*Sirex* sp. *Sirex noctilio* (in Tasmania) *Urocerus* sp. *Xeris* sp.	*Abies concolor***,** *Picea engelmannii*, *Pinus ponderosa, Pseudotsuga menziesiii*

Ibaliidae

Ibalia anceps adults have been captured from mid April to late July and, rarely, in early September (Smith and Schiff 2002). Their main flight period, from early June to mid-July, is well ahead of the *Tremex columba* flight. The range is from Minnesota and Nova Scotia in the North to Colorado, Texas and Florida in the South (Liu and Nordlander 1992).

Ibalia arizonica is recorded from Arizona and New Mexico where conifers grow (Liu and Nordlander 1992). No other information is available.

Ibalia kirki is recorded from Arizona and New Mexico where conifers grow (Liu and Nordlander 1992). No other information is available.

Ibalia leucospoides adults have been captured from mid April to early October. The main flight period is from July to early October (Smith and Schiff 2002). The range is from Alaska and Nova Scotia in the North to California and Florida in the South, where conifers grow (Liu and Nordlander 1992). Flanders (1925) observed that horntails attack nearby *Ibalia*. The parasitoid biology was treated by Hanson (1939).

Ibalia montana adults have been captured in July (Kirk 1975). The range is from British Columbia and Montana in the North to California and New Mexico in the South (Liu and Nordlander 1992).

Ibalia ruficollis adults have been captured from mid July to early October. The main flight period is in August and September (Kirk 1975). The range is from Arizona and northern Mexico (Chihuahua) (Liu and Nordlander, 1992).

Ibalia rufipes adults have been captured from early May to late July. The main flight period is all of July (Kirk 1975). The range is from Oregon and Quebec (it may occur across the boreal zone) in the North to California, Nevada, Arizona and Colorado in the South, where conifers grow (Liu and Nordlander 1992).

Ichneumonidae

Megarhyssa atrata adults have been captured from mid May to early August. The main flight period is in June. The species is divided into two subspecies. The range of *M. atrata atrata* is from Wyoming, Minnesota to Massachusetts in the North to eastern Texas and Georgia in the South (host data by Walsh and Riley 1868, Riley 1870, Thomas 1876, Riley 1888, Packard 1890). The range of *M. atrata lineata* Porter is from Ontario, Quebec, New York and New Hampshire (Townes and Townes, 1960).

Megarhyssa greeni adults have been captured from mid May to early August for *M. greenei greenei* or March, April and September for *M. greenei florida* Townes. The main flight period is in June and early July. The range of *M. greenei greenei* is from Minnesota and Quebec in the North to Alabama and Georgia in the South. The range of *M. greenei florida* Townes is central Florida (Townes and Townes 1960).

Megarhyssa macrura adults have been captured from mid May to late September. The main flight period is in late June and July. This widespread species is divided into three subspecies. The range of *M. macrura lunator* (Fabricius) is east of the Rocky Mountains from South Dakota, Ontario, Quebec and Maine in the North to New Mexico, Texas and Georgia in the South (host data by Walsh and Riley 1868, Riley 1870, Harrington 1882b, Riley 1888 (illustrated on larva of *T. columba* larva), Packard 1890, Felt 1905, Fyles 1917, Herrick 1935). The range of *M. macrura macrura* (Linnaeus) is Chihuahua (Mexico), Texas, South Carolina and Florida. The range of *M. macrura icterosticta* Michener is Utah, Colorado Arizona and New Mexico (Townes and Townes 1960).

Megarhyssa nortoni adults have been captured from late May to early August. The main flight period is in July. The species is divided into two subspecies, both associated with conifers. The range of *M. nortoni nortoni* is from southern British Columbia and southwestern Alberta in the North to southern California and New Mexico in the south. The range of *M. nortoni quebecensis* (Provancher) is from Ontario to Nova Scotia in the North to North Carolina in the South (Townes and Townes 1960).

Rhyssa alaskensis adults have been captured from late May to early September. The main flight period is in June and July. The range is from Alaska and Alberta in the North to California and New Mexico in the South (Townes and Townes 1960).

