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

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 spincolumn 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 μ l of PCR product was mixed with 8 μ l of Exo-SAP (2 μ l Exonuclease I at 10U/ μ l, USB product no. 70073Z, Cleveland, OH; 20 μ l Shrimp Alkaline Phosphatase at 1U/ μ l USB product no. 70092Z, Cleveland, OH); 78 μ l ddH₂O) 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 μ l). 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/ μ l. 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 multiplefunnel 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.

<u>Mouth parts</u>. 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 setalike. 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.

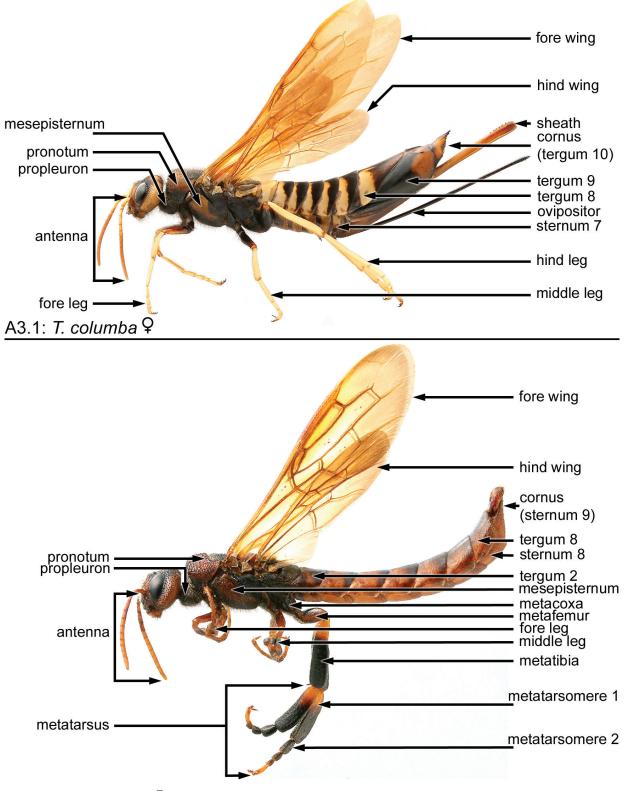
Size is one variable that affects all structures of a specimen, but which normally is not analyzed or discussed in detail. Size range within well sampled siricid species is great. For example, both sexes of *S. noctilio* may range between 8 and 36 mm and similar size variation is true for many other 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.

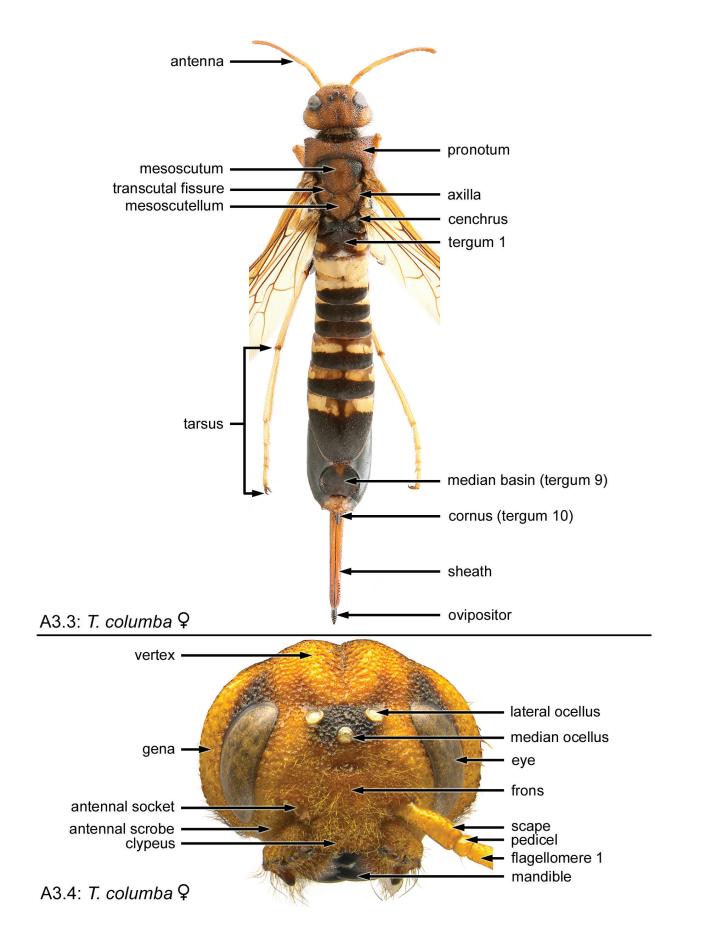
Measurements. When possible, 30 specimens of each sex were measured. Means and standard deviations were calculated using Microsoft Excel software. The main measurements are the length of the basal and apical sections of the ovipositor sheath and the maximum length of the fore wing. Because a limited 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

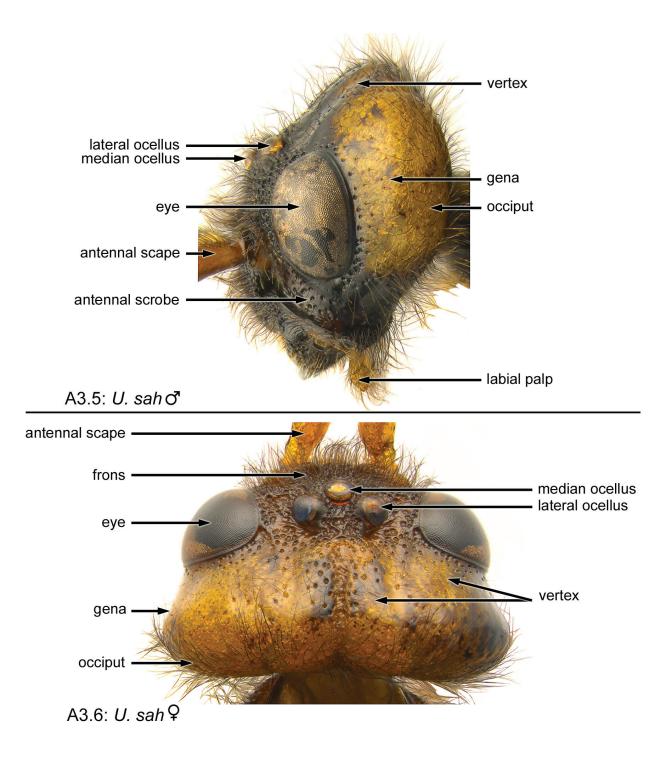
teeth annuli.). For a few species, distances between pits 1 and 2, 4 and 5, and 9 and 10 of the ovipositor relative to the ovipositor diameter (including lance and lancet) between these pairs of pits is given. Other measurements were recorded as required. Measurements considered useful are given in Tables 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.

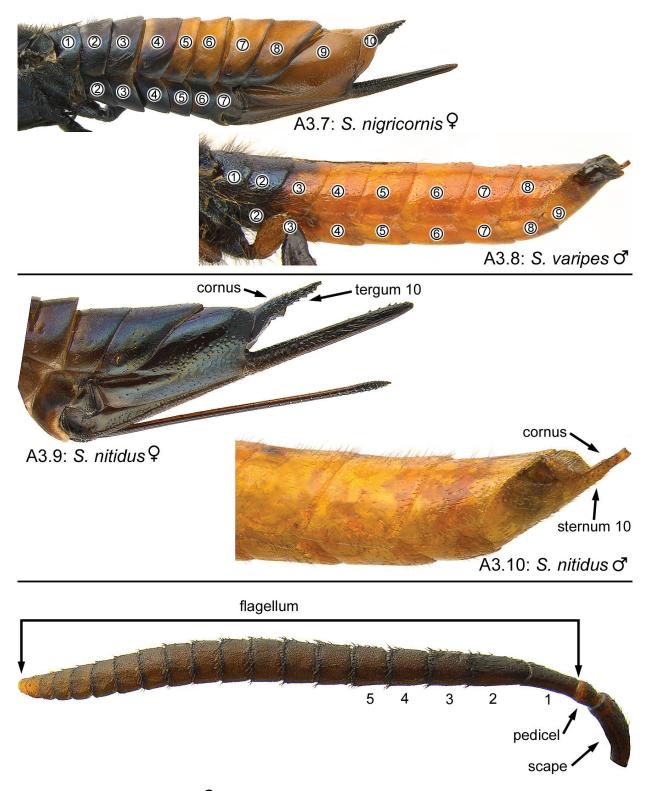
Barcode information. For each specimen the following is recorded: country, year, state/province, specimen code, and number of base pairs.



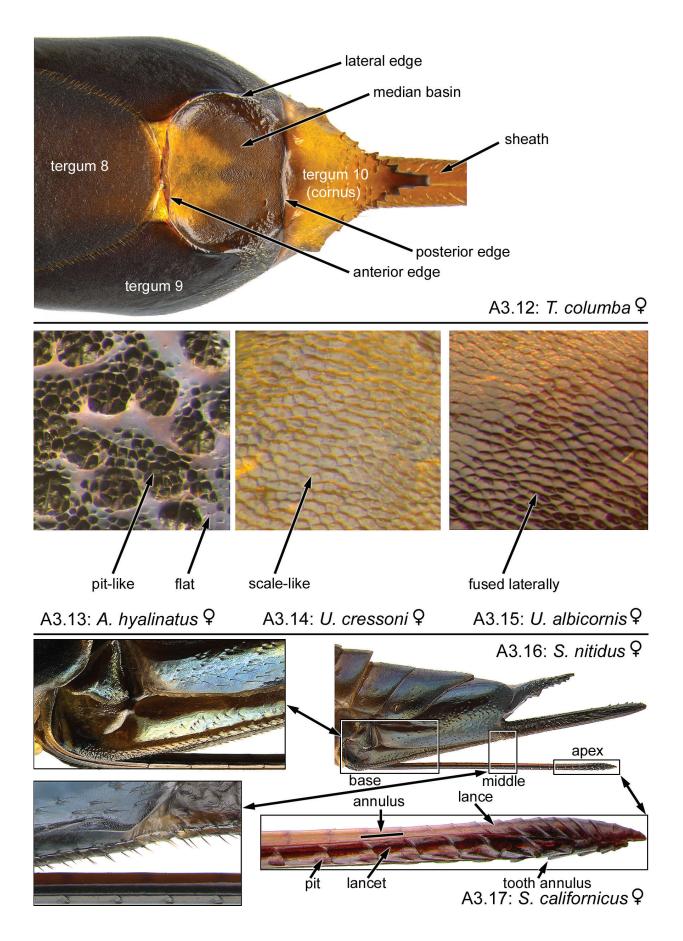
A3.2: T. columba d

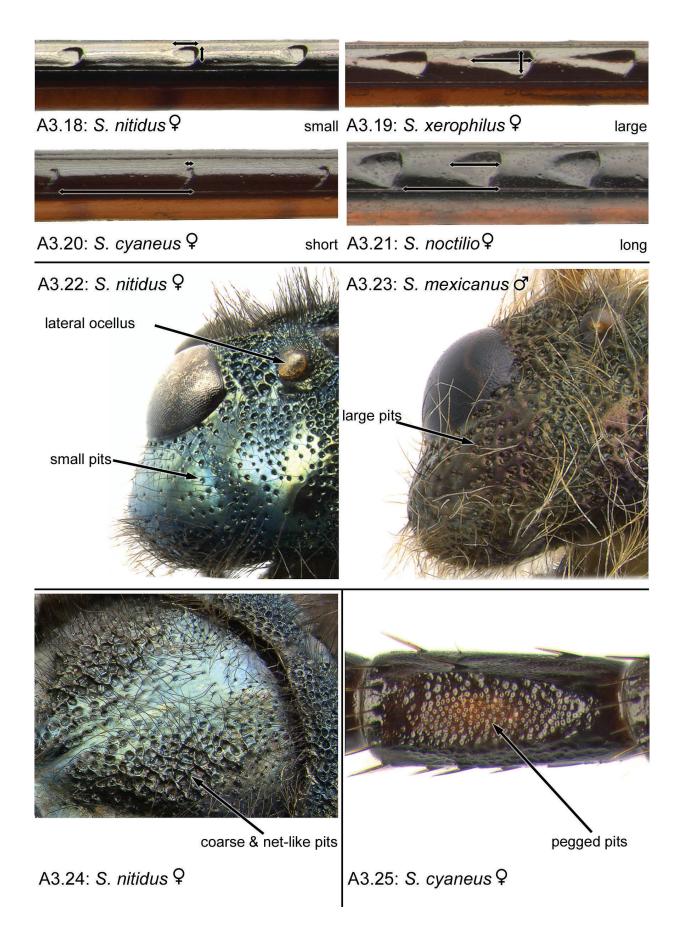


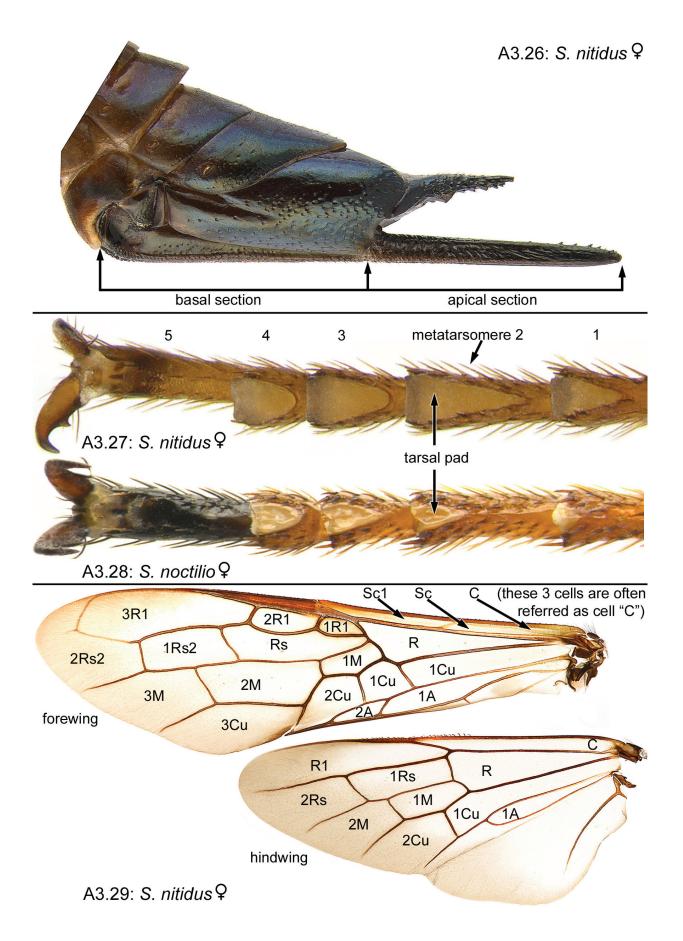


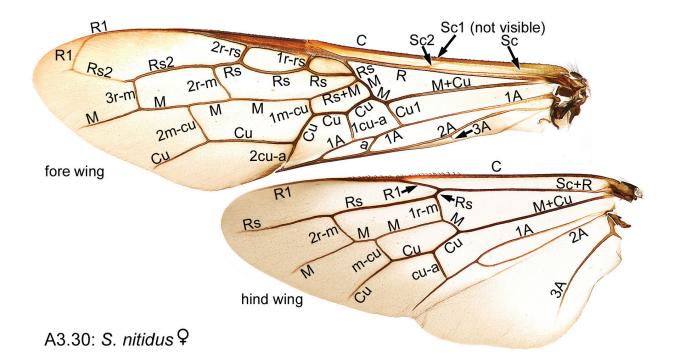


A3.11: E. formosanus Q









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 Šrŭtka 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)	
<i>Thuja</i> 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)	
	<i>Xeris caudatus</i> (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
	Shew hoemio I activitas	Uruguay and eastern North America
	Urocerus albicornis (Fabricius)	
	Urocerus flavicornis (Fabricius)	
Pinus sylvestris	Sirex californicus (Ashmead)	
syrresu is	Sirex nigricornis Fabricius	
	Sirex noctilio Fabricius	Introduced into New Zealand, Australia, Chile, Argentina, Brazil, South Africa
	Sirex noemo i abielus	Uruguay and eastern North America
	Urocerus gigas (Linnaeus)	Introduced into Argentina, Brazil, Chile
	Grocerus gigus (Liillideus)	muoduccu mio Argenuna, Diazii, Cine

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 BETULACEAE	Tremex columba (Linnaeus)	
Carpinus sp.	Tremex columba (Linnaeus)	
FABACEAE		
<i>Robinia</i> sp.	Tremex columba (Linnaeus)	
Robinia pseudoacacia FAGACEAE	Tremex fuscicornis (Fabricius)	
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 JUGLANDACEAE	Eriotremex formosanus (Mat.)	Introduced into southeastern United States
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	Conifer Siricidae	
Ibalia kirki Liu & Nordlander	Perhaps Sirex nitidus (T. W. Harris)	Picea engelmannii
		-

PARASITOID SPECIES	SIRICID SPECIES	TREE HOST & NOTES
Ibalia leucospoides (Hochenwarth)	Sirex sp.	Various conifers genera; common in Pinus
(Fig. A4.3)	S. behrensii (Cresson)	resinosa
	Sirex noctilio Fabricius	
	S. cyaneus Fabricius	
	S. areolatus (Cresson)	
	S. nigricornis Fabricius	
	Urocerus sp.	
	U. albicornis (Fabricius)	
	Xeris sp.	
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	Sirex cyaneus 1 abricius of 5. naturus (1. w. mains)	various conners genera
Megarhyssa atrata (Fabricius) (Fig. A4.4)	Tremex columba (Linnaeus)	See host trees under T. columba
megunyssu unuu (1 abhends) (1 fg. A4.4)	Urocerus sp.	Unlikely host
Magguhuggg guogui Vianali	Tremex columba (Linnaeus)	See host trees under <i>T. columba</i>
Megarhyssa greeni Viereck		
Megarhyssa macrura (Linnaeus) (Fig. A4.5)	Tremex columba (Linnaeus)	See host trees under <i>T. columba</i>
Megarhyssa nortoni (Cresson)	Sirex noctilio Fabricius	Abies concolor, A. grandis, A. lasiocarpa,
	Urocerus albicornis (Fabricius)	A. magnifica, Picea sitchensis, Pinus
	Xeris morrisoni (Cresson)	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	Abies balsamea
	Urocerus albicornis (Fabricius)	
Rhyssa hoferi Rohwer	Siricidae on conifers	Juniperus sp., Pinus edulis, P. ponderosa
Rhyssa howdenorum Townes & Townes	Sirex cyaneus Fabricius	Pinus virginiana
	S. nigricornis Fabricius	
Rhyssa lineola (Kirby) (Fig. A4.6)	Sirex sp.	Abies balsamea, A. fraseri, A. lasiocarpa,
1019550 incom (11109) (11 <u>5</u> .111.0)	Sirex nigricornis Fabricius	Picea sitchensis, Pinus radiata, P. rigida,
	S. <i>cyaneus</i> Fabricius or <i>S. nitidus</i> (T. W. Harris)	Tsuga canadensis
	S. noctilio Fabricius	Isugu cunuuchsis
	Urocerus albicornis (Fabricius)	
	· · · · ·	
	<i>U. flavicornis</i> (Fabricius)	
Rhyssa persuasoria (Linnaeus) (Fig. A4.7)	Sirex areolatus (Cresson)	Abies balsamea, A. concolor, A. lasiocarpa
	<i>S. cyaneus</i> Fabricius	Juniperus scopulorum, Larix decidua, Picea
	S. noctilio Fabricius	engelmannii, Pinus edulis, P. ponderosa, P.
	Xeris sp.	virginiana
Rhyssa ponderosae Townes & Townes	Sirex areolatus (Cresson)	Pinus ponderosa
Pseudorhyssa nigricornis (Ratzeburg)	Cleptoparasite on Rhyssa spp.	Abies balsamea, A. concolor; Picea
(Fig. A4.8)		engelmannii, P. mariana, Pinus ponderosa, Larix laricina
STEPHANIDAE		
Schlettererius cinctipes (Cresson) (Fig. A4.9)	Sirex sp.	Abies concolor, Picea engelmannii, Pinus
- · · · · · · · · ·	Sirex noctilio (in Tasmania)	ponderosa, Pseudotsuga menziesiii
	· /	

Urocerus sp. *Xeris* sp.

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*

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*

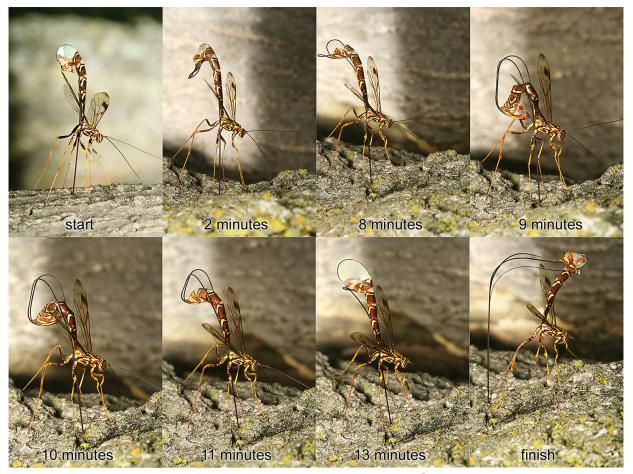
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al. 2005), Urocerus sah in eastern North America (Smith 1987), Urocerus gigas in Chile and Argentina (Smith 1988), Eriotremex formosanus in southeastern United States (Smith 1975b, 1996), and Tremex fuscicornis in Chile (Baldini 2002). Urocerus flavicornis 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 Q



A4.2: Ibalia anceps Q



A4.3: Ibalia leucospoides



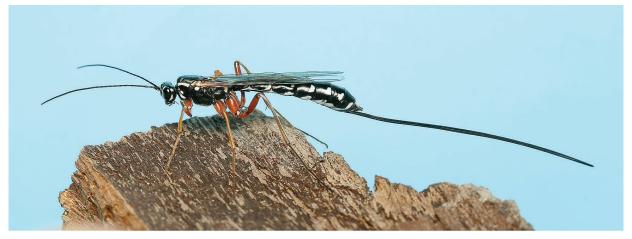
A4.4: Megarhyssa atrata



A4.5: Megarhyssa macrura



A4.6: Rhyssa lineola



A4.7: Rhyssa persuasoria



A4.8: Pseudorhyssa nigricornis



A4.9: Schlettererius cinctipes

B. Key to genera and species

Use of keys

Specimen condition and preparation.

Clean specimens (greasy specimens are quite common in collections) with wings slightly open are needed to view the dorsal surface of the abdomen. At least one antenna and one leg of each pair must be present and complete.

It is often important to know the sex of the specimen to be keyed. Males and females are easily separated. The main sexual differences for all species are on the hind leg and the abdomen.

Female features are:

- Abdomen large, particularly terga 8 and 9 (Fig. A3.1).
- Tergum 9 with a very large median impression (median basin) (Fig. A3.3).
- Tergum 10 developed as a horn (cornus) (Fig. A3.9).
- Long sword-like sheath ventral to abdominal segments 9 and 10 or posterior to sternum 7 covering the ovipositor (Figs. A3.1 & A3.9).
- Hind leg similar in proportions but longer than fore and middle legs (Fig. A3.1).

Male features are:

- Abdomen slender and apical tergum similar to but sometimes a little longer than preceding terga (Fig. A3.2).
- Tergum 8, the last tergum, without a median impression (Fig. C28.3).
- Sternum 9, the last sternum, with a horn (cornus) at apex (Fig. A3.10).
- Abdomen without sword-like extension, and ended at tergum 8 and sternum 9 (Fig. A. 3.2 & A3.10).
- Hind leg clearly enlarged relative to fore and middle legs (Fig. A3.2).

Male identification does not require dissection; female identification usually does. The apical section of the ovipositor sheath should be removed to see the apical half of the ovipositor. To expose the apical half of the ovipositor, insert an insect pin near the apex of the sheath between the ovipositor and the apical section of the sheath. It should break at the junction of the basal and apical sections. Alternatively, the complete ovipositor may easily be pulled out of its sheaths either after relaxing a dried specimen for about 36 hours in a very humid atmosphere (in a closed container) or immediately after pinning an alcohol preserved specimen. To see most or all the ovipositor of a relaxed or recently mounted alcohol preserved specimen, insert an insect pin between the ovipositor and the apical section of the sheath and gently slide the pin toward the base of the sheath. This will force the ovipositor out of the sheath and the apical section of the sheath will return to its normal position (the sheath will not break). Ensure that the ovipositor remains out of the sheath. Use a fine paintbrush dipped in 95% alcohol to remove any dirt from the ovipositor. The specimen is now ready to be keyed.

Lighting

The light source is important. The best light is diffused light. Diffused light could come directly from a daylight fluorescent light (13 watts is usually satisfactory) or is produced with a semi-opaque plastic between the light source and the specimen. The best diffusion is achieved when the plastic is less than 20 mm from the specimen. This type of lighting eliminates all or most glare from smooth surfaces or those with metallic reflections. Such lighting makes structural features very clear and has been used throughout our work as illustrated in the numerous figures. We use a small (5 by 7 cm) piece of transparent plastic (Mylar) placed vertically on a base of modeling clay about 20 mm from the specimen to provide a sharp, glare-free image, of ovipositor pits for example. A dissecting microscope with a magnifying range of 40-60 times is recommended to view a structure clearly.

Key construction

Each couplet is arranged in contrasting pairs of statements labeled, respectively, with upper and lower case letters. Each statement almost always describes one feature of a character. So, different expressions of the same character would be found, for example, in couplet 8A and 8a. Information that is not compared in the alternate part of the couplet is given between brackets. Clarification notes are given in parentheses. Almost all statements of each couplet are illustrated. Each figure in addition to a number has the statement code: a capital or a lower case letter. Two figures with the same statement code may be mentioned to show a range of variation for a character. The illustration shown is not necessarily that of the species named, but is a similar expression of the character to be observed. In these cases, other structures in the figure should be ignored as they do not represent the species keyed. Plates of figures are organized so that the contrasting statements of each character are adjacent to one another. Arrows and morphological terms are added for clarity.

Field guide to Siricidae of North America

Schiff *et al.* (2006) published a key to genera and species of the North American Siricidae. Their excellent illustrations should help anyone without a reference collection trying to identify a specimen. However, the names of many habitus images need to be revised. We refer to such habitus images under each species of our revision. For other modifications see Appendix 2.

1. Key to extant genera of Siricidae

1. A) Minimum distance (at top of eye) between eyes 0.7–1.2 times as long as maximum height of eye (Fig. B1.1). B) Distance between inner edges of antennal sockets 3.5–10.0 times as long as distance from outer edge of antennal socket to nearest edge of eye (Fig. B1.3). C) Flagellomeres flattened dorsoventrally (Fig. B1.5). [Additional character. Eye narrow: 1.7–1.9 times as high as long except in male of *Teredon cubensis* with a long eye (1.3 times as high as long) causing a very narrow gena.] a) Minimum distance (at top of eye) between 1.2–1.6 times as long as maximum height of eye (Fig. 1.2). b) Distance between inner edges of antennal sockets 1.5–2.5 times as long as distance from outer edge of antennal socket to nearest edge of eye (Fig. B1.4). Flagellomeres circular or almost circular in cross section (Fig. B1.6). c) 2(1)A) Fore wing vein 2r–m present (Fig. B1.7). B) Fore wing vein 1cu-a not aligned with vein M, but joining vein Cu near middle or in basal 0.25 between veins 1m-cu and M (Fig. B1.9). C) Hind wing with hamuli present basal and apical to junction of veins R1 and C (as in Fig. B1.11). a) Fore wing vein 2r–m absent (Fig. B1.8). b) Fore wing vein 1cu–a aligned or almost aligned with vein M (Fig. B1.10). Hind wing with hamuli present only apical to junction of veins R1 and C (Fig. B1.12). c)3(2) A) Distance between inner edges of lateral ocelli subequal to distance from outer edge of lateral ocellus to nearest edge of eye (Fig. B1.13). B) Hind wing vein 1r-m slightly longer than vein M; vein M slightly curved (Fig. B1.15). C) Metatarsomere 1 scarcely compressed laterally and lateral surface not twisted when seen in dorsal view (as in Fig. B1.17). D) **Female**: cercus broad at base of cornus (Fig. B1.19). E) Female: tergum 9 with median basin more than 1.5 times as wide as long and median length about 0.5 as long as cornus (Fig. B1.21). Siricosoma Forsius, 1933 [Note. Only one species, Siricosoma tremecoides Forsius, from the Malay Peninsula.] a) Distance between inner edges of lateral ocelli more than 1.5 times as long as distance from outer edge of lateral ocellus to nearest edge of eye (Fig. B1.14). b) Hind wing vein 1r-m clearly shorter than vein M; vein M markedly curved (Fig. B1.16). c) Metatarsomere 1 greatly compressed laterally and lateral surface twisted when seen dorsal view (Fig. B1.18). d) Female: cercus very small at base of cornus (Fig. B1.20). e) Female: tergum 9 with median basin about as wide as long and median length about 2.0 times as long as cornus (Fig. B1.22). [Note. only one species, Teredon cubensis (Cresson) from Cuba.]

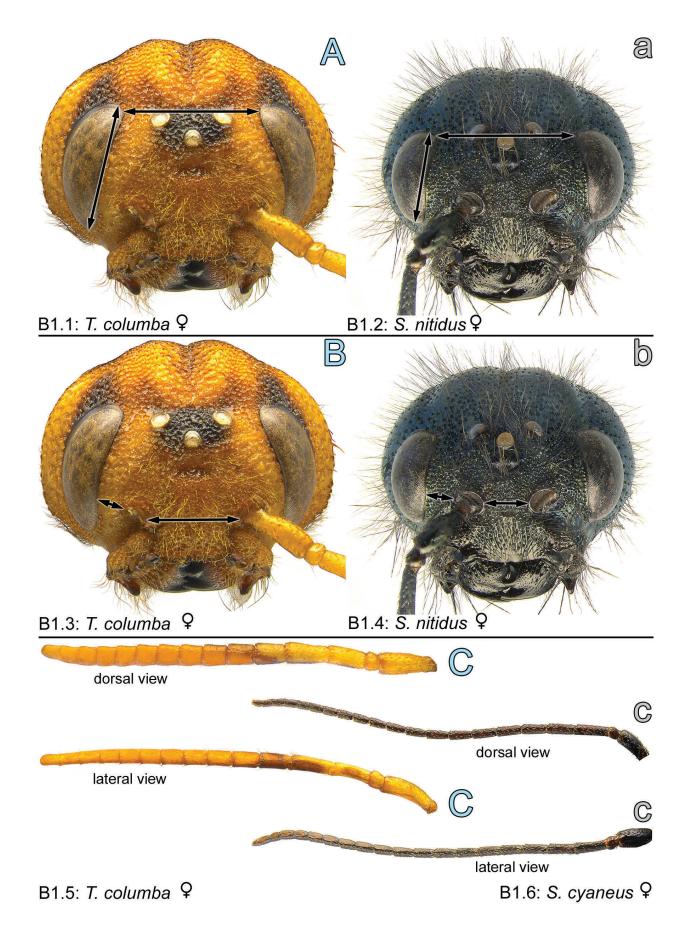
A) Antenna with 11–19 flagellomeres (Fig. B1.23).

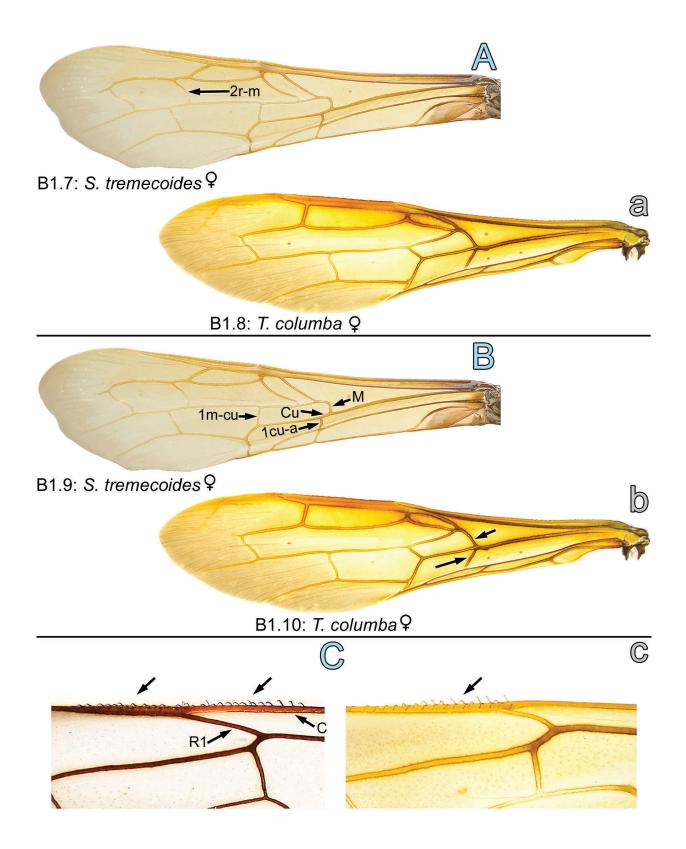
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- B) Fore wing cell 2R1 about 0.5 times as long as cell 3R1; vein 2r-rs joining stigma near middle; stigma gradually attenuated even after junction with vein 2r-rs (Fig. B1.25). C) Male (only E. formosanus studied): antenna as long as length of fore wing costal cell and stigma combined (Fig. B1.27). D) Female: tergum 9 with disc of median basin very convex and lightly to densely pitted (Fig. B1.29). E) **Female:** cercus present and thumb-like (Fig. B1.31). Eriotremex Benson, 1943 [Note. Twelve species restricted to the Oriental region and Papua New Guinea. One species, Eriotremex formosanus, accidentally introduced into southeastern United States.] a) Antenna almost always with fewer than 14 flagellomeres (Fig. B1.24). b) Fore wing cell 2R1 at least 0.63 times as long as cell 3R1; vein 2r-rs joining stigma in apical 0.2–0.33; stigma before junction with vein 2r-rs parallel and beyond junction abruptly attenuated (Fig. B1.26). c) Male: antenna at most as long as length of fore wing costal cell (Fig. B1.28). d) **Female**: tergum 9 with disc of median basin at most slightly convex, but usually flat to concave, and most of surface not pitted (Fig. B1.30). **Female**: cercus absent (Fig. B1.32). e) 5(4) A) Flagellomere 1 about 0.5 times as long as flagellomere 2 (Fig. B1.33). B) Fore wing cell 2R1 at most 0.7 times as long as cell 3R1 (Fig. B1.35). C) Head with setae (exclusive of those on occiput) enlarged at apex, club-like (Fig. B1.37). D) Frons with pits separated by 1-2 pit diameters (surface quite bright because surface between pits smooth) (Fig. B1.39). [Note. Two species known A. hyalinatus (Mocsáry) and A. violaceus Pasteels. Both only recorded from sub-Saharan Africa.] Flagellomere 1 at least 0.7 times as long as flagellomere 2 (Fig. B1.34). a) b) Fore wing cell 2R1 at least 0.85 times as long as cell 3R1 (cell 2R1 commonly subequal or clearly longer than length of 3R1) (Fig. B1.36). c) Head with setae gradually tapering sharply at apex (Fig. B1.38). d) Frons with pits dense and generally in contact with each other (Fig. B1.40). [Note. Thirty three species known. Almost all species restricted to Palaearctic region except for one, Tremex columba Linnaeus, in North America. One species, T. fuscicornis (Fabricius), introduced into the Western Hemisphere.] **6(1)** A) Gena behind eye with short ridge (Fig. B1.41). B) Hind wing without cell 1A (Fig. B1.43). C) Metatibia with one apical spur (Fig. B1.45). D) Female: apical section of sheath without teeth in apical third of dorsal margin (Fig. B1.47). [Note. Ten species known. Three species in Palaearctic region and seven in New World.] a) Gena behind eye without ridge (Fig. B1.42). b) Hind wing with cell 1A (Fig. B1.44). c) Metatibia with two apical spurs (Fig. B1.46). d) Female: apical section of sheath with teeth in apical third of dorsal margin (except in a few species of Urocerus from Asia) (Fig. B1.48). 7(6) A) Fore wing broadly rounded at apex (Fig. B1.49).
 - B) Fore wing with cell 1Rs2 short (2r–m and 3r–m slightly longer than veins Rs2 and M above and below (Fig. B1.51).
 - C) Fore wing with cell 3R1 short (2.2 times as wide as long) (Fig. B1.53).

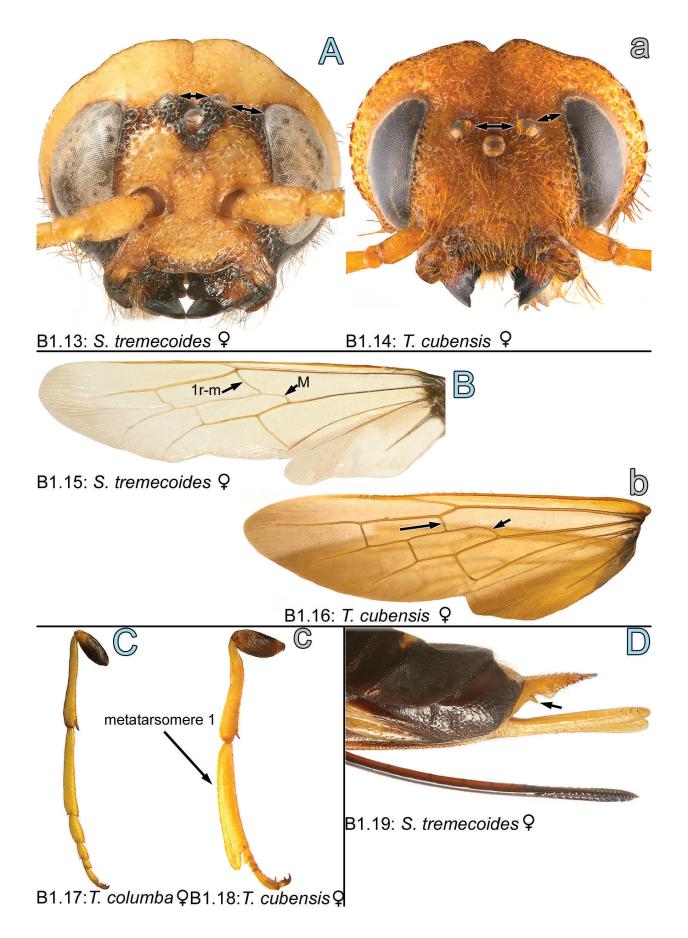
D) Flagellum with 10 or 11 flagellomeres, and middle flagellomeres about 1.5 times as long as high in lateral view (Fig. B1.55). [Note. One species, Sirotremex flammeus Smith, from Mexico. Only males known.] Fore wing angularly rounded at apex (Fig. B1.50). a) b) Fore wing with cell 1Rs2 long (2r-m and 3r-m slightly or very clearly shorter than veins Rs2 and M above and below) (Fig. B1.52). Fore wing with cell 3R1 long (3.0–6.0 times as wide as long) (Fig. B1.54). c) d) Flagellum with 12 or more flagellomeres, and middle flagellomeres at least 2.0 times as long as high in lateral view (Figs. B1.56 & B1.57). 8(7) A) Dark sections of body with dark blue or green metallic reflections (Figs. B1.58 & B1.60). B) Head entirely black with dark blue or green metallic reflections (Fig. B1.62), at most with dark brown on gena behind eye (Fig. B1.63). C) Fore wing with vein Cu1 complete or almost so (Fig. B1.66). [Note. Twenty eight species known. Almost equally divided between the Palaearctic (15 species) and Nearctic (14 species) regions. One species, S. noctilio, introduced into temperate North America, South America, New Zealand, Australia and South Africa.] Dark sections of body without dark blue or green metallic reflections (Figs. B1.59 & B1.61). a) b) Head variably colored, but with at least a pale spot (white, light reddish brown or reddish brown) on gena behind eye in upper half (Figs. B1.64 & B1.65). Fore wing without vein Cu1, at most with a stump or very rarely complete on one wing only (Fig. B1.67). [Additional character. Female: cornus long and constricted in almost all species; rarely small and not constricted as in *Sirex longicauda*.] 9(8) A) Gena densely pitted (Fig. B1.68). B) Fore wing vein 2r-m displaced apically and joined to cell 3M (Fig. B1.70). C) Pronotum with vertical surface mainly smooth, with pits medially and along dorsal margin (Fig. B1.72). D) Female: tergum 9 with median basin about as wide as long, and with short and slightly divergent ridge edges at base; cornus narrow (Fig. B1.74). [Note. Two species recorded from China, eastern Russia and Japan.] a) Gena with almost no pits (Fig. B1.69). b) Fore wing vein 2r-m more basal and joined to cell 2M (Fig. B1.71). Pronotum with vertical surface almost completely pitted (Fig. B1.73). c) d) **Female**: tergum 9 with median basin about 2.0 times as wide as long, and with long and very divergent ridge edges; cornus wide (Fig. B1.75).

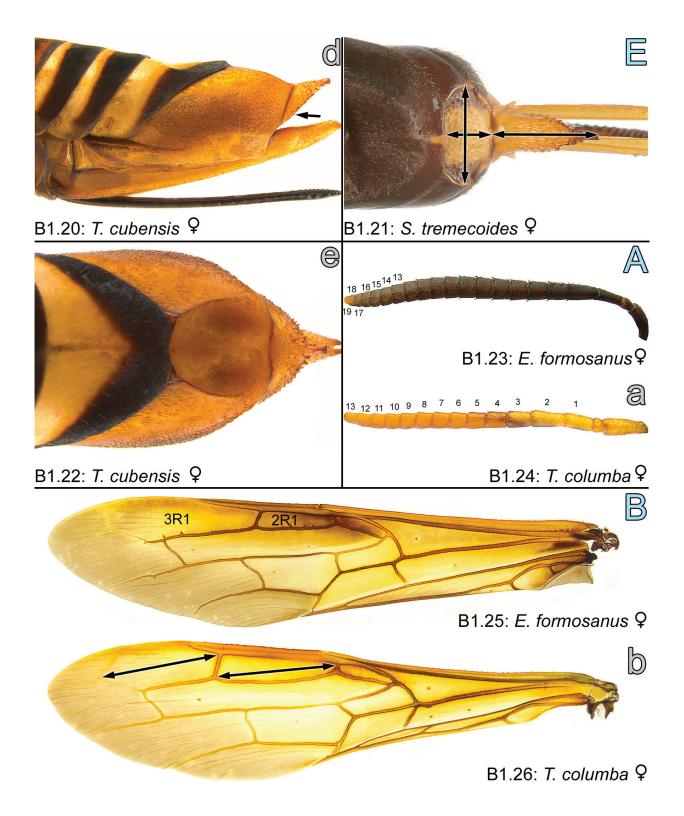
[Note. Thirty three known species. Most (28 species) restricted to Palaearctic region and few (7) in New World. Two of the New World species, *Urocerus gigas* and *U. sah*, introduced.]

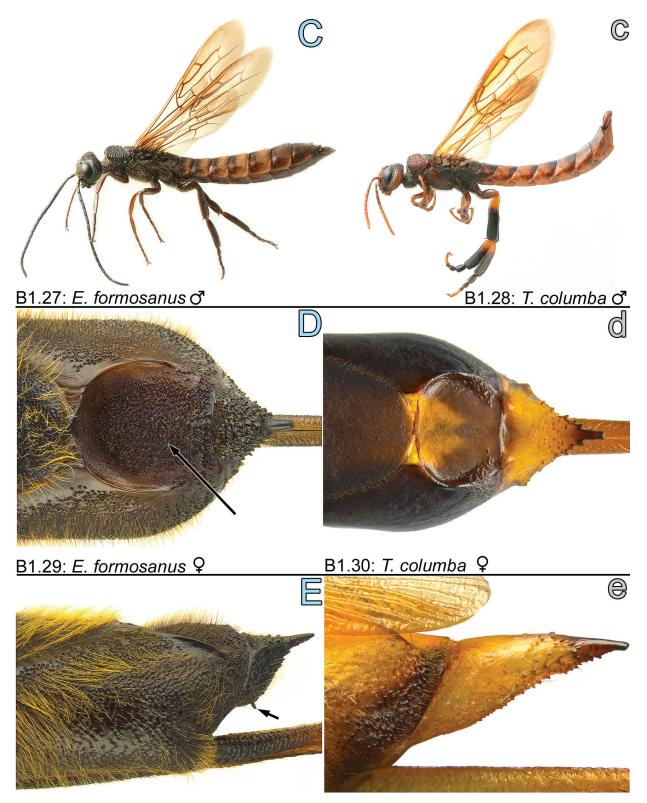




B1.12: T. columba Q

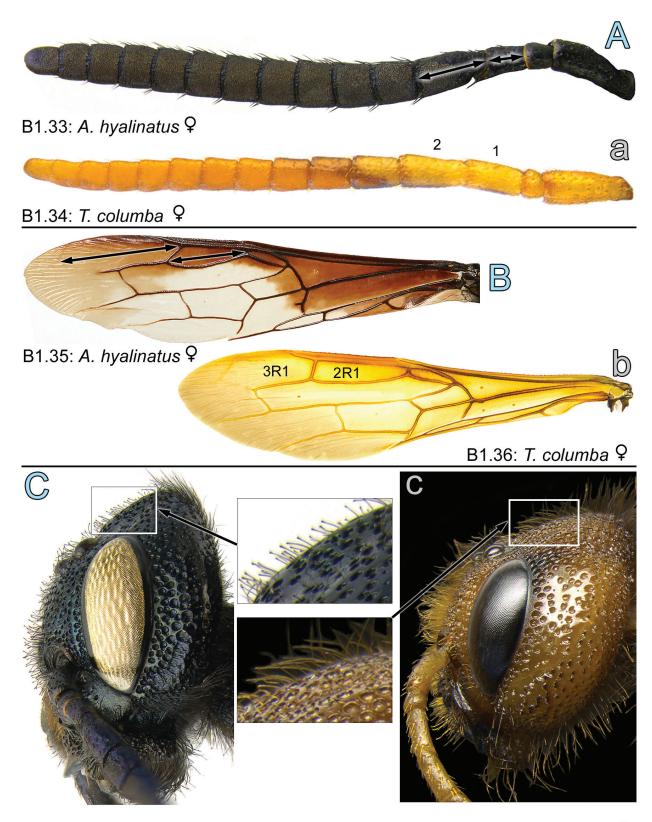






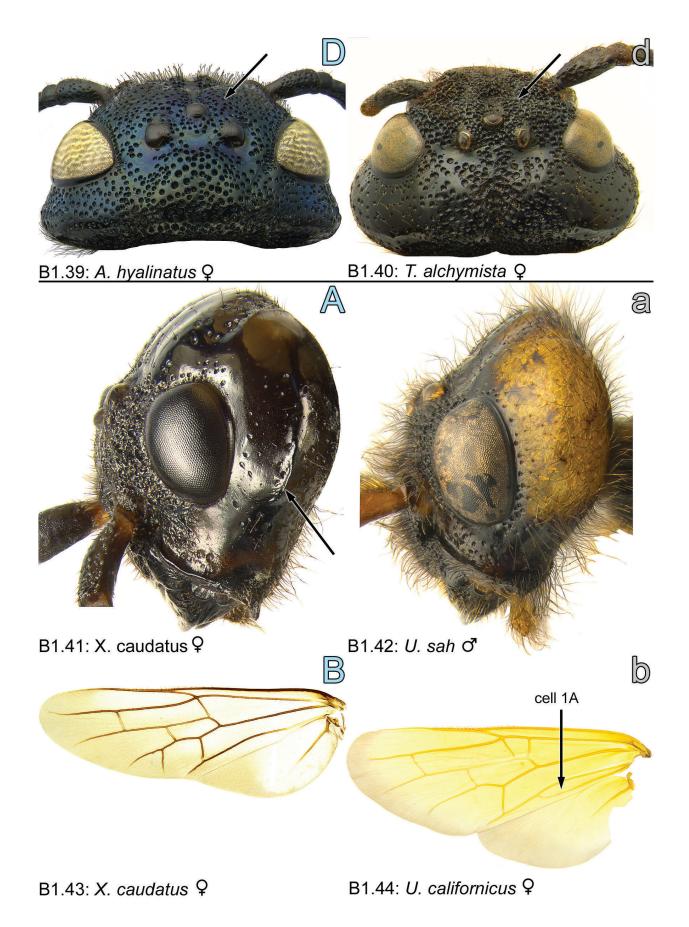
B1.31: E. formosanus Q

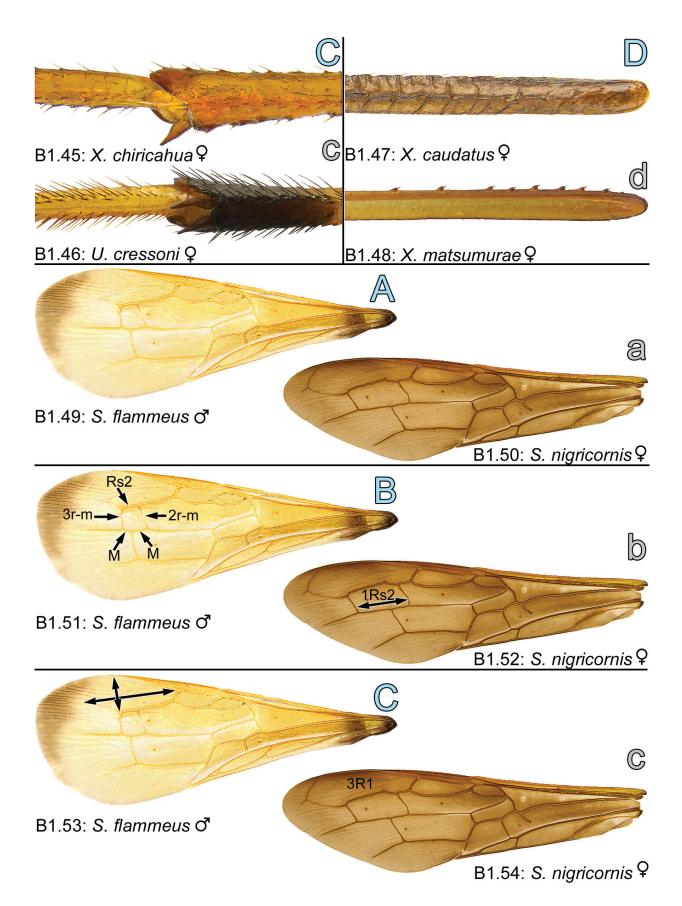
B1.32: T. fuscicornis Q

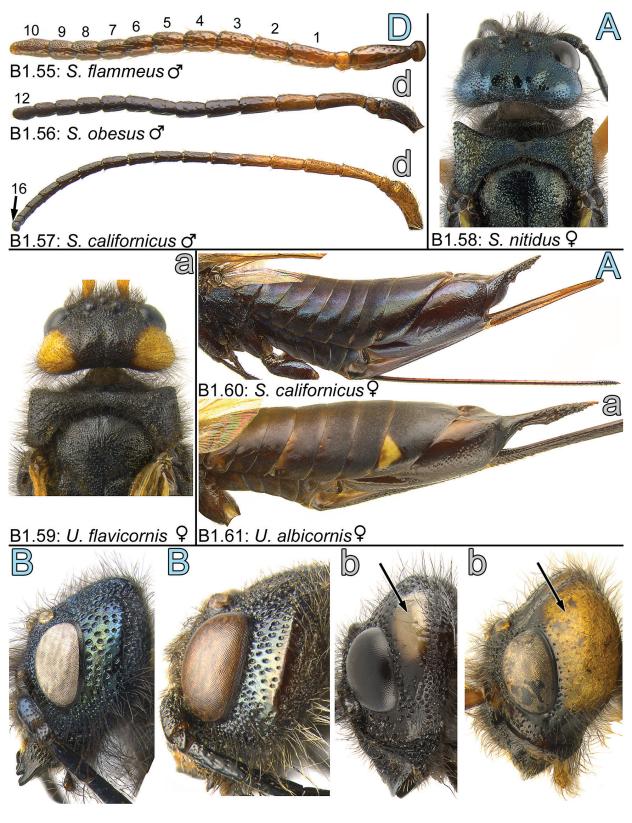


B1.37: A. hyalinatus Q

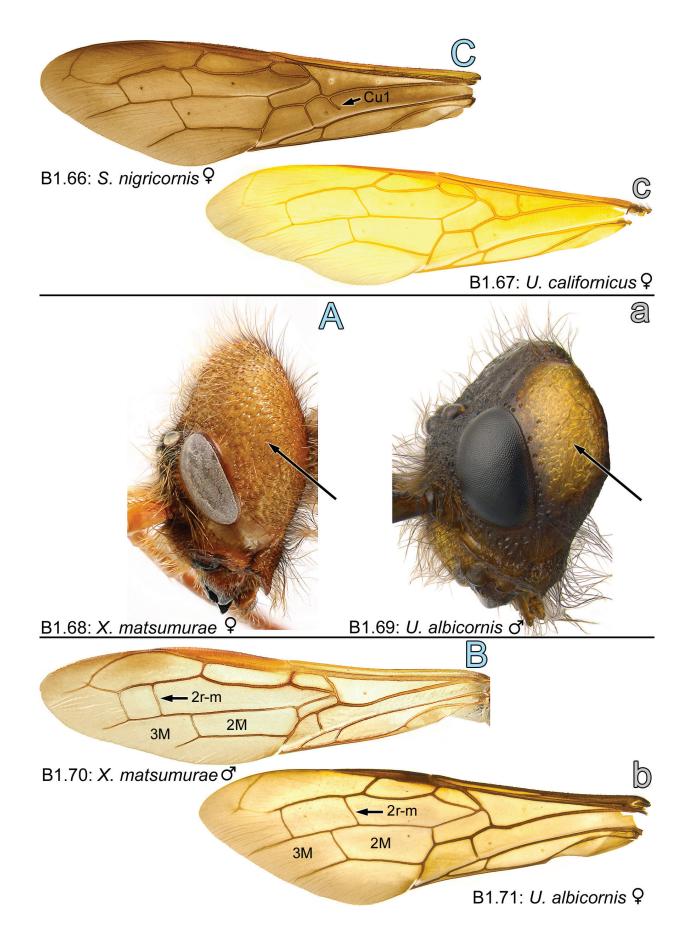
B1.38: *T. columba*♀

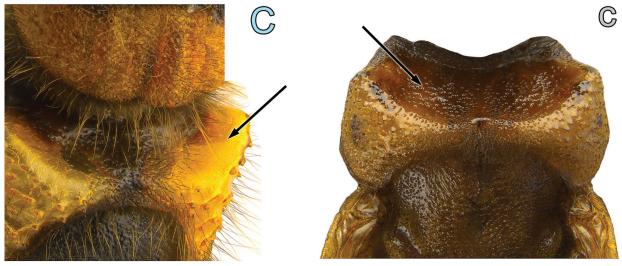






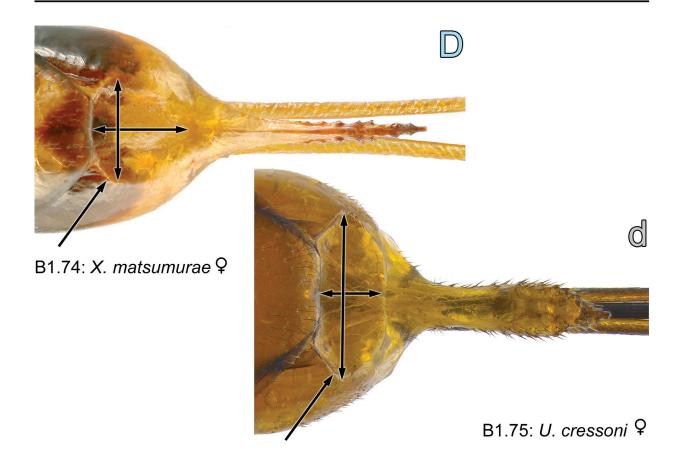
B1.62: S. nigricornisQ B1.63: S. behrensiiQ B1.65: U. saho