Rhyssa creveiri adults have been captured from late May to early September. The main flight period is in June. The range is from Minnesota, Ontario and Nova Scotia in the North to North Carolina in the South (Townes and Townes 1960).

Rhyssa hoferi adults have been captured from April to August. The main flight period is in July (Kirk 1975). The range is from Colorado to Arizona (Townes and Townes 1960).

Rhyssa howdenorum adults have been captured in April and June. The range is Alabama, Georgia, Nebraska, North Carolina, South Carolina and Virginia (Townes and Townes 1960, Kirk 1974).

Rhyssa lineola adults have been captured from mid May to late September. The main flight period is in July and August. The range is from southern British Columbia and Nova Scotia in the North to Wyoming and South Carolina in the South (Townes and Townes 1960).

Rhyssa persuasoria adults have been captured from late May to early September. The main flight period is late May to early July (Kirk 1975). The range is from

southern British Columbia, Minnesota, Quebec and New Hampshire in the North to California, Arizona and North Carolina in the South (Townes and Townes 1960). The biology was treated by Hanson (1939).

Rhyssa ponderosae adults have been captured in April, May and June. The range is California (Townes and Townes 1960).

Pseudorhyssa nigricornis adults are cleptoparasites of *Rhyssa*. Adults have been captured from late May to late June (Townes and Townes 1960). Females search for an oviposition shaft of *Rhyssa* and oviposit into it with their narrower ovipositor. Wet siricid frass and vaginal gland secretions are attractants. The larva of *P. nigricornis* eliminates the *Rhyssa* larva and develops on the siricid larva (Couturier 1949, Spradbery 1969, Spradbery 1970).

Stephanidae

Schlettererius cinctipes adults have been captured from early June to early September. The main flight period is in July (Kirk 1975). The range is from southern British Columbia and Idaho in the North to California and Arizona in the South (Townes 1949, Aguiar and Johnson 2003). It has become established recently in eastern North America (Smith 1997). The biology was studied by Taylor (1967).

5. Distribution

The ranges of native species of Siricidae are grouped in six major distribution patterns. The transamerican distribution pattern extends from the Atlantic to the Pacific coasts, usually centered in the boreal zone from Alaska to Newfoundland. The following species have this distribution pattern: *S. nitidus*, *U. flavicornis* and *X. melancholicus*. Occasionally a species with a more temperate range will be found from British Columbia to Newfoundland. The following species has this distribution pattern: *U. albicornis*.

Ranges restricted to regions farther south (usually the southern boreal zone or further south) are divided into eastern and western distribution patterns.

The eastern distribution pattern varies greatly in extent. A range could extend as far west as east of the Cascades Mountains. Only one species shows such a wide range: *Tremex columba*. This species is centered in eastern Northern America but one color form occurs from the eastern edge of the prairie ecotone west to the eastern edges of the Great Basin. A more typical eastern range is one that extends from the Atlantic coast between Nova Scotia and the Gulf of Mexico to at most regions east of the Rocky Mountains and north of the prairie ecotone. The following species have this distribution pattern: *S. cyaneus* (south of New York the range is restricted to the high Appalachian Mountains), *S. nigricornis*, *U. cressoni* and *U. taxodii* (this species was previously known to occur only in southeastern United States, but following its recent discovery in Ontario its range now fits with the above distribution pattern).

The western distribution pattern occurs from the Rocky Mountains to the Pacific coast and also includes the coniferous zone of highlands in the prairies such as the Cypress Hills in Alberta and the Black Hills in South Dakota. The following species have this distribution pattern: *S. abietinus*, *S. areolatus*, *S. behrensii*, *S. californicus*, *S. longicauda*, *S. varipes*, *U. californicus*, *X. indecisus*, and *X. caudatus*. These species extend widely from British Columbia down to California and probably northernmost Mexico south of California. Most have ranges extending north into southern British Columbia, but the ranges of *S. abietinus* and *S. californicus* extend as far north as southern Yukon or northernmost British Columbia. The range of *X. tarsalis* is restricted to the Pacific coast.