B1.72: X. matsumurae o

B1.73: *U. sah* ♀



2. Key to New World Species of *Sirex*

Females 1 A) Metafemur black (Fig. B2.1) Metafemur light reddish brown (Fig. B2.2) [Doubtful specimens from Alaska and Yukon key out through a) both parts of the couplet.] 2(1)A) Metatarsomere 2 4–5 times as long as high (Fig. B2.3). B) Sheath with basal section relative to apical section less than 0.8 (Fig. B2.5). C) Ovipositor with more than 38 annuli. [Additional character: Fore wing vein 3A clearly present.] a) Metatarsomere 2, 1.5–3.5 times as long as high (Fig. B2.4). b) Sheath with basal section relative to apical section greater than 0.9 (Fig. B2.6). c) Ovipositor with fewer than 37 (usually 29–31) annuli. 3(2) A) Tibiae and tarsi reddish brown (Fig. B2.7). B) Ovipositor with 13–18 annuli outlined by annulus line only (Fig. B2.11) followed more distally by 23–28 annuli with pits before teeth annuli (Fig. B2.9); 10-15 annuli (anterior to teeth annuli at apex of ovipositor) each with a ridge extending from pit to ventral margin (Fig. 2.9). C) Sheath with basal section relative to apical section less than 0.53 (if between 0.53 and 0.61, use only A and B) (See Fig. B2.5 for measurements). Tibiae and tarsi dark brown or black (Fig. B2.8). a) b) Ovipositor with all annuli before apical teeth annuli with pits (Fig. B2.12); 5-7 annuli (anterior to teeth annuli at apex of ovipositor) each with a ridge from pit to ventral margin (Fig. B2.10). Sheath with basal section relative to apical section greater than 0.61 (if between 0.53 and 0.61, use only a and b) (See Fig. B2.5 for measurements). 4(2) A) Abdomen mostly reddish brown and abdominal segment 10 entirely light reddish brown (Fig. B2.13). B) Gena behind eye with a weakly outlined ridge (rounded and not sharp) (Fig. B2.16). C) Ovipositor pits (if necessary, remove apical section of sheath to see pits) 0.2 times as long as a annulus near middle or aligned with base of apical section of sheath (Fig. B2.18), and tibiae black and tarsi reddish brown. [Additional character: Fore wing vein 3A present and extended along posterior wing margin. Ovipositor with very small pits at base. a) Abdomen black (Fig. B2.14), or mostly reddish brown and abdominal segment 10 with cornus black at least apically (Fig. B2.15). b) Gena behind eye without ridge (Fig. B2.17). c) Ovipositor pits (if necessary, remove apical section of sheath to see pits) 0.12 times as long as a annulus (Figs. B2.20 & B2.21), or 0.3–0.7 times as long as an annulus near middle or aligned with base of apical section of sheath (Fig. B2.19), or if as C then tibiae light reddish brown.

5(4)	 A) Metatarsomere 2 with tarsal pad slightly shorter than ventral length of tarsomere (Fig. B2.22). B) Ovipositor without pits in basal 0.4–0.5 or pits very small at base (Fig. B2.24). C) Tibiae and tarsi light reddish brown (Fig. B2.26) and abdomen black with dark blue metallic reflections (Fig. B2.29), or tibiae and tarsi completely black (one specimen from Alaska). D) Specimen from Alaska, Yukon, north of central Alberta and probably northernmost British Columbia [Additional character: Head dorsally with diameter of pits 0.15–0.25 that of lateral ocellus.]
_	 a) Metatarsomere 2 with tarsal pad about half as long as ventral length of tarsomere (Fig. B2.23). b) Ovipositor with medium to large pits on all annuli before teeth annuli (Fig. B2.25). c) Tibiae and tarsi black (Fig. B2.27), or light reddish brown (Fig. B2.28) and most of abdomen reddish brown (Fig. B2.30). d) Specimen clearly south or east of region described in D.
6(5)	 A) Fore wing darkly tinted (Fig. B2.31a) or clear with darkly tinted bands near middle and apex (Fig. B2.31b).
_	a) Fore wing clear and slightly yellow tinted (Fig. B2.32).
7(6)	 A) Gena in lateral view (Fig. B2.33) and in dorsal view (Fig. B2.35) with most pits relatively larger and 0–1 diameters apart (only a few pits farther apart). B) Ovipositor pits near base (e.g., annuli 3–5) as long as pits of middle annuli or pits aligned with base of apical sheath section (0.3 or more than 0.37 times as long as annulus) (Fig. B2.37).
_	 a) Gena in lateral view (Fig. B2.34) and in dorsal view (Fig. B2.36) with most pits relatively smaller and 1–3 diameters apart (rarely, pits touching). b) Ovipositor pits near base (e.g., annuli 3–5) shorter (about 0.25 as long as annulus) than pits of middle annuli or pits aligned with base of apical sheath section (about 0.3 times as long as annulus) (Fig. B2.38).
8(7)	 A) Metatarsomere 2 in lateral view about 1.5 times as long as high (Fig. B2.39), and ventral tarsal pad about 0.5–0.7 times as long as tarsomere. B) Mesoscutum with discal pits usually without tooth-like processes except at middle; some processes fused laterally into irregular transverse ridges (Fig. B2.41). C) Abdomen black. D) Ovipositor with pits near middle or pits aligned with base of apical section of sheath (if necessary, remove apical section of sheath to see pits) about as long as high and small, their length 0.3 as long as annulus (Fig. B2.43).
_	 a) Metatarsomere 2 in lateral view 2.0–2.5 times as long as high (Fig. B2.40), and ventral pad 0.3–0.5 times as long as tarsomere. b) Mesoscutum with most discal pits with tooth-like processes; most processes fused in many directions forming a net-like pattern (Fig. B2.42). c) Abdomen black or mainly reddish brown. d) Ovipositor with pits near middle or pits aligned with base of apical section of sheath (if necessary, remove apical section of sheath to see pits) 1.4–1.8 times as long as high and their length 0.37–0.45 as long as annulus (Fig. B2.44).

- 9(6) A) Femora brown.
 - B) Mesoscutum with most discal pits with processes; processes usually fused in many directions forming a net-like pattern (Fig. B2.45).
 - C) Fore wing without vein 3A (Fig. B2.47).

D) Ovipositor with pits (if necessary, remove apical section of sheath to see pits) near middle or aligned with base of apical section of sheath about 3.0 times as long as wide, their anterior end long and furrow-like (Fig. B2.49).

E) Ovipositor thin and long: annulus length divided by ovipositor diameter at annulus between pits 1 and 2 = 1.9-2.4, and between pits 12 and 13 = 1.5-2.1 (Fig. B2.51).

Sirex xerophilus Schiff, n. sp.

a) Femora black though sometimes dark brown dorsally.

b) Mesoscutum with most discal pits usually mainly round with tooth behind large pits; some processes fused laterally into irregular transverse ridges (Fig. B2.46).

c) Fore wing with vein 3A (Fig. B2.48).

d) Ovipositor with pits (if necessary, remove apical section of sheath to see pits) near middle or pits aligned with base of apical section of sheath 1.2–1.3 times as long as wide, their anterior end not extended as narrow furrow (Fig. B2.50).

e) Ovipositor thick and short: annulus length divided by ovipositor diameter at annulus between pits 1 and 2 = 1.3, and between pits 12 and 13 = 1.0 (Fig. B2.52).

10(1) A) Abdomen posterior to segment 2 or 3 almost completely reddish brown (Fig. B2.53).

B) Gena (Fig. B2.55) and vertex (Fig. B2.57) with pits large (diameter 0.3–0.4 times that of lateral ocellus) and dense (on gena and vertex pits 0.0–0.5 pit diameter apart).

C) Metatarsomere 2 1.7 times as long as high (Fig. B2.59).

[Additional characters. Metatarsomere 2 in ventral view with tarsal pad 0.9 times as long as tarsomere. Sheath with apical section clearly shorter than basal section, their junction aligned between 15th and 16th annuli of ovipositor. Cornus in dorsal view short and clearly angular.]

a) Abdomen black with dark blue metallic reflections (Fig. B2.54).

b) Gena (Fig. B2.56) and vertex (Fig. B2.58) with pits smaller (diameter 0.1–0.25 that of lateral ocellus) and scattered (on gena pits 4–10 pit diameters apart, and on vertex 2.0–8 pit diameters apart).

c) Metatarsomere 2 2.0–3.6 times as long as high (Fig. B2.60).

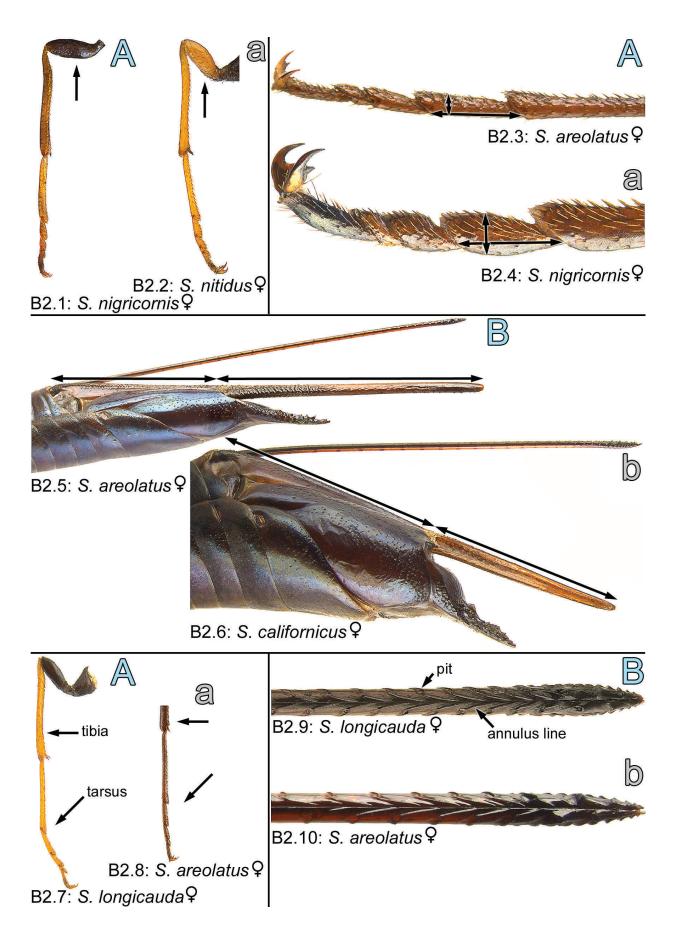
- **11(10)** A) Head posterodorsally with setae each with or without small pit at base (Fig. B2.61).
 - B) Mesoscutum with most discal pits mainly round with tooth behind larger pits, giving a rasp-like pattern; few processes fused laterally into irregular transverse ridges (Figs. B2.63 & B2.64).
 - C) Metatarsomere 2 with tarsal pad 0.3–0.4 times as long as tarsomere (Fig. B2.66).

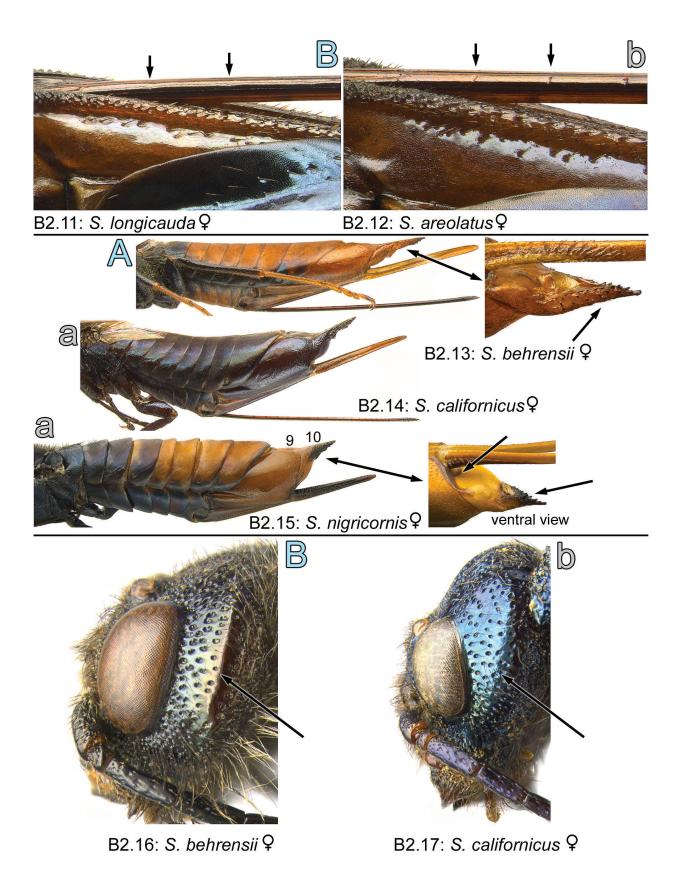
D) Ovipositor pits (if necessary, remove apical section of sheath to see pits) near middle or pits aligned with base of apical section of sheath at least 0.5 as long as annulus length (Fig. B2.68).

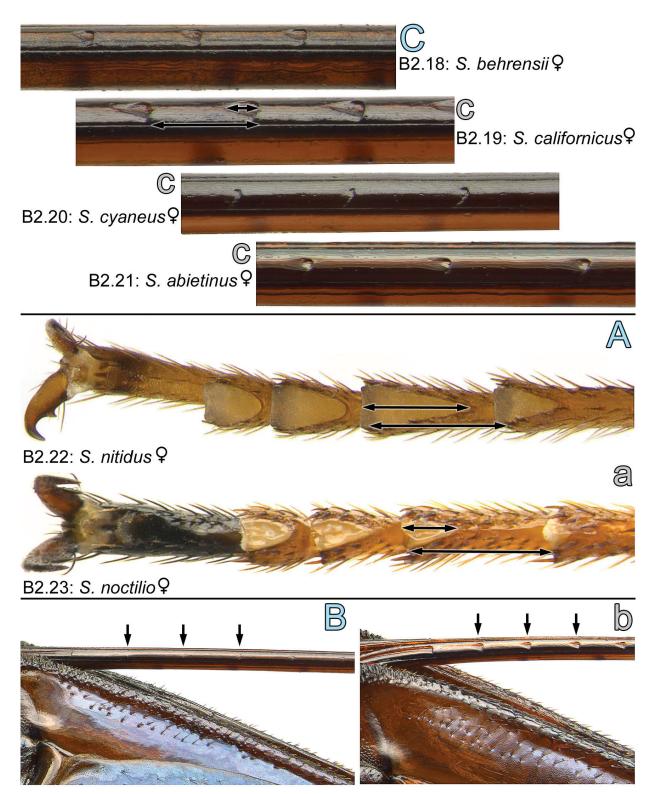
[Additional character. Metatarsomere 5 black or dark brown.]

-Sirex noctilio Fabricius, 1793
- a) Head posterodorsally with setae with large, clearly outline pit at base (Fig. B2.62).
- b) Mesoscutum with most discal pits with processes; processes usually fused in many directions forming a net-like pattern (Fig. B2.65).
- c) Metatarsomere 2 with tarsal pad 0.4–0.5 or 0.8 times as long as tarsomere (Fig. B2.67).
- d) Ovipositor pits (if necessary, remove apical section of sheath to see pits) near middle or pits aligned with base of apical section of sheath 0.1–0.4 times as long as annulus (Figs. B2.69–B2.71).

12(11)	A) Tibiae light reddish brown and their dorsal surface almost always with dark blue with metallic reflections (Fig. B2.72).
	[Additional characters: Ovipositor pits near middle or aligned with base of apical section of sheath (if necessary, remove apical section of sheath to see pits) 1.5–2.0 times as long as wide and 0.3–0.4 times as long as length of annulus (Fig. B2.71). Fore wing clear, faintly yellow tinted, and without dark bands at middle and
	apex.]
	Sirex varipes Walker, 1866
-	a) Tibiae completely light reddish brown (Fig. B2.73).
12(10)	
13(12)	A) Fore wing clear with dark bands at center and apex or completely darkly tinted (Fig. B2.74).B) Metarsomere 5 completely black (Fig. B2.76).
	C) Metatassomere 2 with tarsal pad about 0.5 times as long as ventral length of tarsomere (Fig. B2.78).
	D) Ovipositor pits near middle portion or pits aligned with base of apical section of sheath 1.5–2.0 times as long as wide and 0.3–0.4 as long as annulus length (Fig. B2.80).
_	a) Fore wing clear, faintly yellow tinted, and with at most a dark band at apex (Fig. B2.75).
	b) Metarsomere 5 entirely light reddish brown or almost black in apical half (Fig. B2.77).
	c) Metatarsomere 2 with tarsal pad about 0.8 times as long as ventral length of tarsomere (Fig. B2.79).
	 d) Ovipositor either without pits in basal 0.4–0.5, or pits present, almost as long as wide, and at most 0.25 times as long as annulus length (Figs. B2.81 & B2.82). 14
14(13)	A) Ovipositor pits near middle or pits aligned with base of apical section of sheath 0.15–0.25 as long as
	annulus and present even on annulus 2 but much smaller than pits at middle; ovipositor annulus lines clearly outlined in basal 0.3–0.4 (Fig. B2.83).
	[Additional character. Lancet with length of annulus 10 1.27–1.85 times as long as width of ovipositor at this annulus.]
_	a) Ovipositor pits near middle portion or pits aligned with base of apical section of sheath 0.0–0.14 times as long as annulus and pits absent in basal 0.4–0.5 of ovipositor; ovipositor annulus lines in basal 0.3 weakly outlined near dorsal edge or not outlined at all (Fig. B2.84).
15(14)	A) Sheath with basal section relative to apical section less than 0.87 (if between 0.87–1.0, use only B and C).
B)	Lancet with length of annulus 10 greater than 1.82 times as long as width of ovipositor at this annulus (if between 1.76–1.82, use A and C) [based on 26 specimens, we found no values below 1.85] (Fig. B2.85).
C)	Cornus usually long (about 2.0 times as long as wide) and broad in basal half (Fig. B2.87).
_	a) Sheath with basal section relative to apical section greater than 1.0 (if between 0.87–1.0, use b and c).
	 b) Lancet with length of annulus 10 less than 1.76 times as long as width of ovipositor at this annulus (if between 1.76–1.82, use a and c) [based on 40 specimens, we found no values below 1.77] (Fig. B2.86). c) Cornus usually short (about 1.5 times as long as wide) and narrow in basal half (Fig. B2.88).
	Sirex cyaneus Fabricius, 1781