Species in southwestern United States that occur east of the Sierra Nevada and as far north as southern Utah and Colorado correspond to a variation of the western distribution pattern. All are probably found in Mexico at least along the Sierra Madre Occidental where there is a rich diversity of conifers. The following species show this distribution pattern: *S. obesus*, *S. xerophilus*, *S. mexicanus*, *X. chiricahua* and *X. morrisoni*.

Species found south of the Isthmus of Tehuantepec are part of a distribution pattern probably associated with the Guatemalan highlands. Only *X. tropicalis* has this pattern.

The Caribbean distribution pattern in the Greater Antilles is the most unusual. So far only two species have this pattern: *S. hispaniola* (pine forests above 1000 m) and *T. cubensis* (low elevation).

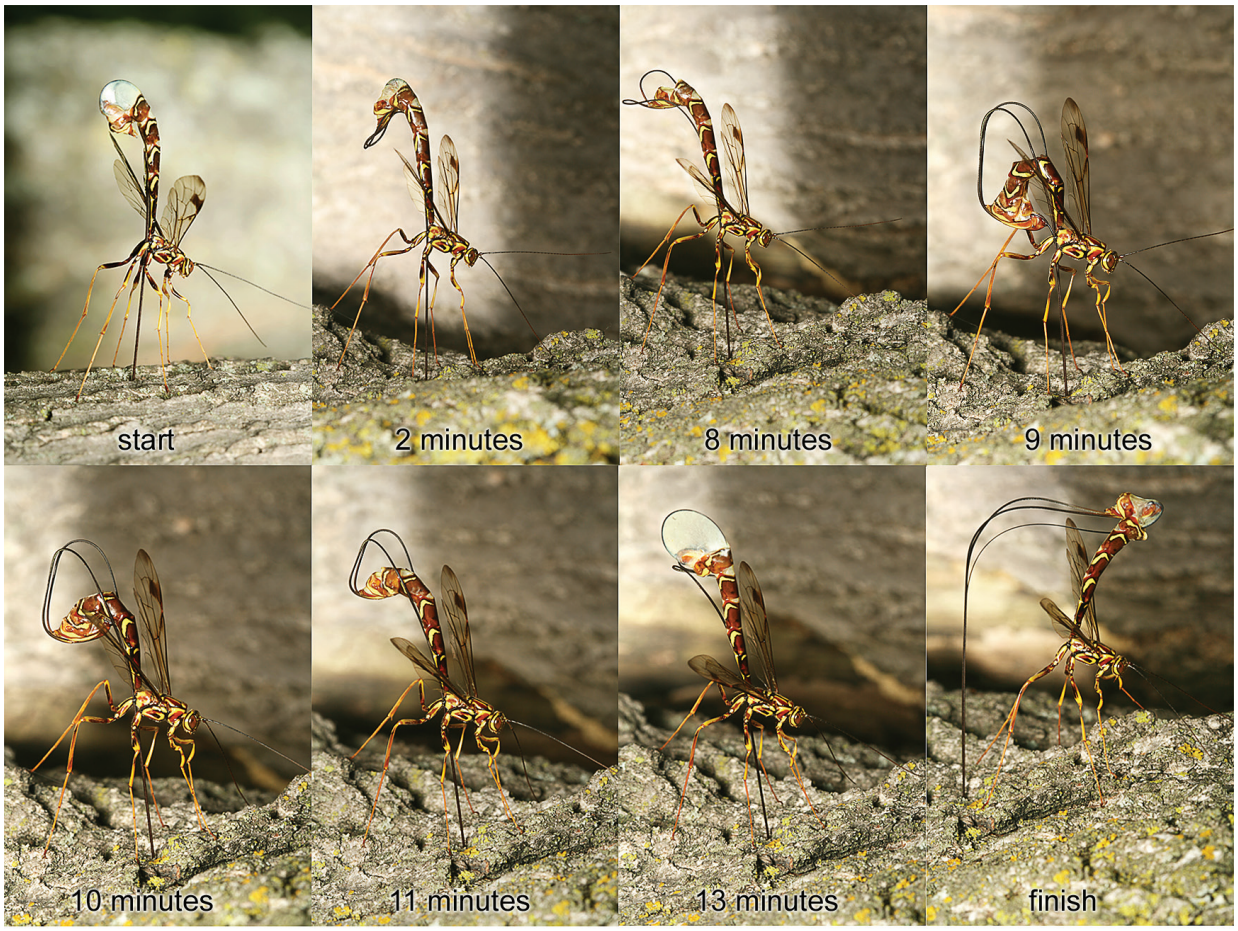
The association of Siricidae with tree trunks and wood have pre-adapted them for worldwide travel, mostly by means of human activity involving international transport of wood products and untreated logs. Their concealed larvae and frequently a multi-year life cycle means they usually remain unnoticed until they become established in areas far outside their native ranges. The primary example is *Sirex noctilio*, native to the Palaearctic region, which has become established in pine plantations in Australia, New Zealand, southern South America, South Africa and, most recently, eastern North America. Numerous other alien siricids have been intercepted at Western Hemisphere ports of entry. The distribution patterns of the species that are now established in the new areas are in flux because all are still expanding their ranges.