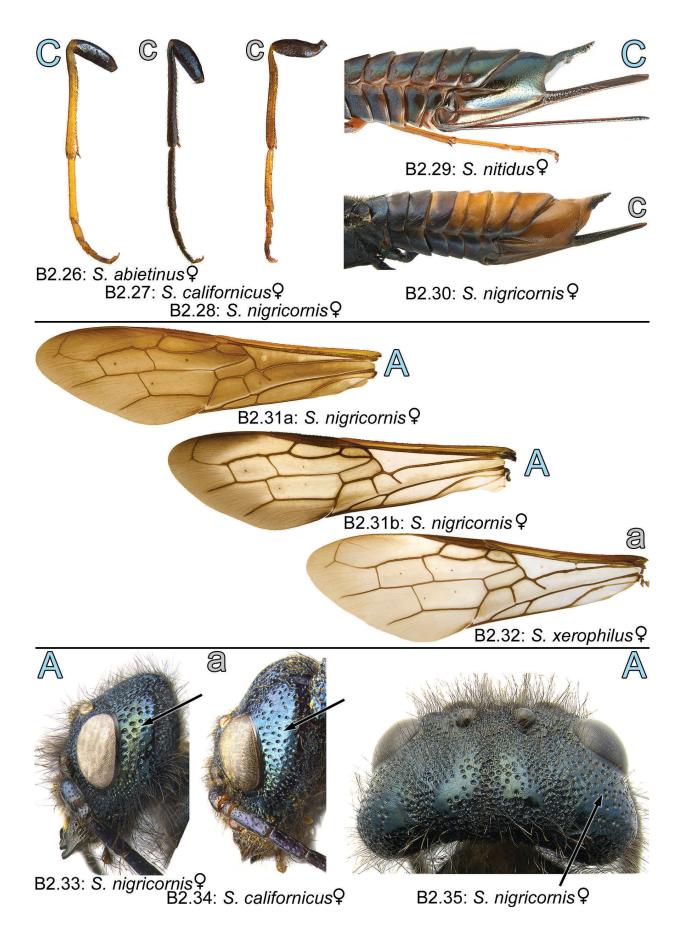


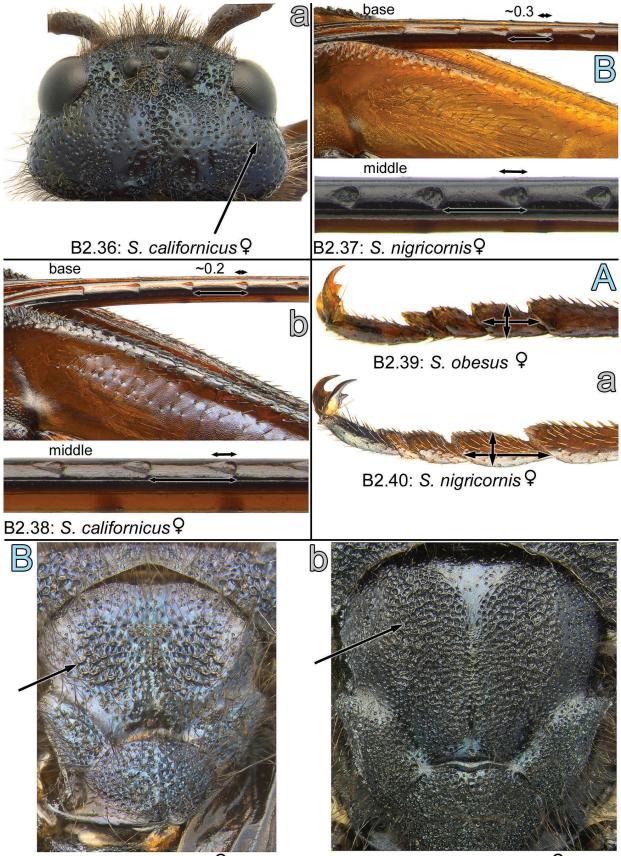




B2.24: S. abietinus Q

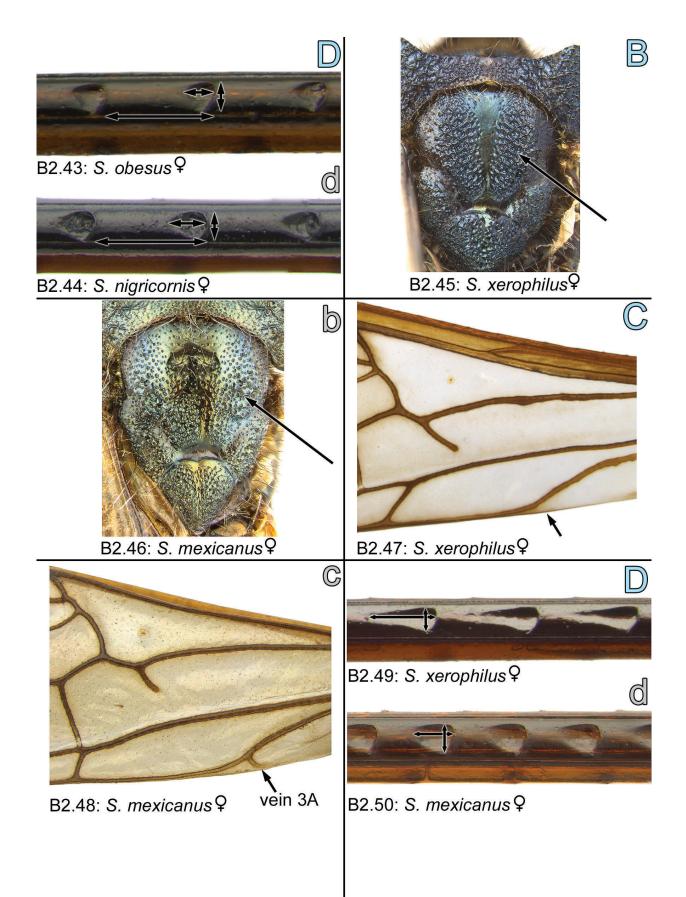
B2.25: S. californicus Q

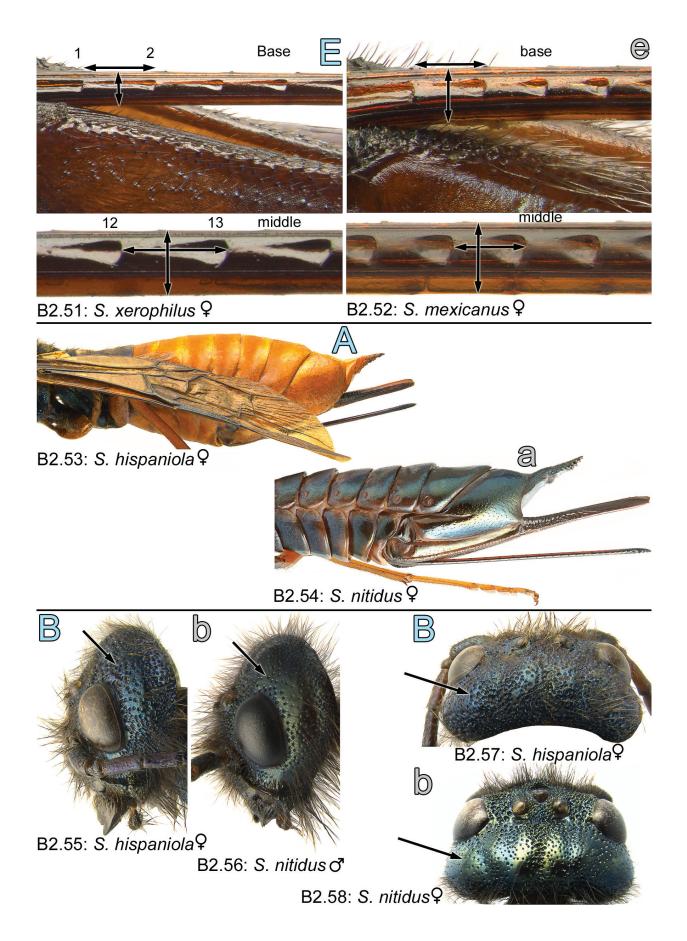


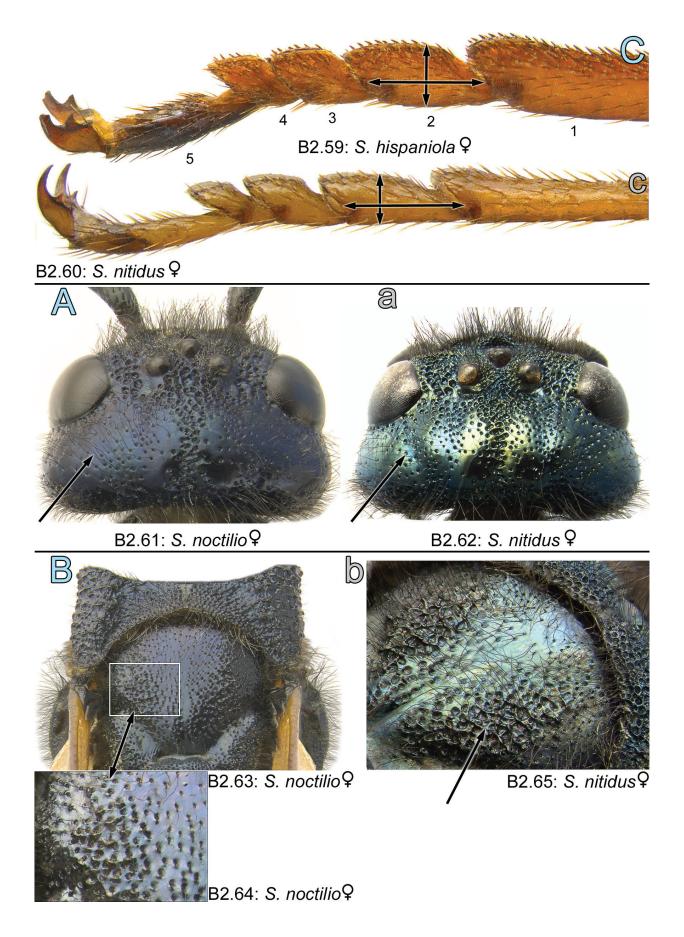


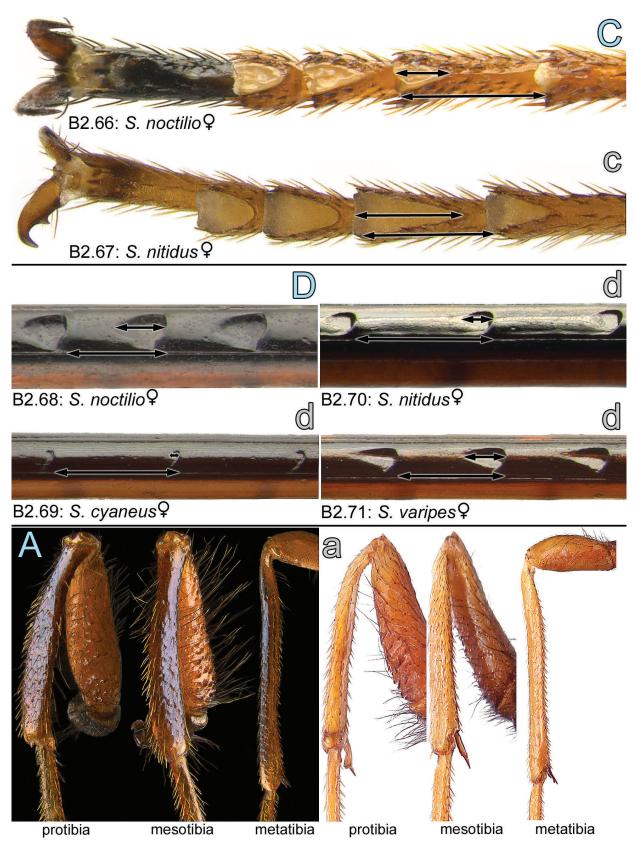
B2.41: S. obesus Q

B2.42: S. nigricornis Q



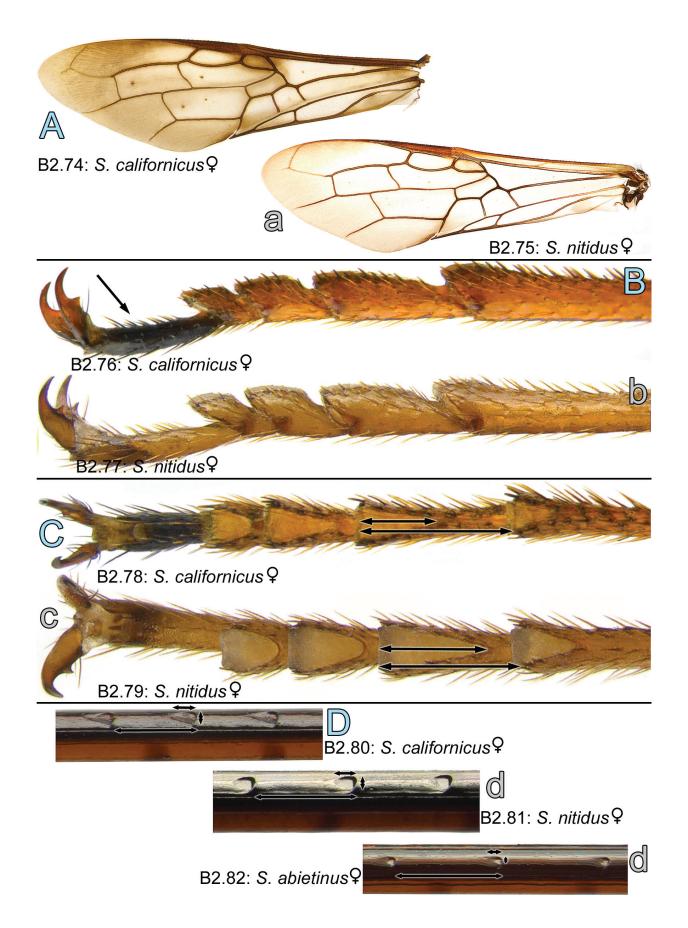


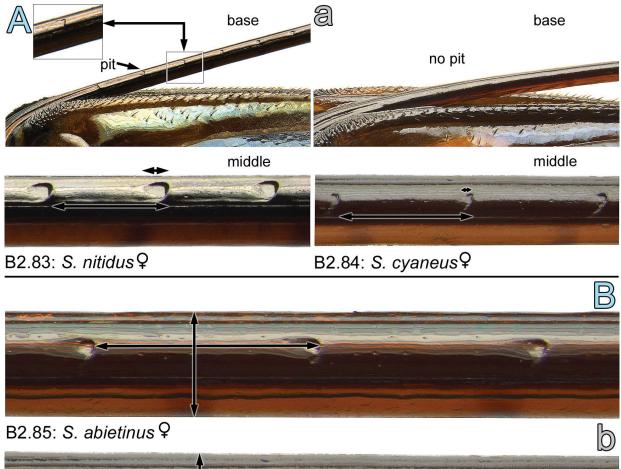


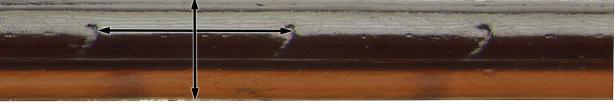


B2.72: S. varipes Q

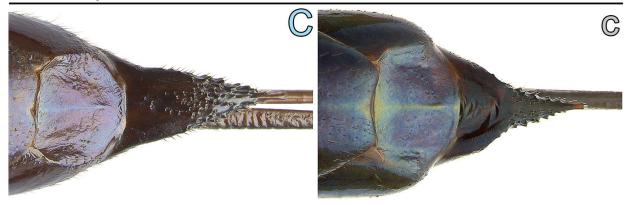
B2.73: S. nitidusQ







B2.86: S. cyaneus Q



B2.87: S. abietinus Q

B2.88: S. cyaneus Q

Males

1	A) Metafemur black (Fig. B2.89).	2
_	a) Metafemur mainly reddish brown (Figs. B2.90–B2.92).	_
2(1)	 A) Legs completely black (including base of metatibia) (Fig. B2.93). [Additional characters. Head with dorsal surface coarsely pitted, but pits scattered.] Sirex areolatus (Cresson, 1868) 	8
_	a) Fore and middle legs with tibiae and tarsi reddish brown or paler (mesotibia and/or mesotarsomere partly brown or black on dorsal surface in some species) (Figs. B2.94 & B2.95).	1
3(2)	A) Head with dorsal surface finely pitted and the pits scattered (Fig. B2.96).	
_	 a) Head with dorsal surface coarsely and densely pitted (Fig. B2.97). [Additional characters. Abdomen black except for segments 5 and 6 (rarely an additional segment), or abdomen light reddish brown except for anterior segments.] Sirex nigricornis Fabricius, 178 	or
4(3)	 A) Metatibia with extreme base light reddish brown (Fig. B2.98). B) Mesotibia and/or mesotarsomere 1 with dorsal surface light reddish brown and with brown or black spectorsally (spot size varies from small to large) (Fig. B2.100). Sirex nitidus (T. W. Harris, 1841 [Notes. Many specimens of this color form seen from Alaska, northernmost British Columbia, and the Yukon Territory, an Saskatchewan east to Newfoundland. In a few of these specimens, abdomen completely black. In Alaska, femora commonly 	.) .d
_	 black, and mesotibia and mesotarsomeres 1–3 widely black a) Metatibia with base more widely light reddish brown (Fig. B2.99). b) Mesotibia and mesotarsus completely light reddish brown (Fig. B2.101). Sirex longicauda Middlekauff, 194 	
5(1)	 A) Metafemur completely reddish brown; metatibia light reddish brown or black (Figs. B2.102 & B2.103). B) Gena black with dark blue metallic reflections (Fig. B2.105). 	
-	 a) Metafemur reddish brown, and black along dorsal surface; metatibia brown (Fig. B2.104). b) Gena brown posterodorsally (Fig. B2.106). [Additional characters. Metatibia and metatarsus brown, not reddish brown or black; dorsal surface of hea coarsely and densely pitted.] Sirex behrensii (Cresson, 1880) 	d
6(5)	 A) Metatibia and metatarsus reddish brown or paler, and base of metatibia not obviously pale (Fig. B2.107). B) Gena posterodorsally with pits mostly touching (except <i>S. californicus</i>) one another to about one diameter apart, only a few pits farther apart (Fig. B2.110). 	
_	 a) Metatibia and at least metatarsomeres 1–3 almost completely black, and metatibia clearly light reddis brown at base or black (Figs. B2.108 & B2.109). b) Gena posterodorsally with pits mostly 1–3 diameters apart, the pits rarely touching (Fig. B2.111). 1 	h

7(6)	 A) Antenna black or, at most, pedicel and flagellomeres 1 and 2 brown (Fig. B2.112). B) Fore wing clearly yellow tinted, especially the cells posterior to costal cell and stigma (Fig. B2.114).
	[Additional character. Head densely pitted dorsally.]
_	 a) Antenna with at least scape, pedicel and flagellomeres 1–5 light reddish brown (Fig. B2.113). b) Fore wing clear, scarcely tinted (Fig. B2.115). 8
8(7)	A) Antenna with scape, pedicel and flagellomeres 1–3 or 4 light reddish brown, remaining flagellomeres black (Fig. B2.116).
	B) Head dorsally with scattered pits and pit diameter 0.15–0.3 times lateral ocellus diameter (Fig. B2.118). <i>Sirex californicus</i> (Ashmead, 1904)
_	a) Antenna almost completely reddish brown or paler (apical 2–4 flagellomeres darker in a few specimens) (Fig. B2.117).
	b) Head dorsally densely pitted and pit diameter 0.3–0.4 times lateral ocellus diameter (Fig. B2.119).
9(8)	A) Coxae black (as in Fig. B2.120)
	B) Mesoscutum submedially with net-like arrangement of polygonal pits with distinct raised margins; pit diameter 0.5–1.0 times lateral ocellus diameter (Fig. B2.122).
_	a) Coxae completely reddish brown (Fig. B2.121).
	b) Mesoscutum submedially with mostly round pits usually separated from one another, and usually without raised margins; pit diameter 0.3–0.7 times lateral ocellus diameter (Fig. B2.123).
10(6)	A) Metatibia at base widely light reddish brown (Fig. B2.124).
	B) Head with setae posterodorsally behind eye each with a small pit at their base or without pit (Fig. B2.127). C) Mesoscutum submedially with small pits, each usually with a tooth behind (giving a rasp-like pattern), the $(F_{i}, F_{i}) = (F_{i}, F_{i})$
	tooth usually not fused laterally with others (Fig. B2.129). <i>Sirex noctilio</i> Fabricius, 1793
_	a) Metatibia at base narrowly light reddish brown (Figs. B2.125 & B2.126).
	 b) Head with setae posterodorsally behind eye each with a deeply outlined pit at their base (Fig. B2.128).
	c) Mesoscutum submedially with moderate to large pits, each often surrounded with raised margins forming a net-like pattern (Fig. B2.130).
11(10)	A) Mesotibia and/or mesotarsomere 1 with brown to black spot on dorsal surface (Fig. B2.131).
_	a) Mesotibia and metatarsomere 1 completely light reddish brown (Fig. B2.132).
	12 [Note. In the range of balsam fir in Alberta and perhaps Saskatchewan, males of <i>S. cyaneus</i> matching above two couplets cannot be segregated with certainty using this character. Elsewhere this character almost always (99%) works.]
12(11)	A) Abdomen with tergum 8 (in most specimens) and sterna 8 and 9 (in all specimens) black or mainly so (Fig. B2.133).
	B) Western Alberta and eastward.
	[Note. In western Alberta the apex of abdomen is light reddish brown. Character works from Manitoba eastward. No males seen from Saskatchewan.]
_	a) Abdomen with apical segments light reddish brown (Fig. B2.134).
	b) Rocky Mountains and westward.
	Sirex abietinus Goulet, n. sp.

13(11) A) Mesotibia dark brown on about 0.5 of outer surface and dark spot not expanded on inner and lateral surfaces; mesotarsomere 1 or 1 and 2 dark brown (Fig. B2.135).

B) Metatibia with base narrowly light reddish brown, the length of reddish brown area about as long as minimum width of tibia (Fig. B2.137).

C) Abdomen with tergum 7 and sterna 7 and 8 black (Fig. B2.139) or light reddish brown (Fig. B2.140) (if the latter, use A, B, and D).

D) Across North America where spruces grow.

- a) Mesotibia black on about 0.7 of outer surface, and partly or completely covering lateral and inner surfaces; tarsomeres 1 and 2 or 1–3 black (Fig. B2.136).

b) Metatibia with base very narrowly light reddish brown, the length of reddish brown area shorter than minimum width of tibia (Fig. B2.138).

- c) Abdomen with apical segments light reddish brown (as in Figs. B2.140 & B2.141).
- d) Rocky Mountains westward.

3. Key to Species of *Tremex*

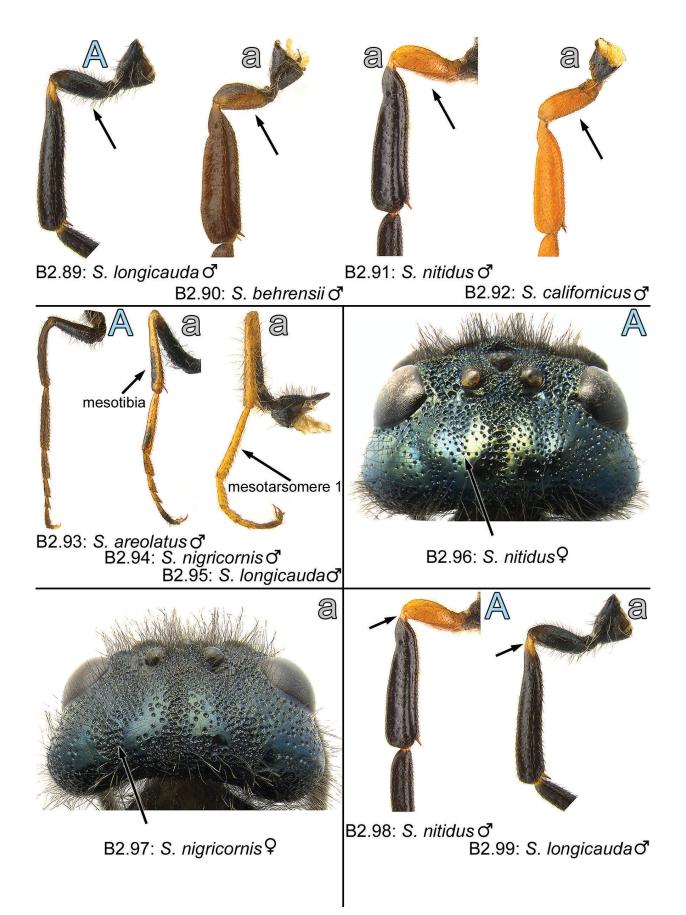
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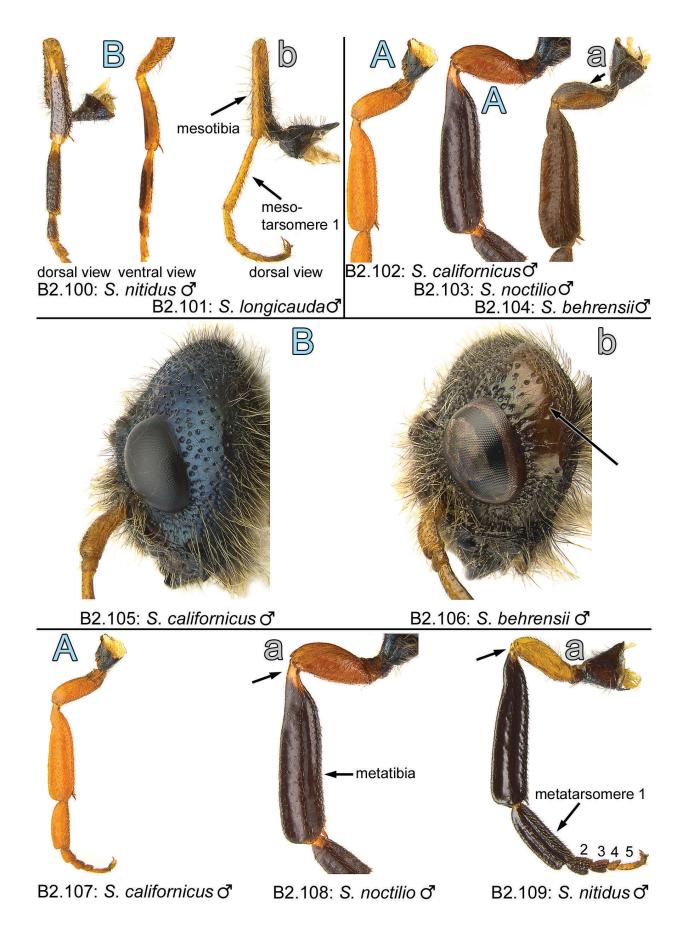
- A) Body setae generally short; frons in lateral view with setae about 0.5 times as long as distance between inner edges of lateral ocelli (Fig. B3.1).
 - B) Female: cornus in lateral view with lateral edge protruded and angular in basal 0.3 (Fig. B3.3).

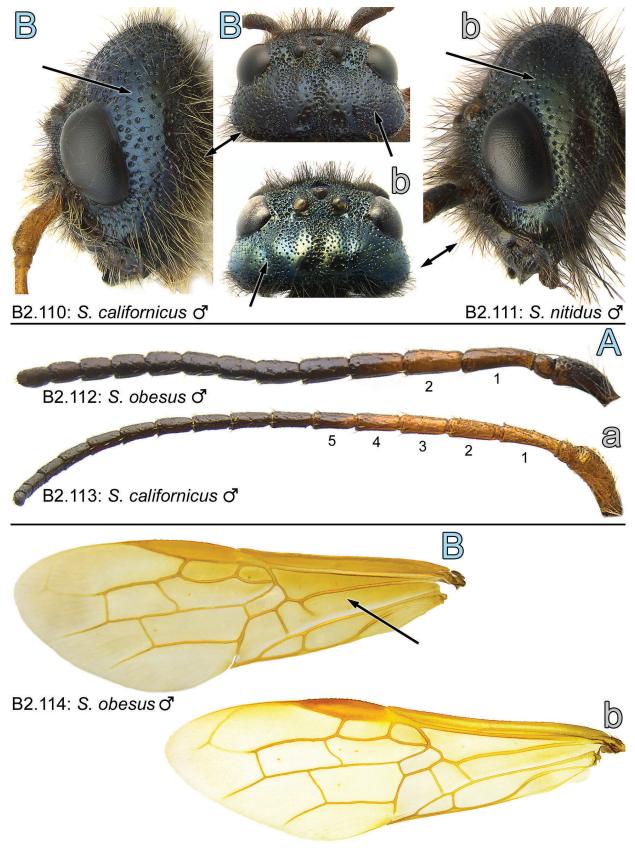
C) **Female**: abdominal tergum 9 laterally with slightly raised, semicircular pit anterior to each seta and pit clearly separated from other such pits (Fig. B3.5).

- D) Female: metatarsomere 2 in lateral view with dorsal edge clearly convex (Fig. B3.7).
- E) Male: metatarsomere 5 as long as metatarsomere 2 (Fig. B3.9).

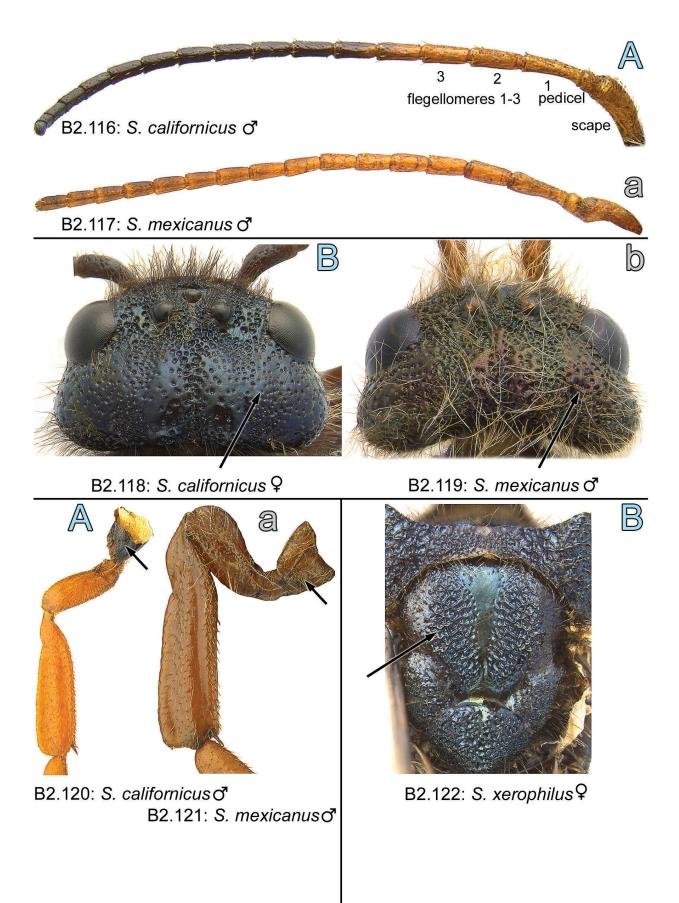
- a) Body setae generally long; frons in lateral view with setae about as long as or longer than distance between inner edges of lateral ocelli (Fig. B3.2).
 - b) **Female**: cornus in lateral view with lateral edge straight in basal 0.3 (Fig. B3.4).
 - c) **Female**: abdominal tergum 9 laterally with distinct circular pit surrounding each setae, and pit contiguous with other such pits (Fig. B3.6).
 - d) Female: metatarsomere 2 in lateral view with dorsal edge almost straight (Fig. B3.8).
 - e) Male: metatarsomere 5 as long as metatarsomere 2 + 3 (Fig. B3.10).

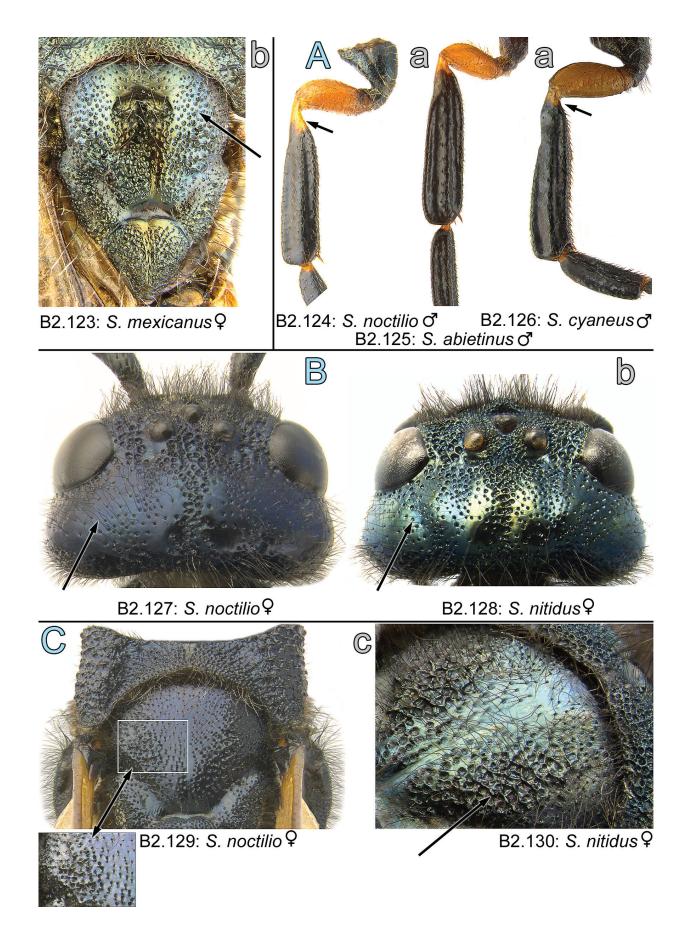


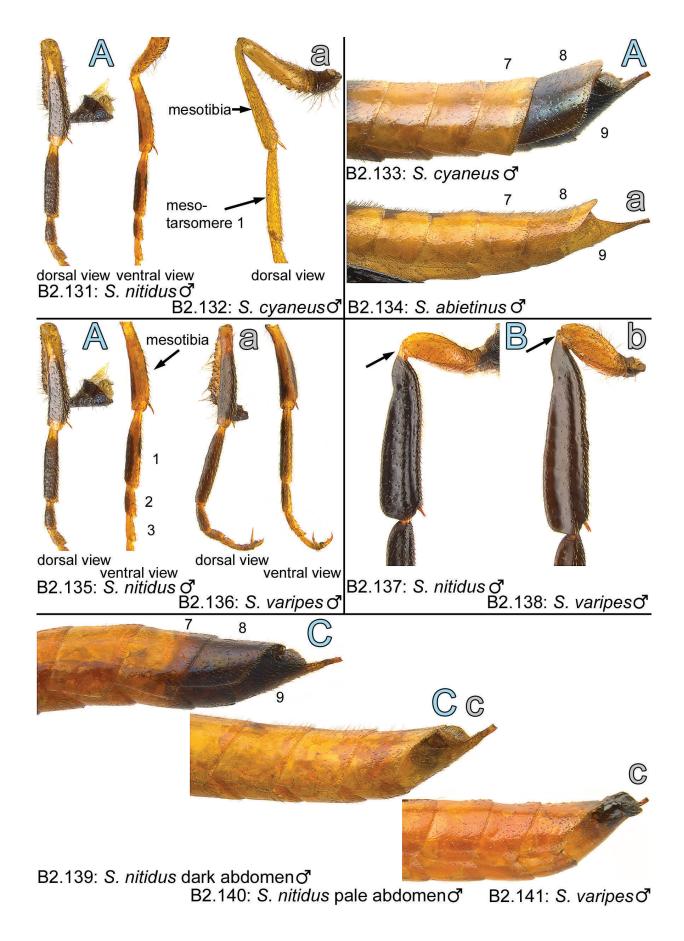


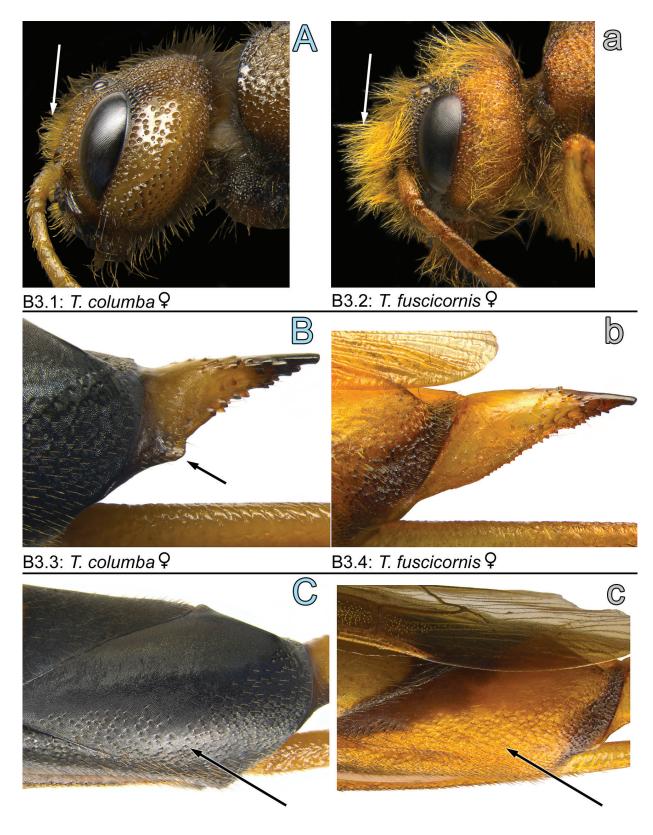


B2.115: S. californicus o



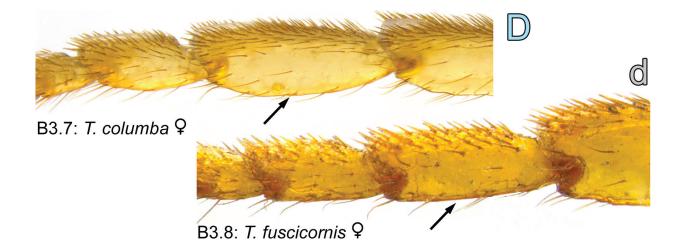


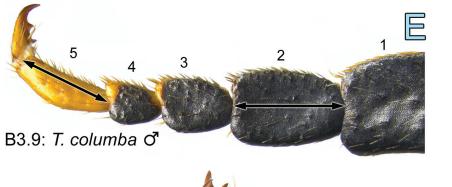


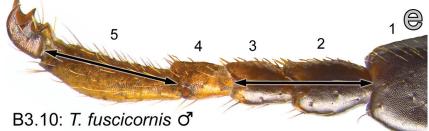


B3.5: T. columba Q

B3.6: *T. fuscicornis*♀







4.	Key	to	Species	of	Urocerus
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Females

1	A) Abdomen black with light reddish brown transverse bands on at least segment 2 and anterior half of segment 8 (Fig. B4.1).						
	B) Protarsomeres 2–5 reddish brown (Fig. B4.4).						
	[Additional character. Flagellum completely light reddish brown.]						
_	 a) Abdomen black with or without white lateral spot on tergum 8 (Fig. B4.2), or partly to completely reddish brown but without light reddish brown transverse bands (Fig. B4.3). b) Protarsomeres 2–5 black (Fig. B4.5). 						
	4						
2(1)	 A) Abdominal segment 7 light reddish brown (may be black at side) and segment 9 black (Fig. B4.6) or almost completely light reddish brown. B) Bronotum black (Fig. B4.8) 						
	B) Pronotum black (Fig. B4.8).C) Metatibia almost completely light reddish brown except for brownish spot on median surface in apical 0.2 (Fig. B4.10).						
	D) Vertex covered with densely spaced pits (Fig. B4.12).						
	a) Abdominal segment 7 black and segment 9 with light reddish brown transverse band in apical 0.5 (Fig.						
_	 a) Abdominal segment 7 black and segment 9 with light reddish brown transverse band in apical 0.5 (Fig. B4.7). b) Pronotum reddish brown (Fig. B4.9). 						
	c) Metatibia mostly black except for a yellowish transverse band in basal 0.3 (Fig. B4.11).						
	d) Vertex mostly smooth with few pits except along posterior edge of eye, just behind ocelli and on median longitudinal furrow (Fig. B4.13).						
	Urocerus sah (Mocsáry, 1881)						
3(2)	A) Tergum 8 entirely, tergum 9 in posterior half and tergum 10 entirely (except posterolateral corners in some specimens) light reddish brown (Fig. B4.14).						
	B) Sheath with apical section more than 1.52 times as long as basal section (if between 1.31 and 1.52, use A). <i>Urocerus gigas</i> (Linnaeus, 1758)						
_	a) Tergum 8 in basal half and only cornus on tergum 10 light reddish brown; (tergum 8 rarely completely black) (Fig. B4.15).						
	b) Sheath with apical section less than 1.31 times as long as basal section (if between 1.31 and 1.52, use a). 						
4(1)	A) Antenna with at least basal 0.25–0.7 black, the remaining antennomeres white but brown to black at apex of last segment (Fig. B4.16).						
	B) Cornus completely reddish brown to light reddish brown (Fig. B4.18).						
	 C) Tergum 8 sublaterally with microsculpture reticulate between spiracle and pitted sculpticells dorsally and sculpticells clearly scale-like (Fig. B4.20). 5 						
_	a) Antenna with at most the three to four basal antennomeres black, the remaining antennomeres white, or						
	remaining antennomeres white except for 3–7 apical antenomeres brown (Fig. B4.17).b) Cornus usually black, rarely partly light reddish brown (Fig. B4.19).						
	 c) Tergum 8 sublaterally without (at most suggested) microsculpture between spiracle and pitted sculpticells dorsally (Fig. B4.22) or reticulation outlined and sculpticells flat and scarcely elevated posteriorly (Fig. B4.21). 						

5(4) A) Abdomen reddish brown at least in apical half (including cornus) (Fig. B4.23).

B) Tergum 9 with dorsal surface lateral to tergum 8 entirely smooth and without reticulation, lateral surface reticulate but sculpticells flat and scarcely elevated posteriorly (best seen in posterior view of segment) (Fig. B4.25).

C) Metatarsomere 2 in lateral view about 2 times as long as high (Fig. B4.27), and in ventral view tarsal pad about half as long as tarsomere.

D) Sheath with length of apical section less than 1.39 times basal section (**if between** 1.39 and 1.45, use A–C).

a) Abdomen black, except cornus light reddish brown (Fig. B4.24).

b) Tergum 9 with dorsal surface lateral to tergum 8 smooth only medially near segment 8 and median basin, otherwise clearly reticulate laterally and sculpticells clearly scale-like (best seen in posterior view of segment) (Fig. B4.26).

c) Metatarsomere 2 in lateral view about 3 times as long as high (Fig. B4.28), and in ventral view with tarsal pad more than 0.7 times as long as tarsomere.

d) Sheath with length of apical section greater than 1.45 times basal section (**if between** 1.39 and 1.45, use a-c).

- A) Flagellum completely yellowish to light reddish brown (Fig. B4.29).
 - B) Wings clearly yellow tinted (Fig. B4.31).
 - C) Metatarsomere 2 about 4.0 times as long as high (Fig. B4.33).

D) Tergum 8 sublaterally without microsculpture between spiracle and pitted sculpticells dorsally, the surface shiny (Fig. B4.35).

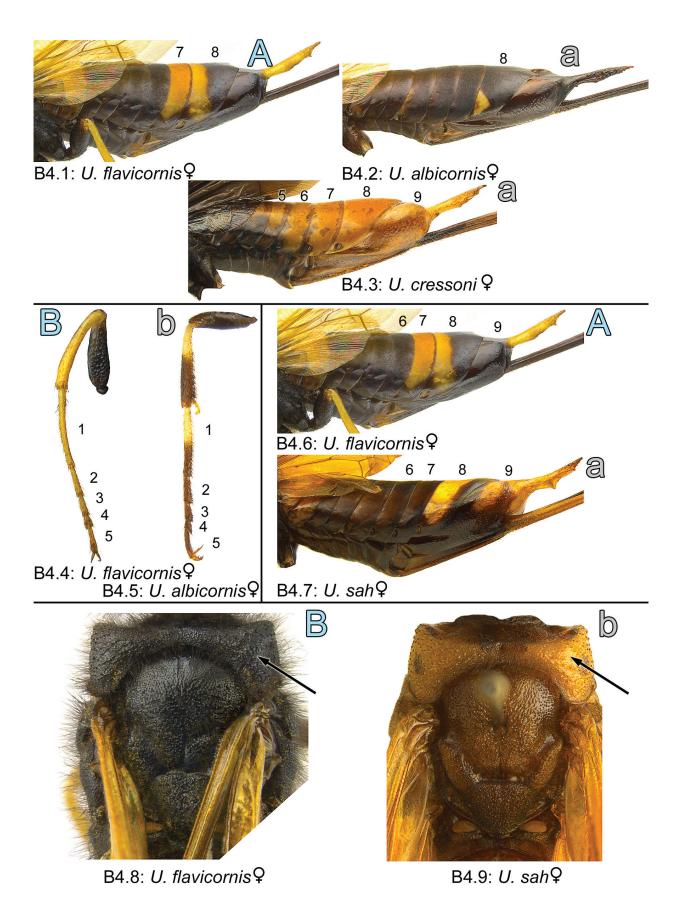
a) Flagellomere 1 or 1 and 2 black, except for brown apical flagellomeres 3–7, remaining flagellomeres white to light reddish brown (Fig. B4.30).

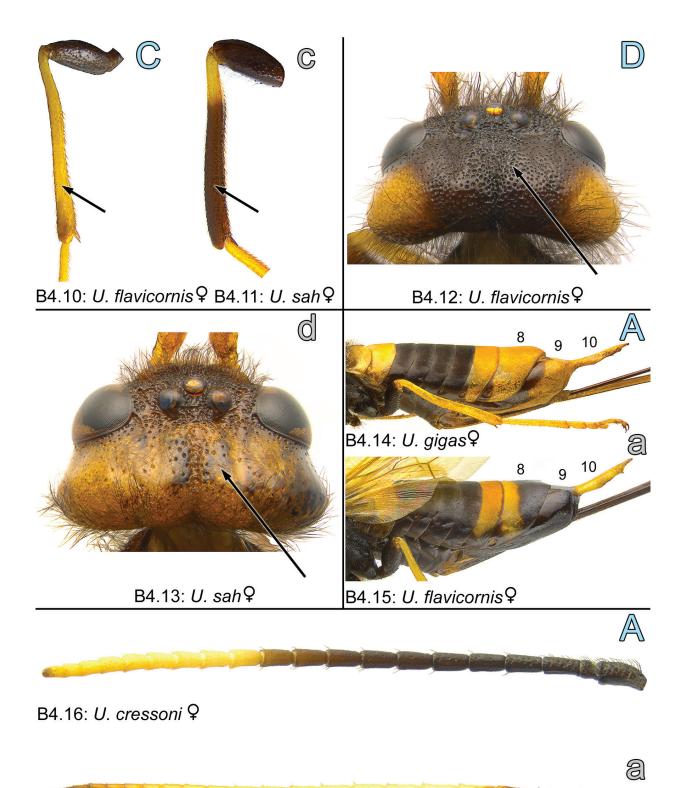
b) Wings darkly tinted (Fig. B4.32).

- c) Metatarsomere 2 about 2.5 times as long as high (Fig. B4.34).
- d) Tergum 8 sublaterally with microsculpture and with clearly outlined meshes between spiracle and pitted sculpticells dorsally (Fig. B4.36).

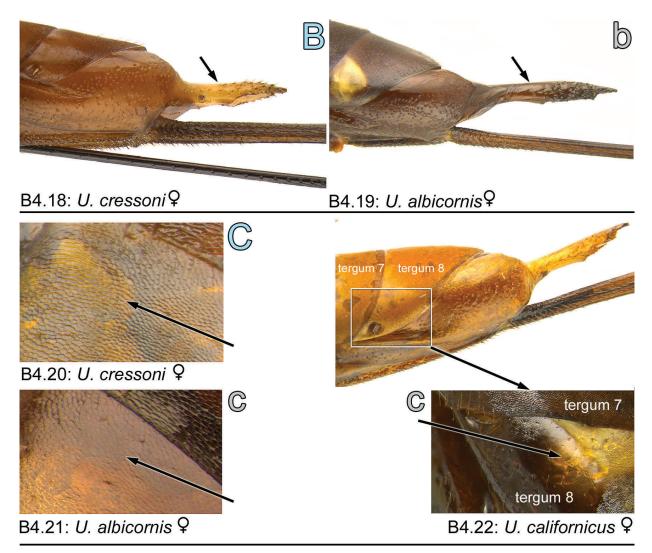
.....Urocerus albicornis (Fabricius, 1781)

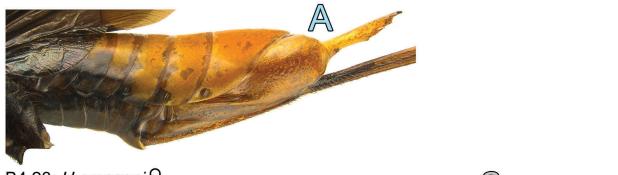
6(4)





B4.17: U. albicornis Q

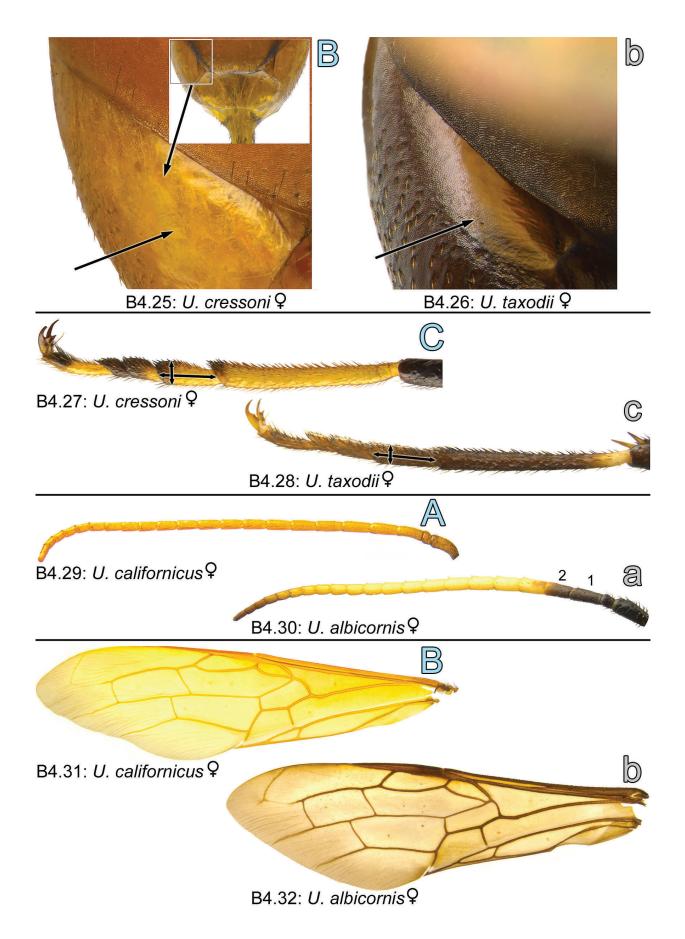


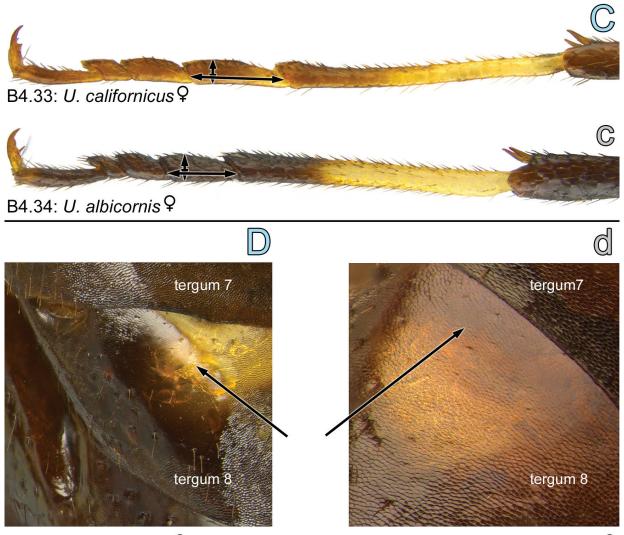


B4.23: U.cressoni Q



B4.24: *U. taxodii*♀





B4.35: U. californicus♀

B4.36: U. albicornisQ

Males

1	A) Antenna black at base and sharply white to light reddish brown in apical half (Fig. B4.37).B) Abdomen with apical segments light reddish brown (Fig. B4.41) and metatibia mainly to completely black (Fig. B4.43).
_	 a) Antenna black (Fig. B4.38), black and light reddish brown at base (pale and dark portions not sharply divided) (Fig. B4.39), or completely light reddish brown (Fig. B4.40).
	b) Abdominal segments 7–9 or 8 and 9 black (Fig. B4.42) and metatibia mainly black (Fig. B4.44), or apical abdominal segments light reddish brown and metatibia reddish brown or mainly black (if the latter, use a).
2(1)	A) Femora, tibiae, tarsi, head capsule except yellow genal spot, and thorax completely black (Figs. B4.45 & B4.47).
_	a) Femora black except reddish brown at apex; metatibia in basal 0.25, protarsus mesotarsus and mesotibia, metatarsomeres 1 and 2 at base, and head capsule ventrally light reddish brown; pronotum reddish brown (Figs. B4.46 & B4.48).
	Urocerus taxodii (Ashmead, 1904)
3(1)	A) Head mainly to completely reddish brown (Fig. B4.49) or genal white spot extending dorsally to median area.
	B) Antenna light reddish brown (Fig. B4.51).
_	 a) Head completely or mainly black in dorsal half, and with white genal spot restricted to area behind eye (Fig. B4.50).
	b) Antenna black (Fig. B4.53), pale at base shifting to brown or black at apex (Fig. B4.52), or very rarely completely light reddish brown (if the latter , use a).
4(3)	A) Head without pits on much of dorsal surface except pits usually present and usually small near posterior edge of eye, behind ocelli and along longitudinal median furrow (Fig. B4.54).
	B) Head capsule black in at least ventral half (Fig. B4.56).C) Metafemur black and reddish brown in apical third, metatibia brown except basal fifth, metatarsomere 1
	brown except for reddish brown base and apex (Fig. B4.58); mesofemur black except apex; mesotibia and mesotarsomeres 1 and 2 light reddish brown; abdominal segments 7 (totally or partly), 8 and 9 black (Fig.
	B4.60).
_	a) Head with large pits on much of dorsal surface except pits absent on genal spot behind eye (Fig. B4.55).
	b) Head capsule completely light reddish brown (Fig. B4.57).
	c) Femora, tibiae (except light reddish brown basal third of mesotibia, most of protibia and all of protarsus) and at least tarsomeres 1 and 2 of middle and hind legs reddish brown (Fig. B4.59); abdominal segments 7–9 light reddish brown (Fig. B4.61).
	Urocerus californicus Norton, 1869
5(3)	A) Metatarsomere 1 in lateral view 5.5–8.2 times as long as high (if between 5.5 and 6.3, use B) and its base with light reddish brown area about twice as long as high (Fig. B4.62).
	B) Metatibia generally more than 7.0 times as long as high (if between 6.8–8.5, use A) (Fig. B4.64).
	[Additional characters. Apex of metatarsomere 1 with narrow reddish brown transverse band. Head (except for white spot on gena) and pronotum black.]
	[Note. If specimen from North America, then the character "A" range is 5.5–8.0 for <i>U. flavicornis</i> and 4.0–5.2 for <i>U. albicornis</i> , and the character "B" range is 5.5–7.0 for <i>U. albicornis</i> and 6.8–9.0 for <i>U. flavicornis</i> .]

- a) Metatarsomere 1 in lateral view 4.0–5.5 times as long as high (if between 5.5–6.3, use b) and its base with light reddish brown area about 1.0 or 1.5 times as long as high (Fig. B4.63).
 - b) Metatibia generally less than 6.8 times as long as high (**if between** 6.8–8.5, use a) (Fig. B4.65).
- 6(5) A) Abdominal tergum 7 at least mainly black (Fig. B4.66).

B) Metatarsomere 1 in lateral view 4.0–4.4 times as long as high (**if between** 4.5–5.2, use A), its base with light reddish brown area about as long as high and its apex black or dark brown (Fig. B4.68).

[Additional characters. Abdomen with tergum 2 usually black; antenna usually black at least apically; pronotum dorsally usually partly to mostly reddish brown, rarely entirely black; head usually partly or mostly reddish brown ventral to antennal sockets.]