Five exotic species from the Palaearctic and Oriental regions have become established in the Western Hemisphere: *Sirex noctilio* in southern South America (Iede *et al.* 1998) and eastern North America (Hoebeke *et*

al. 2005), *Urocerus sah* in eastern North America (Smith 1987), *Urocerus gigas* in Chile and Argentina (Smith 1988), *Eriotremex formosanus* in southeastern United States (Smith 1975b, 1996), and *Tremex fuscicornis* in Chile (Baldini 2002). *Urocerus flavicornis* has been reported from Brazil (Ries 1946) but it has not been confirmed since.

Interceptions at ports of entry give an idea of the movement of species. Benson (1943, 1963) reported *Sirex areolatus, S. cyaneus, Urocerus albicornis, U. californicus,* and *U. flavicornis*, as adventive but not established in Britain. We have seen and studied numerous intercepted specimens from Canada, New Zealand and United States. No doubt there are many other records of interceptions awaiting discovery in collections of various countries. We summarize data from Canada and the United States, based on identified adults found in collections. In the United States, records for the past 40 years (DRS unpublished) indicate that more than 12 species have been intercepted in incoming wood, dunnage, or other wood products. They originated from more than 20 countries and were intercepted at 30 different ports of entry, mostly along the eastern and western seaboards, and a few at the Mexican border. Many unidentified intercepted larvae could include additional species. Other than *Sirex noctilio*, the only exotic Siricidae known to be established in the United States are *Urocerus sah* and *Eriotremex formosanus*. It is surprising that more species of Siricidae have not become established because interceptions include species of *Sirex, Urocerus, Xeris*, and *Tremex*. At least six species of *Sirex* have been intercepted from Europe, eastern Asia, and Mexico. Based on adults, the earliest interception record for *S. noctilio* is 1978. Since then, it has arrived from at least six European countries and been intercepted at seven different ports along the eastern seaboard. *Urocerus gigas* is the most commonly intercepted species of *Urocerus*, mostly from European countries. Western Palaearctic and Asian species of *Xeris* have been intercepted at eastern and western ports; and several species of *Tremex*, mostly from eastern Asia, have been intercepted at western ports.

Within Canada and United States, siricid wasps have been found outside their native range emerging from imported structural wood. Eastern United States records for *Sirex areolatus, S. behrensii, S. longicauda,* and *S. varipes* from homes and other buildings result from importations in wood from the western United States (Smith 1979, Smith and Schiff 2002). They often emerge from structures several years after wood is used for construction. Records indicate that only *S. areolatus* may have become established in the southeastern states.



A4.1: *Megarhyssa macrura* ♀

A4.2: *Ibalia anceps* ♀

A4.3: *Ibalia leucospoides*

A4.4: *Megarhyssa atrata*

A4.5: *Megarhyssa macrura*

A4.6: *Rhyssa lineola*

A4.7: *Rhyssa persuasoria*

A4.8: *Pseudorhyssa nigricornis*

A4.9: *Schlettererius cinctipes*