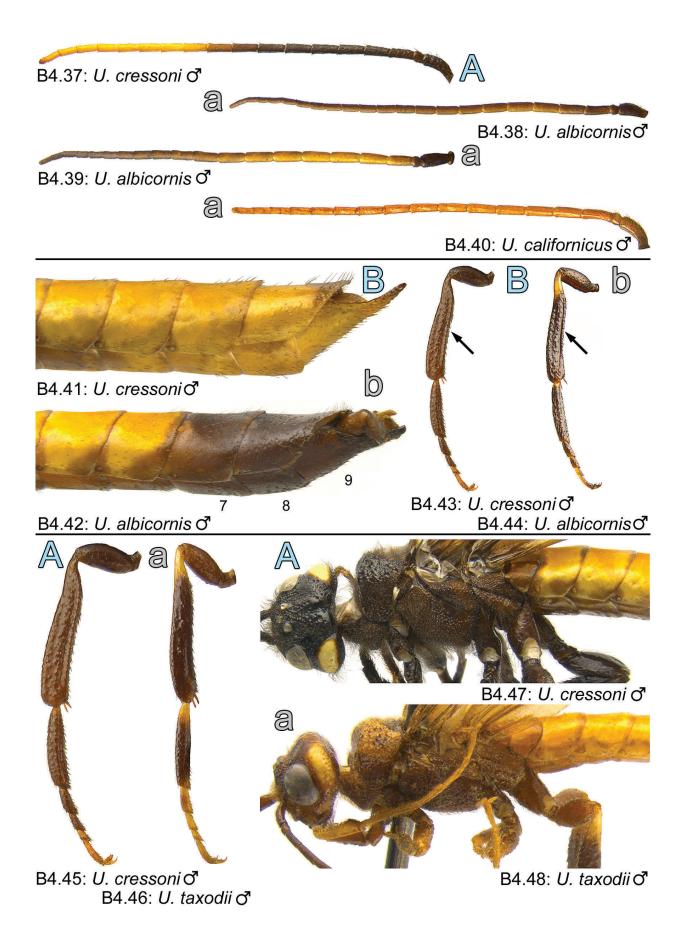
......Urocerus albicornis (Fabricius, 1781)

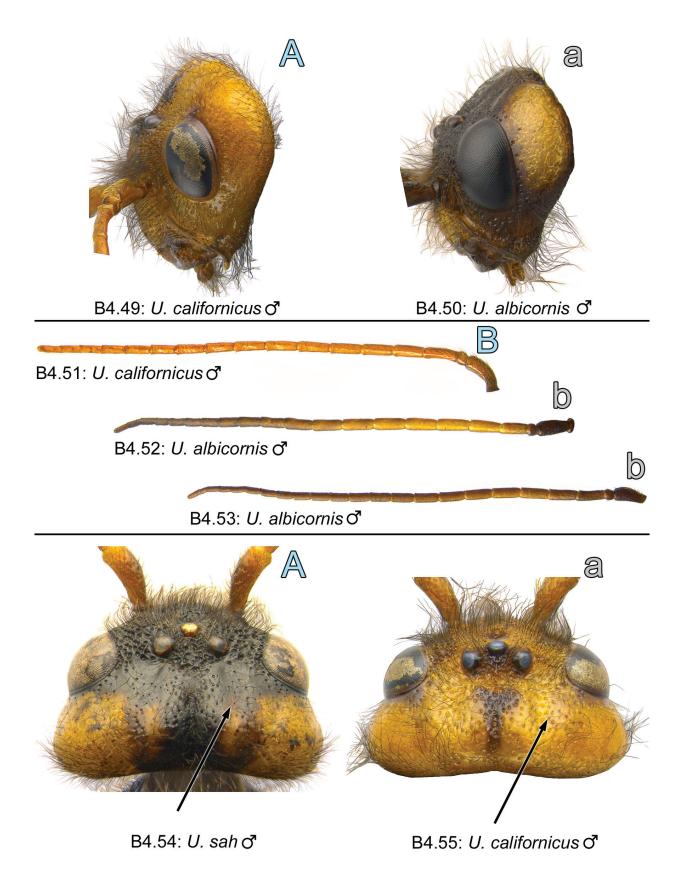
a) Abdominal tergum 7 mainly or completely reddish brown (Fig. B4.67).

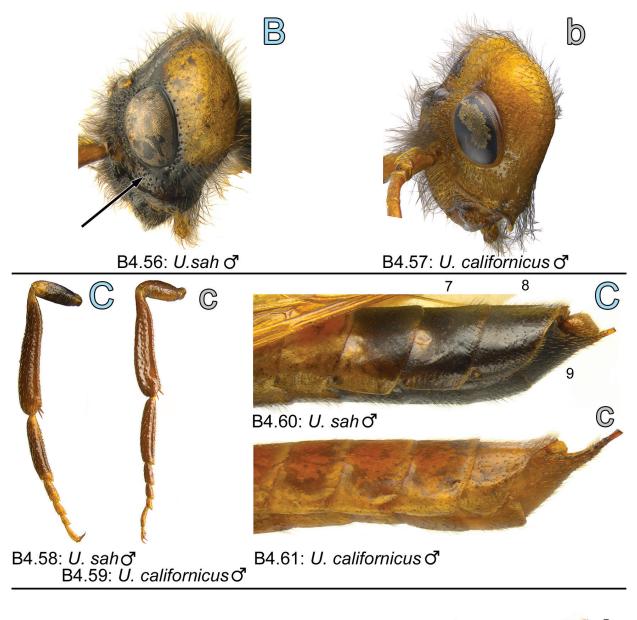
b) Metatarsomere 1 in lateral view 5.3–6.3 times as long as high (**if between** 4.5–5.2, use a), its base with light reddish brown area about 1.5 times as long as high and its apex reddish brown (Fig. B4.69).

[Additional characters. Abdomen with tergum 2 reddish brown, rarely black; antenna usually entirely white, rarely darkened in apical 0.25; pronotum black dorsally, rarely with white area laterally on vertical surface ventral to anterolateral corner; head rarely with reddish brown spots ventral to antennal sockets.]

.....Urocerus gigas (Linnaeus, 1758)

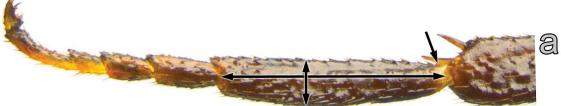




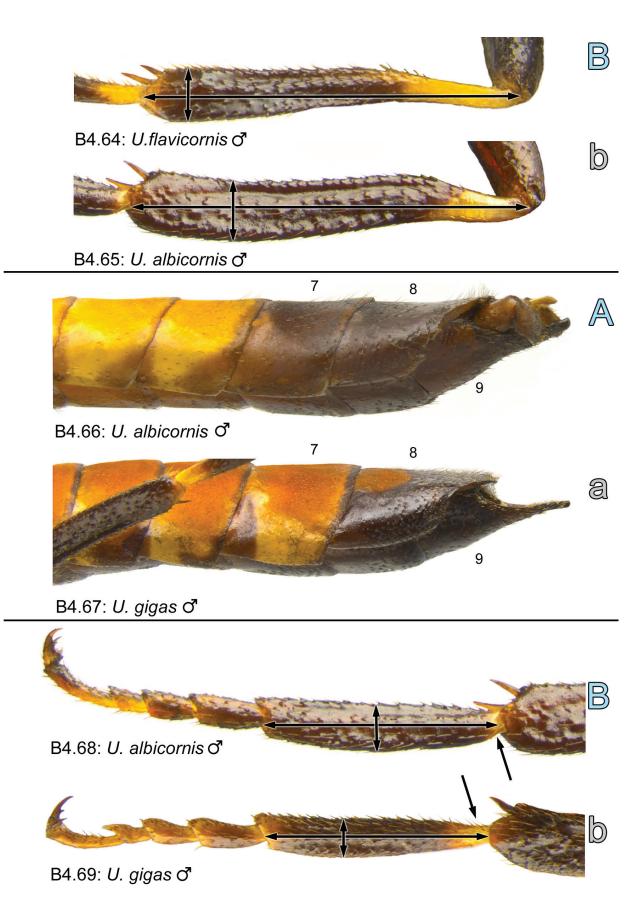




B4.62: U. flavicornis o



B4.63: U. albicornis o



5. Key to Species of Xeris

1 A) Gena in dorsal view with lateral angle not prominent (Fig. B5.1), the maximum distance between outer genal edges at most about as wide as maximum distance between outer edges of eyes (Fig. B5.3).

B) Maximum eye height in lateral view 0.53–0.61 times maximum head height (measured from genal ridge) (Fig. B5.5).

C) Female: tibiae black and tarsi light reddish brown (Fig. B5.8).

D) **Female**: sheath with length of basal section about 0.5 times length of apical section (Fig. B5.11); apical section without longitudinal ridge between dorsal and ventral edges (Fig. B5.11, insert).

E) **Female**: ovipositor with pit on each annulus anterior to teeth annuli at apex (Fig. B5.14) and each pit with anterior apex extending toward preceding annulus as a shallow furrow (as in middle and end Fig. B5.14); sheath with junction of basal and apical sections aligned between annuli 8 and 9 of ovipositor.

- a) Gena in dorsal view with lateral angle more prominent (Fig. B5.2); the maximum distance between outer genal edges at least slightly wider than maximum distance between outer edges of eyes (Fig. B5.4).
- b) Maximum eye height in lateral view at most 0.51 times maximum head height (measured from genal ridge) (Figs. B5.6 and B5.7).
- c) Female: tibiae and tarsi similar in color: black (Fig. B5.8) or light reddish brown (Fig. B5.10).

d) **Female**: sheath with length of basal section at most 0.46 times length of apical section (Figs. B5.12 and 13); apical section with longitudinal ridge between dorsal and ventral edges (insert in Fig. B5.13).

e) **Female**: ovipositor with pit only on apical 5–7 annuli anterior to teeth annuli (very small pit may be present on one or more additional annuli anteriorly) (Fig. B5.14); each pit with anterior end sharp and round, and shorter than 0.5 times annulus length (as in end Fig. B5.15); sheath with junction between of basal and apical sections aligned between 2 and 3, 3 and 4, or 4 and 5 annuli.

2(1)	A) Wings darkly tinted over most or all of surface (Fig. B5.16).						
_	a) Wings very lightly tinted or clear except for lightly tinted apical 0.25 (Fig. B5.17). [Note. Some specimens of <i>X. indecisus</i> could key through either alternate of this couplet.]						
3(2)	 A) Gena below eye and genal ridge (including adjacent occiput) densely pitted (Fig. B5.18). B) Gena with transverse ridge dorsal to mandible, broadly rounded and coarsely pitted (Fig. B5.20). C) Female: legs black (Fig. B5.22). D) Female: sheath with basal section 0.4 times as long as apical section (Fig. B5.24). Xeris tropicalis Goulet, n. 						
_	[Note. Male not known, but character A and B will help recognit a) Gena below eye and genal ridge (including adjacent occiput) with or without a few pits, the surface sh	ion.]					
	 (Fig. B5.19). (Fig. B5.19). (Fig. B5.19). (Female: at least tibiae and tarsi light reddish brown (Fig. B5.23). (Female: sheath with basal section at most 0.35 times as long as apical section (Fig. B5.25). 	4					
4(3)	 A) Gena narrow, its maximum length from eye to genal ridge at most 0.50 times as long as maximum length (Fig. B5.26). B) Female: coxae and femora black (Fig. B5.28). C) Female: flagellum brown or black in basal 0.3, gradually becoming light reddish brown in apical 0.6 (1) 	eye					
	B5.30). 	80)					

a) Gena wide, its maximum length from eye to genal ridge at least 0.50 times as long as maximum eye length (Fig. B5.27).

b) **Female**: coxae brown usually becoming reddish brown apically, and femora light reddish brown (Fig. B5.29).

c) Female: flagellum entirely light reddish brown (Fig. B5.31).

5(2) A) Vertex between eye and postocellar furrows with large, densely spaced pits over most of surface (many pits polygonal) (Fig. B5.32).

B) Gena below eye and genal ridge (including adjacent occiput) densely pitted; clypeus, face, frons and vertex with setae about 2.0 times as long as posterior ocellus (Fig. B5.34).

C) Female: coxae black and rest of legs light reddish brown (Fig. B5.36).

D) Male: metatibia with dorsal edge in lateral view very deeply indented in basal 0.3 (Fig. B5.39).

[Additional character. Pronotum in dorsal view with broad white longitudinal band along the lateral margin between anterior and lateral angles.]

a) Vertex between eye and postocellar furrows with mostly small, more sparsely spaced pits over most of surface (pits round) (Fig. B5.33).

b) Gena below eye and genal ridge (including adjacent occiput) with or without a few pits, the surface shiny; clypeus, face, frons and vertex with setae at most as long as posterior ocellus (Fig. B5.35).

c) **Female**: coxae either completely light reddish brown (Fig. B5.37) **or** brown shifting to reddish brown apically (Fig. B5. 38).

- d) Male: metatibia with dorsal edge in lateral view shallowly indented in basal 0.3 (Fig. B5.40).
- **6(5)** A) Gena with white spot behind eye (very rarely absent) not extending to genal ridge (Fig. B5.41).

B) Gena with few, small pits between dorsal and ventral limits of genal ridge (Fig. B5.43).

C) **Female**: abdomen black and coxae completely light reddish brown except near articulation of coxa to thorax (Fig. B5.45).

- D) Female: flagellum black, at most dark brown in apical 0.25 (Fig. B5.48).
- E) Male: femora mainly or completely light reddish brown (Fig. B5.51).

[Additional character. Pronotum in dorsal view with broad longitudinal band along lateral margin between anterior and lateral angles.]

– a) Gena with white spot behind eye large, extending to genal ridge (Fig. B5.42).

b) Gena with numerous, larger pits between upper and lower limits of genal ridge (Fig. B5.44).

c) **Female**: abdomen black and coxae mainly brown laterally, becoming reddish brown near apex (Fig. B5.47) **or** abdomen mainly reddish brown and coxae reddish brown or procoxae at least brown laterally, becoming reddish brown apically (Fig. B5.46).

d) **Female**: flagellum black, becoming light reddish brown (in specimens with black abdomen) (Fig. B5.49), **or** completely reddish brown (in almost all specimens with reddish brown abdomen and very rarely with those with black abdomen) (Fig. B5.50).

e) Male: femora or at least metafemur completely or almost completely black (Fig. B5.52).

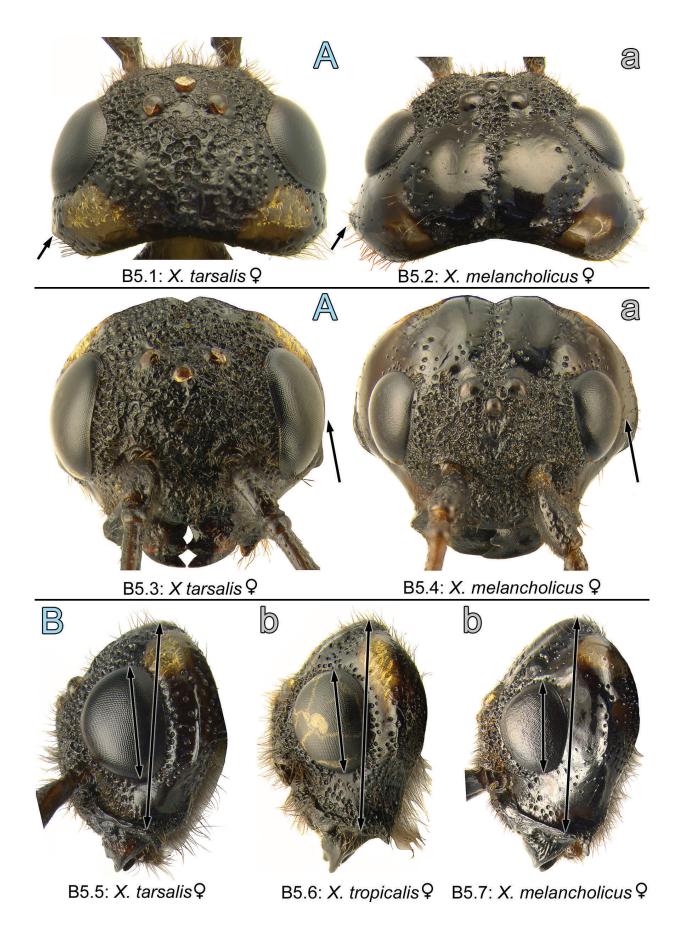
[Note. Females with either black or reddish brown abdomens are found together except in southwestern United States where females with black abdomens have not been recorded.]

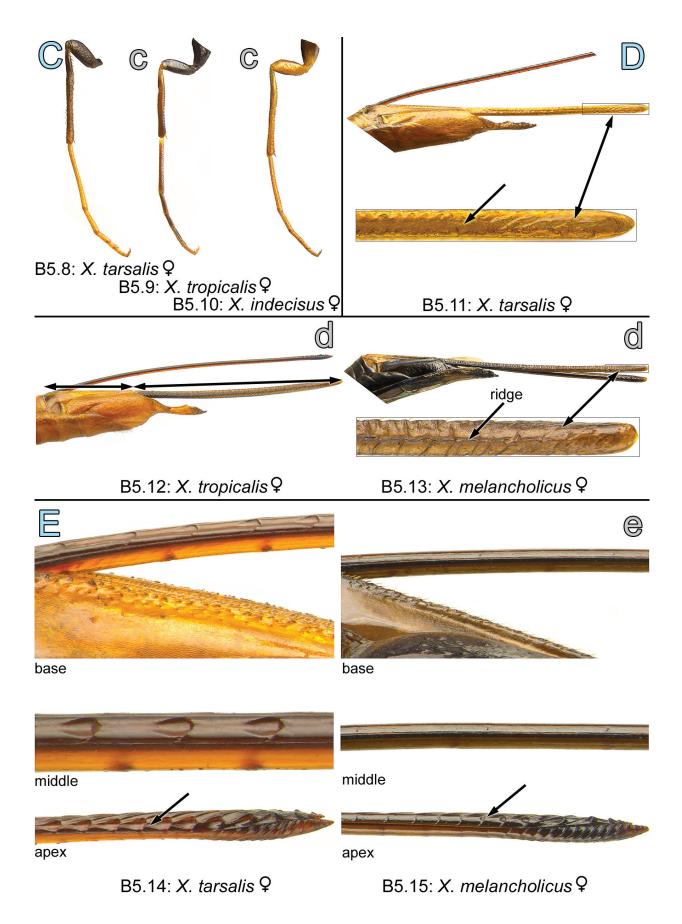
7(6) A) Female: sheath with basal section less than 0.25 times length of apical section (if 0.25–0.27, use B) (Fig. B5.53).

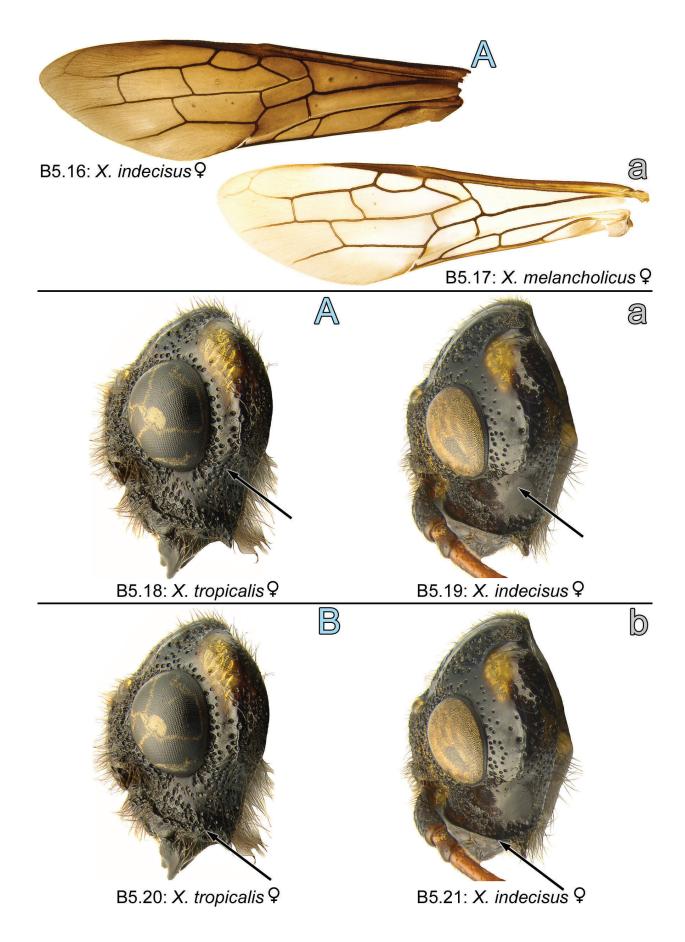
B) Range west of the cordillera from Alaska and British Columbia south to mountains of California and Northern Mexico, and east of cordillera in Alberta and perhaps as far east as north central Saskatchewan.

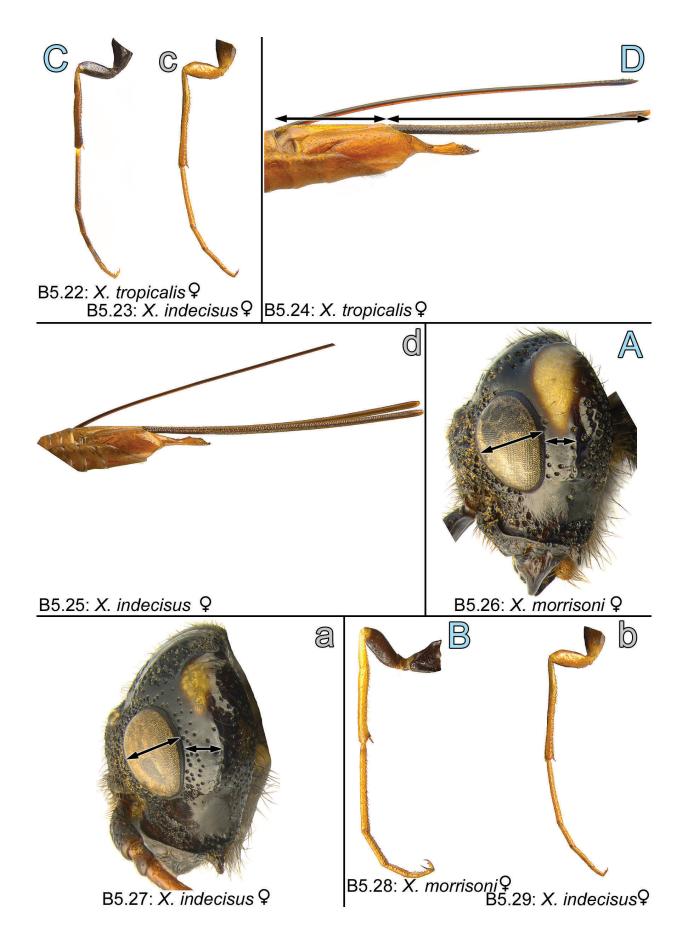
- [Note. Both sexes are difficult to recognize on morphological features, but can be distinguished by the CO1 barcode sequence. The general range is a good indication. This species occurs in the Rocky Mountains westward. East of the Rocky Mountains, in central Alberta, both species occur sympatrically.]
- a) Female: sheath with basal section more than 0.27 times length of apical section (if 0.25–0.27, use b) (Fig. B5.54).
 - b) Range from Alberta to Nova Scotia and south east of the prairie region Michigan to Maine.

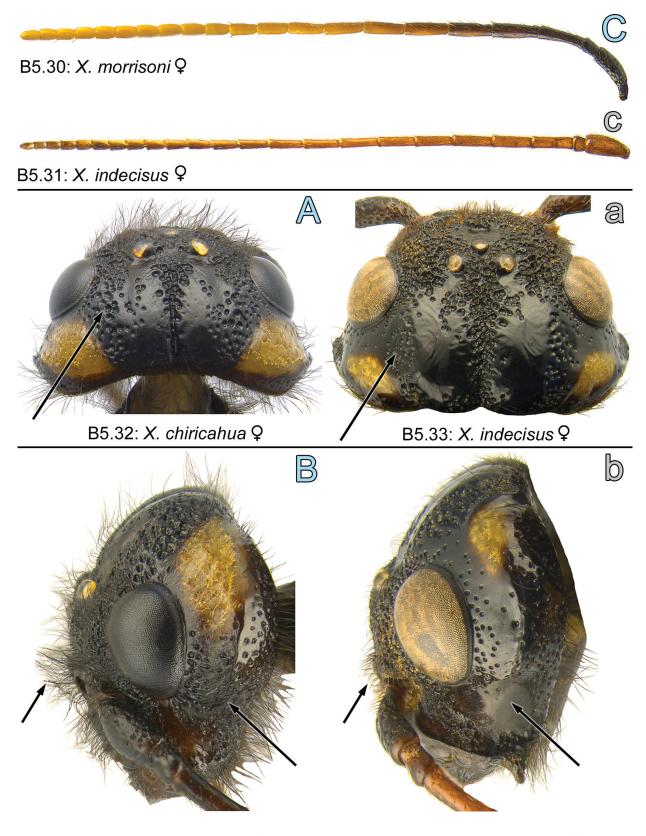
[Note. Both sexes are difficult to recognize on morphological features, but can be distinguished by the CO1 barcode sequence. The general range is a good indication. This species occurs east of the Rocky Mountains and is sympatric with X. melancholicus in central Alberta (perhaps as far east as north central Saskatchewan.]





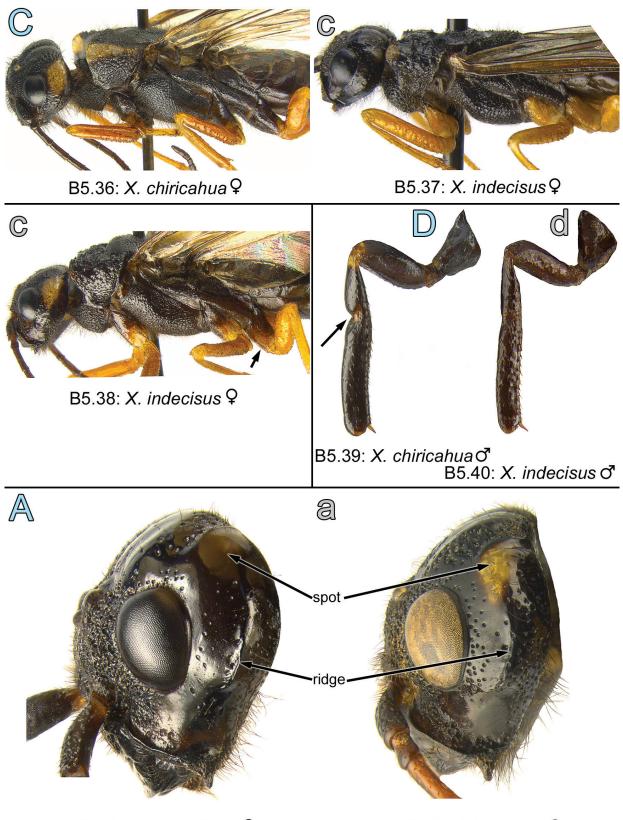






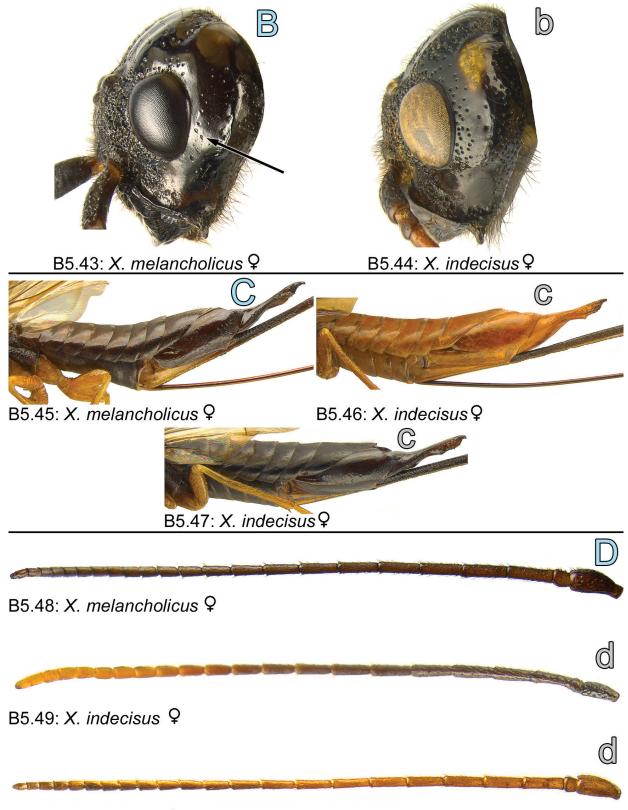
B5.34: X. chiricahuaQ

B5.35: X. indecisus Q

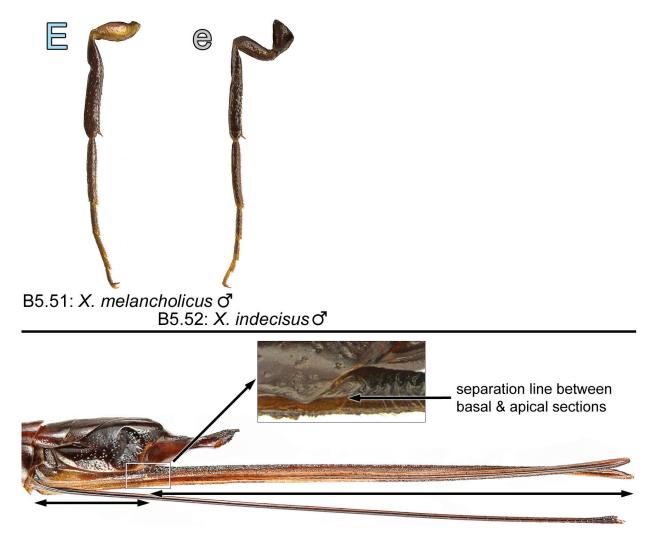


B5.41: X. melancholicus Q

B5.42: X. indecisus Q



B5.50: X. indecisus ♀



B5.53: X. caudatus ♀



B5.54: X. melancholicus Q

C. Taxonomic treatment

1. Family Siricidae

Diagnostic combination

Both sexes of Siricidae are easily distinguished from all Symphyta (and probably all Hymenoptera) by the collar-like pronotum, and the cornus (horn) present on tergum 10 in **females** and on sternum 9 in **males**.

Description

General. Body length 7–38 mm, slender and mostly covered with long, more or less entangled setae. Males and females of the same species often differ considerably in color pattern and adults of most species may show great variation in size.

Head. In frontal view, head markedly constricted below the eye (Fig. A3.4). Malar space with well defined horizontal antennal groove between eye and mandible, sharply outlined ventrally. In posterior view, foramen magnum widely separated from mouth opening by occiput (Fig. C1.1). Mouthparts. Labrum small, fingerlike and hidden under clypeus. Mandible with three teeth. Maxillary palp with 1 article; labial with 2 or 3 articles. Antenna. Scape with ventral surface flattened and concave, fitting into antennal groove when retracted (Fig. C1.2); pedicel wider than long and about 0.25 times as long as scape; flagellum with 4-30+ flagellomeres, flagellomere 1 as long as, longer, or shorter than following flagellomere (Fig. A3.11); flagellomeres each with sensory oval impression (often quite sharply outlined especially in female) on part or most of ventral surface (males in some genera, without sensory oval impression on apical flagellomere) (Fig. A3.25).

Thorax. Pronotum long medially, collar-like with anterior margin slightly concave, and with acute anterolateral corners (Fig. C1.3). Propleura widely touching medially. Mesonotum with median lobe usually without notauli (except in Xeris, notauli slightly outlined in anterior third and far in front of scutellum) and each lateral lobe transversely divided by a wide, deep oblique furrow (possibly the precursor of the transscutal fissure) extending from scutellum posteromedially toward base of fore wing (Fig. C1.4). Tegula very small and mostly hidden under pronotal angle (the "tegula" of authors probably refers to the humeral plate). Mesoscutellum with a small, very narrow and sharply outlined posteromedian appendage. Legs. Tibial spur number: 1 (protibia), 1 (mesotibia), and 1 or 2 (metatibia). Tarsal pad (pulvillus) present on tarsomeres 1-4 and integrated within ventral surface of tarsomeres (slightly extended posteriorly in fresh specimens) (Figs. A3.27 & A3.28), without microtrichae,

either smooth or papillate with scattered sensilla, almost as long as ventral length of tarsomeres 3 and 4, 0.4-0.8 times length of tarsomere 2, and 0.1-0.2 times length of tarsomere 1. Protibia with one row of spatula-like setae along posterodorsal margin. Pro- and mesotibiae with dorsal and ventral surfaces curved, commonly appressed to body. Pro- and mesofemora clearly longer than metafemur, their ventral or dorsoventral surface rasp-like, with numerous transverse ridges (Fig. C1.5). Female with tarsomere 1 0.7–1.0 times length of corresponding tibia. (Fig. C1.6). Male with hind leg greatly modified: tibia and tarsomeres 1-3 either thicker (Fig. C1.7) or compressed laterally and leaf-like (much less so on fore and middle legs) (Fig. C1.8); metatibia in lateral view with dorsal edge sinuate or sharply constricted in basal 0.3 and ventral edge sinuate in basal 0.3. Wings. Fore wing cell 3R1 enlarged toward apex (especially apical to vein 3r-m) and cell apex far from wing margin; fore wing veins R1 and Rs2 faint, ending in a short petiole (Fig. C1.9); stigma very narrow; cell 1M much narrower (about 0.5 as wide) than cell 2M (Fig. C1.9); vein 2A with basal portion clearly outlined; vein 3A present or absent (Fig. C1.9). Hind wing with only one set of hamuli along edge, either only apical to vein R1 or apical and basal to vein R1 (Figs. B1.11 & B1.12); anal cell absent, or present and with apical petiole almost reaching wing edge (Fig. A3.29).

Abdomen. Tergum 1 divided medially (Fig. C1.10). Terga 2-8 with pit like sculpticells (surface similar to velvet) over most of median area (except in X. matsumurae) (Fig. C1.11). Female with tergum 8 in dorsal view with disc markedly extended posteriorly (Fig. A3.1); tergum 9 in lateral view greatly lengthened (about 0.3–0.5 times abdomen length) (Fig. A3.1) with sharp longitudinal furrows basolaterally (Fig. C1.12) and median basin dorsally (Fig. A3.12); median basin anteriorly outlined laterally by two sets of short furrows and extended posteriorly to base of tergum 10. Tergum 10 separated at least laterally from tergum 9 by transverse furrow and extended posteriorly as a wide or narrow horn (cornus) ending in a rod-like apex (Figs. A3.1 & A3.12); cercus present or absent anterior to anus, and usually very small when present (Figs. B1.31 & B1.32). Ovipositor. Sword-like, with both lance and lancet subdivided into annuli (Figs. A3.16 & A3.17). Lancet with 12-50 annuli, ventrally smooth (without teeth) but apical 3 or 4 annuli each with a large tooth laterally (Fig. A3.17); annuli before teeth annuli laterally each with apical pit, but pit present on as few as 3–5 apical annuli (Figs. A3.16 & A3.17); if pits absent on basal annuli, the annuli either outlined or not. Male with sternum 8 deeply cleft medially and sternum 9 extended as a triangular horn ending in a rodlike apex (Fig. C1.13).

Taxonomic notes

Viitasaari (1984) and Viitasaari and Midtgaard (1989) introduced sawfly taxonomists to pits on the ovipositor lancet. The character was first used by Kjellander (1945) to distinguish *S. juvencus* from *S. noctilio*. The ovipositor pits turned out to be crucial in deciphering the species of *Sirex* in the New World. Undoubtedly this character will be important in the study of Euroasiatic species of this genus and other genera.

The following keys to families of Hymenoptera include useful features to identify the family Siricidae: Ross (1937), Benson (1938), Smith (1988), Goulet (1992), and Mason (1993).

Range

Based on species listed by Taeger *et al.* (2010) and the species recognized here, there are 122 extant species known worldwide. These are grouped into ten genera classified traditionally in two subfamilies. Ninety-seven species are recorded from the Old World mostly in Eurasia, and 28 native species in the New World are known from Guatemala and the Dominican Republic north to the tree line in North America. Except for the introduced *Sirex noctilio*, *Urocerus gigas* and *Tremex fuscicornis* in South America, South Africa, Australia, and New Zealand, and two native species in equatorial Africa, there are no extant species in the southern hemisphere. Siricidae are not known from oceanic islands.

In the New World, Siricidae are represented by seven extant genera (including one introduced into southeastern United States) and 33 extant species (including five introduced species). One species, Urocerus patagonicus Fidalgo and Smith - a Paleocene fossil from Patagonia (Argentina) - is the only native species recorded from the southern hemisphere (Fidalgo and Smith 1987). Twentyeight native species are distributed as follows: Sirex – 13 species recorded north of Guatemala and the Dominican Republic, *Sirotremex* – one species restricted to Mexico, Teredon - one species restricted to Cuba, Tremex - one species in temperate regions of Canada, United States and northernmost Mexico, Urocerus - five species from Mexico northward, and Xeris - seven species from Mexico and northward. We have seen fewer than 25 specimens from Mexico representing five species, three of which are new. No doubt numerous species await discovery in the conifer zone of the Mexican highlands.

Notes on affinities

A phylogenetic reconstruction of extant taxa at generic level is proposed (Fig. C1.14). Principles and methods of cladistic analysis and phylogenetic reconstruction are based mainly on Hennig (1966). For each lineage, an indented list of characters is given. For each character, the derived state is given first, followed, in brackets, by the ancestral state and its distribution within Siricidae and out-groups representing earlier lineages of Symphyta.

Affinities of Siricoidea among Symphyta.

The Siricoidea (including Siricidae only) is an isolated lineage in Hymenoptera. It is defined by many unique derived character states. The general relationships among the basal Hymenoptera lineages are best illustrated in Vilhelmsen (2000, 2001). The old concept of Siricoidea is a grade and is paraphyletic. It includes the Anaxyelidae, Siricidae and Xiphydriidae. All members of these three families have a similar sword-like ovipositor in adult females, and their larvae have a rod-like structure on the abdominal apex and develop in wood. Detail studies of external and internal structures redefine the Siricoidea (Vilhelmsen 2001, Schulmeister 2003) and restrict it to one family, the Siricidae. The lineages (out-groups) that precede the Siricoidea starting with the earliest are the Xyeloidea giving rise to the Tenthredinoidea, and then to the Pamphilioidea, followed by the Cephoidea, the Anaxyeloidea and finally the Siricoidea. The Siricoidea are followed by Xiphydrioidea, and all remaining Hymenoptera. Because Anaxyelidae, Siricidae and Xiphydriidae do not share a common ancestor and are part of a transformation series between Xyelidae and the all remaining Hymenoptera, each family was given superfamily status equal to the preceding and following lineages.

- 1 The Siricidae form a monophyletic lineage, united by the nine following derived character states:
 - Pronotum collar-like, the anterior surface vertical and slightly concave with projecting anterolateral angles, and the dorsal and lateral surfaces flat (Fig. C1.3). The unique pronotal shape is probably an adaptation to protect the head during adult emergence from a tree trunk. [In other Hymenoptera the pronotum is not collar-like.]
 - Tergum 10 in **female** and sternum 9 in **male** extending posteriorly as a horn ending in a small tube-like rod (Figs. A3.9 & A3.10). This structure is probably involved in helping the adult emerge from a tree trunk. [This structure is unique to the Siricidae.]
 - Maxillary palp with one palpomere. [Most Hymenoptera have 2–6 palpomeres.]
 - Postgenae broadly meeting medially ventral to the foramen magnum (Fig. C1.1) [In other Symphyta the postgenae do not meet medially ventral to foramen magnum.]
 - Tergum 9 of **female** with median basin (Figs. B1.29 & B1.30). [This structure does not occur in

other Hymenoptera.]

- Mesoscutum with posterior portion divided on each side by a broad furrow between base of fore wing and scutellum (Fig. C1.4). [This is probably the precursor of the transscutal fissure, clearly outlined in Xiphydriidae and many Apocrita. These furrows are absent in earlier lineages.]
- Fore wing with basal portion of vein 2A clearly outlined (Fig. C1.9). [Though considered as part of the ground plan of Hymenoptera, this vein is absent in later lineages of Symphyta and, in our opinion, is a derived character state, not an atavism.]
- Vein 3R1 with apical portion thinly sclerotized and nebulous (Fig. C1.9). [If the cell is close, it is clearly tubular in earlier lineages of Symphyta.]
- Metatibiae and metatarsomeres 1 or 1 and 2 enlarged and wide in male (Fig. A3.2). [In almost all Symphyta, the metatibia and metatarsus are not particularly enlarged and are quite similar to those of the middle leg, but are usually relatively longer.]

Affinities among genera of Siricidae.

The ten extant genera of the Siricidae are included in our phylogenetic reconstruction. The pivotal character is based on the junction of the fore wing vein Rs. This vein originates from vein 1r–rs and its proximal section ends normally at or near the junction of veins Rs and M. In earlier lineages of Symphyta and in one fossil siricid, vein Rs joins M more distally either at vein 1m–cu or on Rs+M.

1a *Sirex, Sirotremex, Urocerus* and *Xoanon* form a monophyletic group, united by the following derived character state:

 Fore wing vein Rs (originating from vein 1r–rs) ends proximally at or very near the junction of veins Rs and M (Fig. A3.30). [In earlier lineages of Symphyta, vein Rs joins M more distally, either at vein 1m–cu or on Rs+M roughly between the junction of vein Rs and M and vein 1m–cu.]

1aa *Sirex* and *Sirotremex* form a monophyletic group, united by the following derived character state:

- Fore wing vein Cu1 present in almost all specimens (Fig. A3.30). [Vein Cu1 is seen in the distantly related Pamphilioidea and is absent in other, earlier lineages of Siricidae. In Siricidae, we do not think that this vein is an atavism, but rather a new vein. In Siricidae veins are commonly added or disappear; we suspect that this vein was an addition.] 1aaa *Sirex* forms a monophyletic group, defined by the following derived character states:

- Ovipositor with ventral edge of the 3–5 apical pits before the teeth annuli clearly ridge-like (Fig. C1.15). [Such a structure is not seen in other Siricidae or other Symphyta. In *Xeris* such a ridge is present only on the last annulus before the teeth annuli, and the pit forms a long trough extending to the dorsal edge of the lancet.]
- Dark areas of body with blue or green metallic reflections (one species of the distantly related *Eriotremex* and one of *Afrotremex* have such metallic reflections). [Metallic reflections are uncommon in Siricidae and generally in Symphyta. We assumed that this state is derived.]

1aab *Sirotremex* forms a monophyletic group, defined by the following derived character states:

- Fore wing broadly rounded at apex (Fig. C1.16). [The fore wing apex is angularly rounded in most Symphyta.]
- Cell 1Rs2 very short (2r-m and 3r-m each slightly longer than veins Rs2 or M) (Fig. C1.16). [This cell is usually long in other Siricidae and most Symphyta.]
- Cell 3R1 very short (2.2 times as wide as long) (Fig. C1.16). [This cell is longer in other species of Siricidae, though it is still long relative to most Symphyta except the Cephoidea and Anaxyeloidea. However, the cell in general outline is typical of Siricidae.]
- Middle flagellomeres short: about 1.5 times as long as high in lateral view (Fig. C1.17). [The flagellomeres are rather short in *Sirotremex* compared to those of early lineages within Siricidae. One expects such short flagellomeres in genera associated with deciduous trees (except larch – a conifer). However, the flagellomeres are round in cross section as in genera of Siricidae associated with coniferous trees rather than dorsoventrally flattened, as in *Tremex*.]
- Head in dorsal view across eyes wider or very slightly narrower than across the genae (behind eyes) (Fig. C1.18). [A common feature of the Siricidae is the marked head enlargement behind the eyes in dorsal view. In a few other species *Xeris tarsalis* (Cresson) and males of *Teredon cubensis* (Cresson) the head is not wider across the eyes than the width across the genae.]
- Note. The female is unknown. Its discovery would probably provide significant additional characters to clarify the relationships of *Sirotremex* with *Sirex*.

1ab *Urocerus* and *Xoanon* form a monophyletic group, united by the following derived character states:

- Sheath with teeth dorsally in apical third of apical section with one bristle near apex of each tooth (Fig. C1.19). (teeth absent in a few species of *Urocerus* from China) [In other siricid genera when the teeth are present each tooth has a very fine seta at its base.]
- **Male** with sterna clearly folded and smooth medially (Fig. C1.20). [Character state scarcely visible (median surface smooth) in other Siricidae and absent in other Symphyta.]
- Ovipositor with pits clearly present in apical 0.25 but still small on last annulus before teeth annuli (Fig. C1.21). [In Siricidae, the lancet pits are large toward apex and are outlined on many or all annuli before the teeth annuli.]

1aba *Urocerus* forms a monophyletic group, defined by the following derived character states:

- Gena without or almost without pits in central area (Fig. A3.5). [The gena is moderately to densely pitted centrally in other species of Siricidae except in a few species of *Xeris*.]
- **Female** with median basin about twice as wide as long, with long and divergent ridge-like edges (Fig. C1.22). [Except in *Siricosoma*, the median basin is not so wide in other genera of Siricidae and, except in *Xeris*, the lateral edges are not so divergent in other genera.]

1abb *Xoanon* forms a monophyletic group, defined by the following derived character states:

- Gena very densely pitted (Fig. C1.23). [The widespread state in Siricidae is less densely pitted at center of gena.]
- Terga without pitted microsculpture even mediobasally. [In other Siricidae the pitted microsculpture is at least present medially on terga 2–8.]
- Fore wing vein 2r-m displaced apically and joined to cell 3M (Fig. C1.24). [In all other extant Siricidae and almost all Symphyta, fore wing vein 2r-m intercepts cell 2M.]
- Male with terga 1–8 densely pubescent. [In other Siricidae at least terga 2–4 are mostly bare.]

1b Xeris, Siricosoma, Teredon, Eriotremex, Afrotremex and Tremex form a monophyletic group, united by the following derived character states:

- Metatibia with one spur (Fig. C1.25). [In earlier lineages of Symphyta, the metatibia has two spurs.]
- Hind wing without anal cell (a single male

of *Teredon cubensis* with cell – it may be an aberration) (Fig. C1.26). [In most Symphyta and earlier lineages of Siricidae, the anal cell is present.]

 Fore wing with vein 1 cu–a joined to vein Cu clearly close to or at junction of veins M and M+Cu (except in *Teredon*) (Fig. C1.27). [In earlier lineages of Symphyta, vein 1cu–a intercepts cell 1M near its middle.]

2a *Xeris* is the earliest lineage of clade 1b and forms a monophyletic group, defined by the following derived character states:

- Gena behind eye with a short vertical ridge (Fig. C1.28). [This is probably not the occipital ridge seen in most Symphyta, as it is found only behind each eye and there is no trough in front of it. Typically, the occipital ridge when present is either completely developed or present only near the mandible.]
- **Female** with anterior edge of median basin clearly narrower than maximum width of basin (Fig. C1.29). [In other Siricidae, the base is relatively wider.]
- Sheath with apical 0.3 of apical section without teeth dorsally (Fig. C1.30). [In Siricidae except *Teredon* and some species of *Urocerus* from China the teeth are present. The presence of teeth is considered an ancestral state within the Siricidae.]
- Note: *Xeris* has been associated traditionally with *Urocerus* (Gauld and Mound 1982, Benson 1943) because of the very long and medially constricted cornus, and the pale spot on the gena. In *Urocerus*, there are species with the cornus shorter and not constricted, similar to that of *Sirex longicauda* or *Siricosoma tremecoides*. Even in *X. tarsalis*, the first lineage of *Xeris*, the cornus is not constricted. Therefore, we think that the long cornus could have been evolved independently in *Xeris* because it does not have the more basal constriction found in *Urocerus* and *Xoanon*).

2b *Siricosoma*, *Teredon*, *Eriotremex*, *Afrotremex* and *Tremex* form a monophyletic group, united by the following derived character states:

- Minimum distance between eyes 0.7–1.2 times maximum eye height (Fig. C1.31, black arrows).
 [In most Symphyta the eye height is clearly less than the minimum distance between eyes.]
- Distance between inner edges of antennae much greater (4.0–10.0) than distance from outer edge of antennal socket to nearest edge of eye: (Fig. C1.31, white arrow). [In almost all Symphyta, the antennal sockets are closer together.]

- Eye long and narrow (1.7–1.9 times as long as high) (Fig. C1.44). [In most Symphyta and early lineages of Siricidae (except *Xoanon*), the eye is moderately narrow (1.2–1.7 times as high as long).]
- Flagellomeres flattened dorsoventrally. [In Symphyta, the flagellomeres are either round or flattened laterally.]

3a *Siricosoma* consists of one species and forms a monophyletic group, defined by the following derived character states:

- Fore wing vein M between veins M+Cu and Rs+M strongly and abruptly curved (Fig. C1.32). [In Symphyta and other Siricidae, vein M is straight, or uniformly and widely curved.]
- **Female** with cercus long and wide at base of cornus (Fig. C1.33). [In Symphyta, the cercus is typically long and narrow; in Siricidae it is very short, thumb- or button-like, articulated or not, or even absent.]
- Tergum 9 with setae in median basin on coneshape tubercles (Fig. C1.34). [In almost all Symphyta and other Siricidae, each seta in medial area is in a pit.]
- Tergum 9 with a wide shallow furrow separating the smooth dorsal surface from the pitted ventrolateral surface (Fig. C1.34). [In other Siricidae, the shallow furrow is absent.]
- Note. *Siricosoma* (from Southeast Asia) and to lesser extent *Teredon* (from Cuba) have character states seen in early lineages of Siricidae. Adults of *Siricosoma* share 10 character states traditionally associated with the Siricinae as defined by Benson (1943). They are:
 - Labial palp with three palpomeres.
 - Both sexes with antenna as long as or longer than fore wing costal cell.
 - Distance between lateral ocelli subequal to distance between lateral ocellus and nearest edge of eye.
 - Gena near lower edge of eye with the surface posterior to edge of pit not elevated as a coarse scale or a low tooth.
 - Metatarsomere 1 in dorsal view not very compressed laterally and lateral surfaces not twisted.
 - Subcosta clearly outlined in basal 0.4 of costal cell.
 - Middle flagellomeres almost twice as long as wide.
 - Hind wing veins 1r-m longer or subequal to M.
 - Tergum 9 with sharp edges of median basin

short (in basal 0.25).

- Tergum 10 with cornus rather long.

Females of *Siricosoma* and *Teredon* have an amazingly similar ovipositor (each annulus of the last ten annuli before the teeth annuli consists of two teeth per annulus with a deep trough between them). If this character state is considered as homologous, then numerous other derived character states would have been evolved twice. Therefore, for reasons of parsimony we do not consider *Siricosoma* and *Teredon* as sister groups. Their ovipositors are considered as convergent.

3b *Teredon, Eriotremex, Afrotremex* and *Tremex* form a monophyletic group, united by the following derived character states:

- Labial palp with 2 palpomeres. [In Symphyta and earlier lineages of the Siricidae, the palp consists of 3–6 palpomeres.]
- Distance between inner edges of lateral ocelli 1.5–2.3 times greater than between lateral ocellus and nearest edge of eye: (Fig. C1.35). [In Symphyta, the lateral ocelli are usually not so close to the edges of eyes.]
- Metatarsomere 1 markedly compressed laterally (about 3 times as high as maximum ventral width) and in dorsal view the lateral surfaces twisted. [In almost all Symphyta, metatarsomere 1 is round or slightly compressed laterally, and is not twisted.]
- Hind wing vein M much longer than vein 1r-m and markedly curved (Fig. C1.26). [In most Symphyta, vein M is not so long.]
- Tergum 9 with median basin sharply outlined laterally for most of its length (Fig. C1.39). [In earlier lineages of Siricidae, the lateral edges are sharp on less than 0.5 of their length.]

4a *Teredon* consists of one species, and the lineage forms a monophyletic group, defined by the following derived character states:

- Flagellum with 3–8 flagellomeres. [In almost all Symphyta except some Pergidae and a very few Tenthredinidae, the antenna has more flagellomeres.]
- Fore wing vein 2r-m basal to vein 2r-rs (Fig. C1.36). [In Symphyta, vein 2r-m is apical to vein 2r-rs.]
- Metatarsomere 1 remarkably compressed laterally and broadly lobed apically (Figs. C1.8, male, and C1.37, female). [In Symphyta, metatarsomere 1 is typically not lobed dorsally.]
- Metatarsomeres 2–4 very short (as long as metatarsomere 5) (Figs. C1.8, male, and C1.37, female). [In Symphyta and other Siricidae

the metatarsomeres 2–4 are much longer than metatarsomere 5.]

- **Male** with metatibia remarkably compressed laterally (Fig. C1.8). [In Symphyta, the metatibia is almost always not or is at most slightly compressed laterally.]
- **Female** with basal and apical sheath sections fused and apical section without teeth along dorsal margin in apical 0.3 (only in *Xeris* and some species of *Urocerus* from China) (Fig. C1.38). [In almost all Symphyta, the sheath is clearly divided into two sections. The lack of teeth in the apical 0.3 is considered derived within Siricidae.]
- Note. *Teredon* still retains some ancestral characters states shared with the early siricid lineages (Siricinae of Benson (1943)), as follows:
 - Hind wing with hamuli both basal and apical to junction of veins C and R1.
 - Middle flagellomeres clearly longer than wide (1.1–1.4 times as long as wide).
 - Fore wing vein 1cu–a joining vein Cu about half way between vein 1m–cu and M.

4b *Tremex*, *Eriotremex* and *Afrotremex* form a monophyletic group, united by the following derived character states:

- Fore wing vein 2r-m absent (Fig. C1.27). [In most Symphyta, vein 2r-m present.]
- Fore wing vein 1cu–a aligned or almost aligned with vein M (Fig. C1.27). [In most Symphyta, vein 1cu–a is between veins M and 1m–cu.]
- Hind wing with hamuli present apical to junction of veins R1 and C though hamuli may be present for a very short distance basally (Fig. C1.26). [In Pamphilioidea, Anaxyeloidea and earlier lineages of Siricidae, the hamuli are also present basal to the junction of veins R1 and C.]

5a *Eriotremex* forms a monophyletic group, defined by the following derived character states:

- **Female** with pits of median basin dense or scattered, deep or shallow and basin very convex (Fig. C1.39). [In Siricidae, the median basin has few or no pits and is not so convex.]
- Body pubescence long and very dense (Fig. C1.40). [In Siricidae, the pubescence is usually short and sparse.]
- Sheath with basal section about twice as long as apical section (Fig. C1.40). [In Siricidae except for *Teredon*, the basal section is subequal or shorter than the apical section.]
- Hind wing with hamuli present for a short distance basal to junction of veins R1 and C (Fig. C1.41). [In Pamphilioidea, Anaxyeloidea and earlier lineages of Siricidae, the hamuli are equally spread basal

and apical to the junction of veins R1 and C.]

5b *Tremex* and *Afrotremex* form a monophyletic group, united by the following derived character states:

- Cercus absent (Fig. C1.42). [In Symphyta, the cercus is present.]
- Flagellum with 12–14 flagellomeres (rarely this low in other Siricidae and only in very small specimens). [In Pamphilioidea, Cephoidea, Anaxyeloidea and most Siricidae, the antenna has more flagellomeres]
- Fore wing cells 2R1 at least 0.6 times to about as long as cell 3R1 (Figs. C30.4 and C1.27); vein 2rrs joining stigma in apical 0.2–0.33; stigma basal to junction with vein 2r-rs parallel and abruptly narrowed apical to junction (Fig. B1.26). [In Siricidae, cell 2R1 is half as long as cell 3R1, vein 2r-rs joins the stigma near the middle, and the stigma gradually narrows apical to junction.]

6a *Afrotremex* forms a monophyletic group, defined by the following derived character states:

- Flagellomere 1 about 0.5 times as long as flagellomere 2 and subequal to flagellomere 3 (Fig. C1.43). [In most Symphyta, flagellomere 1 is subequal to flagellomere 2 and is generally as long as or shorter than flagellomere 3.]
- Head except occiput with setae clubbed at apex (Fig. C1.44). [In Symphyta, setae of the vertex, the frons, the face and the clypeus are apically pointed.]

6b *Tremex* forms a monophyletic group, defined by the following derived character states:

- Fore wing cells 2R1 and 3R1 subequal (Fig. C1.27). [In other Siricidae, cell 3R1 is clearly longer.]
- Note. Fore wing cell 2R1 length relative to cell 3R1 length is the only character state found to define Tremex as a natural lineage but is variable. Since cell 2R1 varies from 0.9-1.5 times as long as length of 3R1 it may perhaps also be shorter, in which case cell 2R1 could be clearly as small as in Afrotremex. We could therefore treat Afrotremex as part of Tremex, as did Benson (1943). The recent tradition is to consider Afrotremex as generically distinct from Tremex, perhaps because this is the only siricid lineage in tropical Africa whereas species of *Tremex* are from temperate zones of the Palaearctic and Nearctic regions. Benson (1943) may have been right in including the rather derived Afrotremex within Tremex, but we have studied only a small portion of the Tremex species and have a limited knowledge of the main lineages

within *Tremex*. Based on the few species studied, adults of *Tremex* show a wide variation in many structures. Therefore, until we better understand the phylogeny of *Tremex*, we follow the status quo in keeping *Afrotremex* generically distinct from *Tremex*.

Classification

Benson (1943) divided eight genera (*Sirotremex* was unknown to him) into two subfamilies, the Siricinae (*Sirex, Siricosoma, Urocerus, Xoanon* and *Xeris*) and the Tremicinae (*Teredon, Eriotremex,* and *Tremex* [*Afrotremex* was recognized as a rather special species but he kept it under *Tremex*]). Gauld and Mound (1982) proposed a formal phylogeny of the Siricidae based on the data provided by Benson (1943). As far as known, the larvae of Siricinae feed on conifers (gymnosperm) trees (hosts known for all genera except *Sirotremex*) and the larvae of Tremicinae are assumed to feed on flowering (angiosperm) trees (hosts known only for *Eriotremex* and *Tremex*). However, some larvae of *E. formosanus* have been reared from conifers in addition to flowering trees.

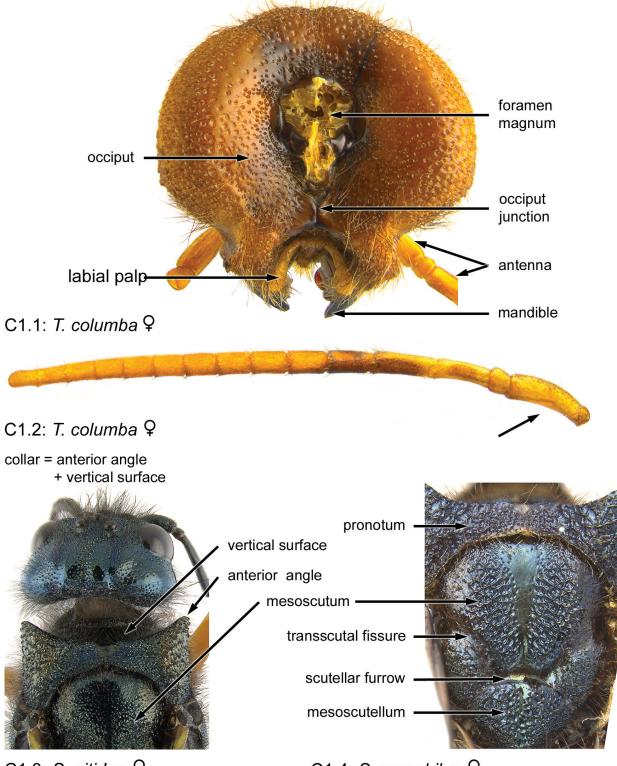
The Tremicinae as defined by Benson (1943) is a natural clade defined by four derived character states not seen in earlier symphytan superfamilies (see character states under "Notes on affinities" under item 2b). The Siricinae as defined by Benson (1943) would have the ancestral state of the above characters. We propose a classification not too different from Benson's. We still recognize the two extant subfamilies of Siricidae, but defined them differently. The Siricinae consists of the genera *Sirex, Sirotremex, Urocerus* and *Xoanon*. It does not include the genera *Siricosoma* and *Xeris*, which are transferred to Tremicinae. This way, both subfamilies are natural lineages defined by shared derived character states (see 1a and 1b above).

A very unusual fossil, *Megapterites mirabilis* Cockerell, 1920, originally assigned to Pseudosiricidae (a junior synonym of Myrmiciidae) was illustrated by Maa (1949) and assigned by him to a new subfamily, Megapterinae, in the Siricidae. Rasnitsyn (1968) changed this classification by giving Megapterinae family status and then (Rasnitsyn 1969), based on the lack of forwing 2m-cu, moved Megapteridae to Myrmiciidae. Lutz (1986) moved *M. mirabilis* to the Formicidae and synonymized *Megapterites* under *Formicium* in the subfamily Formiciinae. Here we move *M. mirabilis* back to Siricidae for the following reasons.

The fossil consists of the apical 0.7 of a fore wing with the anal region missing (Fig. C1.45). Several features support our view that it is a sawfly of the family Siricidae. All studies of *M. mirabilis* agree that the wing is of a hymenopteran because the presence of a sclerotized stigma, and the pathways of veins M and CU are typical of Hymenoptera. Does *M. mirabilis* belong to Symphyta? Vein 1r-rs is widespread in Symphyta but does not occur in Apocrita. Is M. mirabilis a Siricidae? The very long cell 3R1 relative to 2R1, vein R1 at the apex of cell 3R1 far removed from the wing margin, the obvious petiole at the apex of cell 3R1, and cell M being much smaller than cell 2M are derived character states of Siricidae and support inclusion of M. mirabilis in Siricidae. The absence of vein 2m-cu, pointed out by Rasnitsyn (1968), may be a damaged section of the wing, as suggested by the marked divergence of veins M and CU and the lack of an anal region.

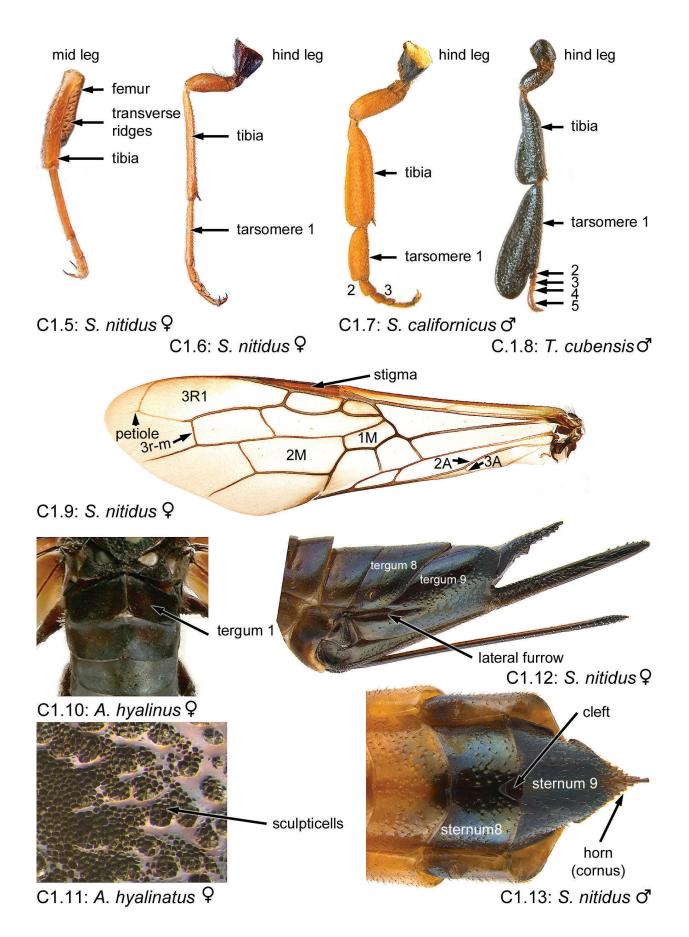
Megapterites mirabilis represents a distinct lineage with special ancestral character states not seen in other Siricidae. Vein Rs behind vein 1r-rs is aligned with vein 1m-cu, (vein directed from midway along vein Rs+M to vein M in Siricinae and Tremicinae), and the veins at the apex of cell 3R1 are tubular (nebulous in Siricinae and Tremicinae). Both character states are common and widespread features of Symphyta. The very long cell 3R1 relative to cell 2R1 and the associated small cell 1M could be considered as shared derived character states of *M. mirabilis* relative to Siricinae and Tremicinae. Therefore, we agree with Maa (1949) that Megapteritinae is a subfamily of Siricidae and Tremicinae.

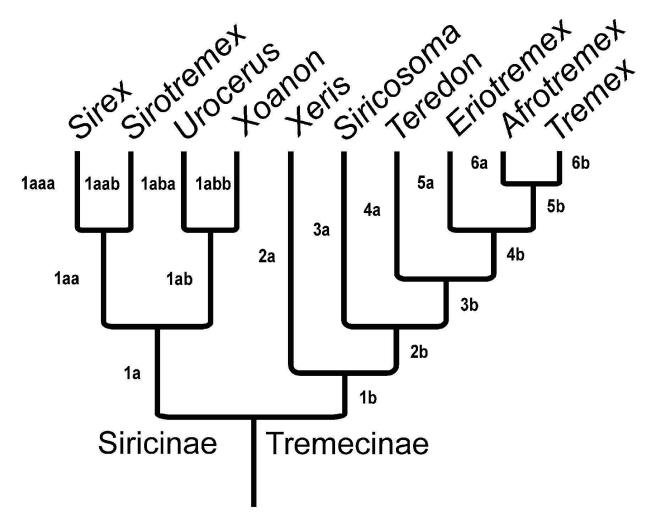
As defined here, the family Siricidae consists of three subfamilies: Megapteritinae, with one extinct species, *Megapterites mirabilis* Cockerell, 1920; Siricinae, with six genera [4 extant and two extinct genera, and the species, *Urocerites spectabilis* (Heer 1867) – according to Maa (1949), and *Eoxeris klebsi* (Brues 1926) – based on Maa's description]; and Tremicinae, with 6 genera [all extant].



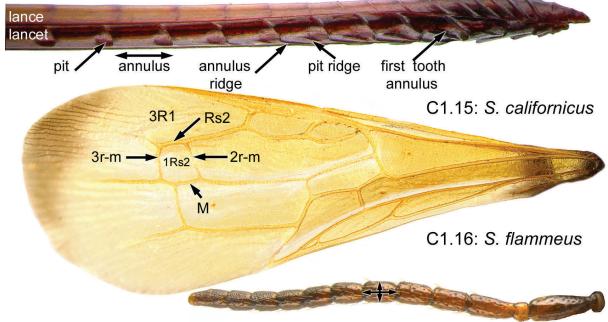
C1.3: S. nitidus Q

C1.4: S. xerophilus Q

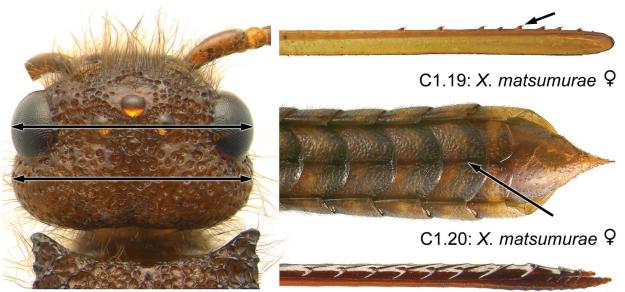




C1.14: Siricidae Phylogenetic Tree



C1.17: S. flammeus



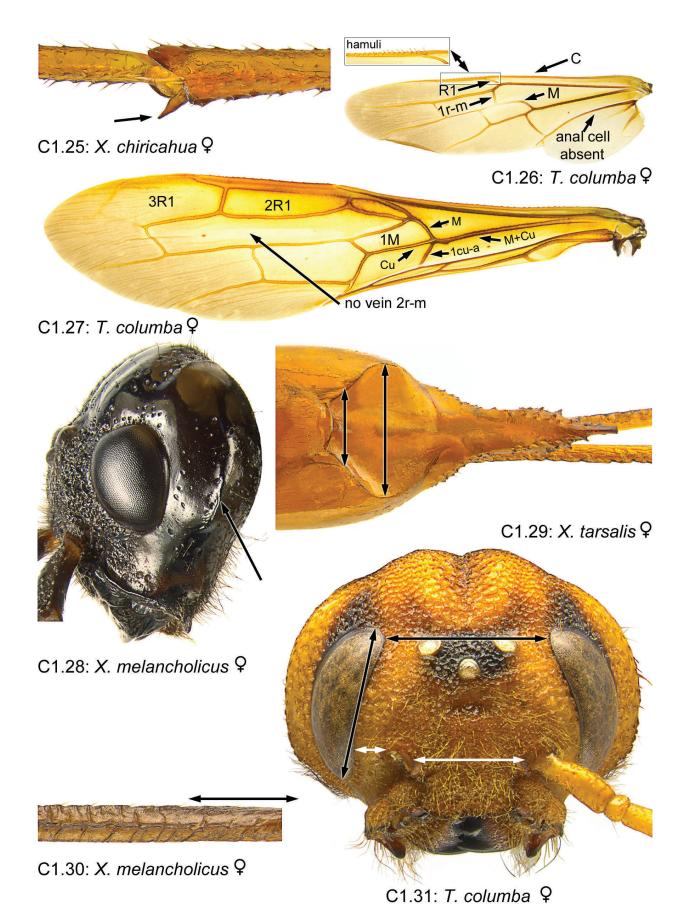
C1.18: S. flammeus o

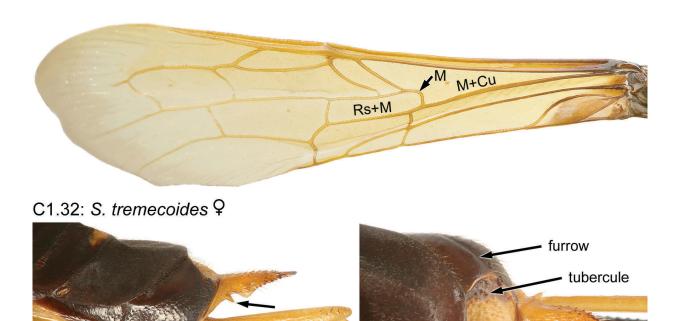
C1.21: U. californicus Q



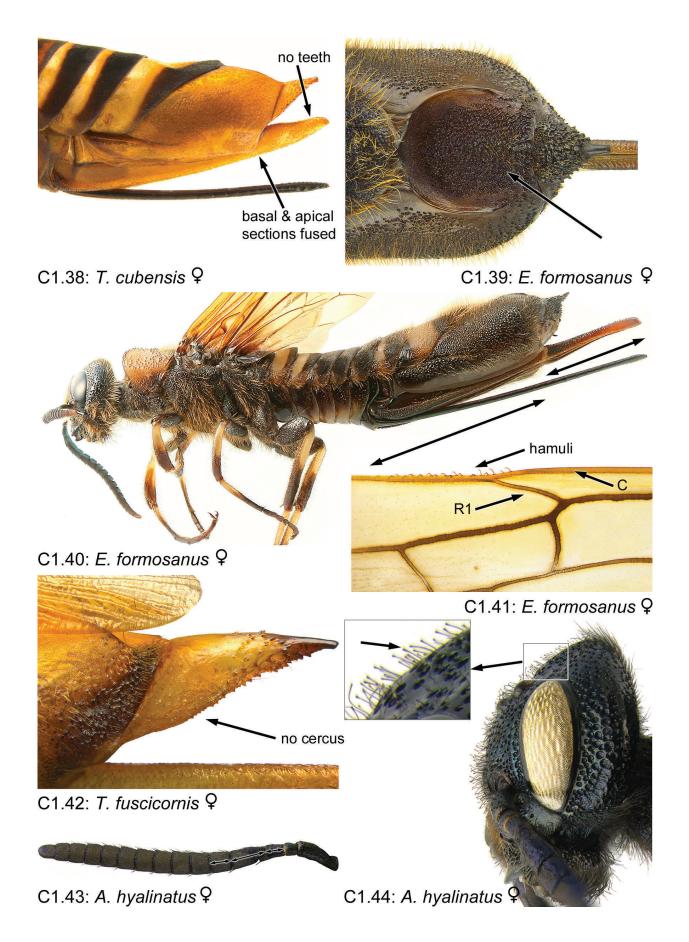


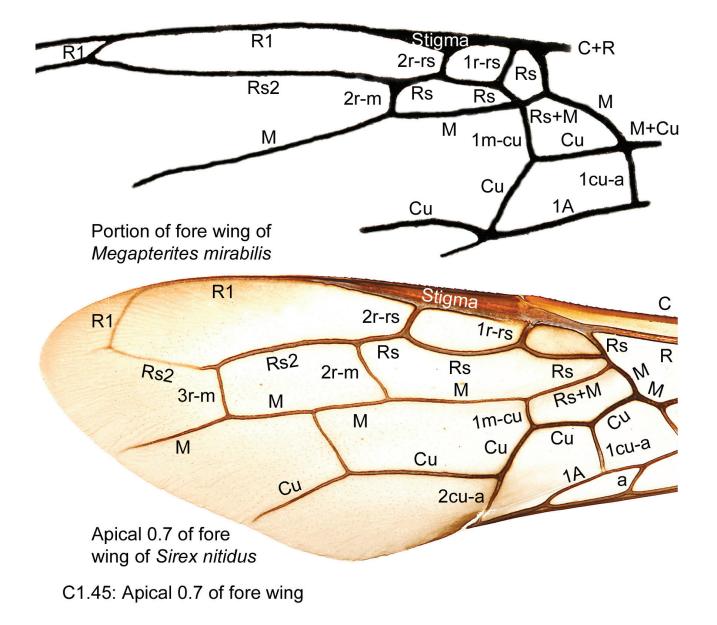
C1.24: X. matsumurae o





C1.33: S. tremecoides Q C1.34: S. tremecoides Q hind leg tibia tarsomere 1 C1.36: T. cubensis Q C1.36: T. cubensis Q C1.37: T. cubensis Q





2. Subfamily Siricinae

Diagnostic combination

Both sexes of Siricinae are recognized by the fore wing junction of vein Rs originating from vein 1r–rs and ending typically at veins Rs and M (Fig. A3.30).

Diversity and Hosts

There are four genera and 64 extant species in the world, and three genera and 18 native species in the Western Hemisphere. Taeger *et al.* (2010) recognized 7 genera; here we synonymized one of these (*Neoxeris*) and transferred *Siricosoma*, *Xeris* and *Neoxeris* (a new synonym of *Xeris* discussed under this genus) to the Tremicinae. All reared specimens (three genera with known hosts) of Siricinae were from conifers.



C3.1: S. nitidus \mathcal{P} with pale femora

3. Genus Sirex Linnaeus

Fig. C3.1 (live female, habitus)

- *Sirex* Linnaeus, 1760 [1761]: 396. Type species: *Sirex juvencus* Linnaeus designated by Curtis (1829: plate 253).
- *Sirex* subg. *Paururus* Konow, 1896: 41, 43. Type species: *Sirex juvencus* Linnaeus designated by Rohwer, 1911. Objective synonymy by Bradley (1913: 9).

Diagnostic combination

Both sexes of *Sirex* are recognized by presence of the fore wing vein Cu1, the dark areas of the body with dark blue or green metallic reflections, the gena without ridge behind eye, and without a white spot dorsally. **Females** also have the cornus in dorsal view not constricted near the middle.

Description

Color. Black portions of body with dark blue or green metallic reflections, remaining pale surfaces, if present, light reddish brown to reddish brown.

Head. Antennal sockets with distance between their inner edges 1.5–2.0 times distance between inner edge of eye and outer edge of socket (Fig. C3.2). Distance between inner edges of lateral ocelli about as long as distance between outer edge of lateral ocellus and nearest edge of eye (Fig. C3.3). Maximum distance between outer edges of eyes clearly less than maximum width of head (thus, in frontal view, genal edge completely visible and not intersected by outer edge of eye) (Fig. C3.2). Minimum distance between inner edges of eyes about 1.5 times maximum eye height (Fig. C3.2). Gena without ridge behind eye and without white spot (at most

with brown spot in males of one species) (Fig. C3.4), with large pits, each with posterior edge not elevated as low tooth. Head with setae sharp at apex. Antenna with 12 or more flagellomeres (the smallest specimens have the lowest number), and middle flagellomeres in dorsal view 1.5–3.0 times as long as wide; middle and apical flagellomeres with sensory pits over all except outer surface, apical 5–10 flagellomeres each with sensory oval impression on inner dorsal and inner ventral surfaces.

Thorax. Pronotum smooth or pitted over less than 0.5 of anterior surface. Mesoscutum densely pitted over median 0.5-0.7 only. Mesotarsomere 1 in lateral view not enlarged, its dorsal and ventral edges almost parallel and base of tarsomere at most 0.7 times its maximum width. Metatibia with two apical spurs, in male metatibia in lateral view 3.5-5.6 times as long as maximum width. In female, metatarsomere 2 in lateral view 1.5–5.0 times as long as maximum height. Metatarsomere 5 shorter than metatarsomere 2 or metatarsomeres 2 + 3. Fore wing with apex acutely and angularly rounded, with vein 2r-m joined to cell 2M (as in Fig. B1.71), with vein 2r-m present, with cell 1Rs2 clearly wider than long, with cell 3R1 3.0-3.8 times as wide as long, with cell 2R1 about 0.5 times as wide as cell 3R1, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even distal to junction with vein 2r-rs (Fig. A3.30), with vein Cu1 almost always fully developed, with vein 1cu-a joining vein Cu about mid way between veins 1m-cu and M, with vein 2A adjacent to posterior edge of wing for 0.25 times length of cell 1A length (Fig. A3.30), and with vein 3A absent or present but short. Hind wing with anal cell 1A (as in Fig. 1.44); hamuli clearly present both basal and apical to junction of veins R1 and C (Fig. B1.11).

Abdomen Female. Cornus in dorsal view short or long, lateral edges markedly to slightly convergent, but not constricted (Figs. B2.87 & B2.88). Tergum 9 with lateral

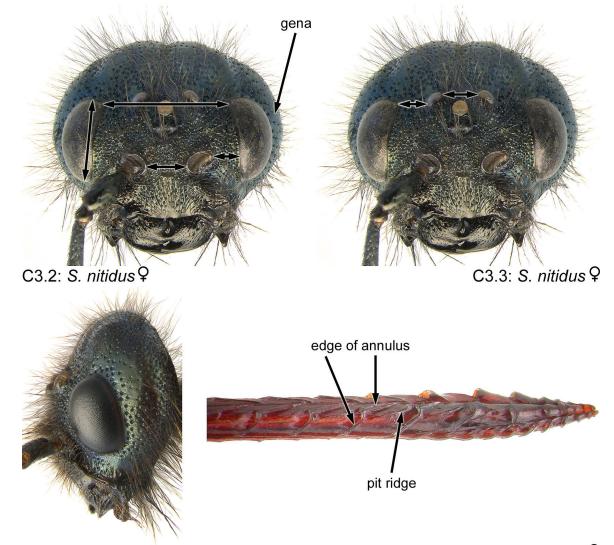
edges of median basin slightly divergent, straight or almost so, and sharply outlined for less than 0.3 times median length of basin (Figs. B2.87 & B2.88), and with basin base (outlined by black furrows laterally) 0.85-1.5 times as wide as median length of basin. Cercus present but very small and wart-like. Sheath. Length of basal section 0.4–1.4 times as long as apical section; apical section without longitudinal lateral ridge, and with teeth in apical third of dorsal margin and each tooth usually with small seta at base (as in Fig. B1.48). Ovipositor. Lancet with any of annuli 10-17 aligned with the junction of basal and apical sections of sheath; first two or three annuli anterior to teeth annuli each with clearly outlined, open ended pit extending along most of annulus and most pits with ventral edge ridged; pits anterior to first annulus before teeth annuli large to very large and edge of annulus below pit sharply and acutely produced and clearly outlined to ventral edge of lancet (Fig. C3.5).

Diversity and distribution

Sirex is diverse in the Northern Hemisphere with 28 extant species (15 known from the Palaearctic region) (Taeger and Blank 2011, Taeger *et al.* 2010). This is the most diverse genus in the New World with 14 species, one of which, *S. noctilio*, was introduced from the Old World. The genus is widespread across North America. More species are expected from the Mexican highlands and perhaps the large Caribbean islands. We studied six Palaearctic species in addition to the Nearctic ones.

References

References provided here mostly emphasize the taxonomic literature. Slippers and Haugen (2009) maintain an extensive bibliography (about 430 papers) on all aspect of *Sirex*, and their links to other information.



C3.4: S. nitidus o

C3.5: S. abietinus Q

4. Sirex abietinus Goulet, n. sp.

Fig. C4.1 (female habitus) Fig. C4.2) (male habitus) Fig. C4.4 (map)

- *Sirex juvencus* race *cyaneus* Bradley, 1913: 14 (not *S. cyaneus* Fabricius, 1781: 419); accepted as subspecies by Ries 1951: 83, Middlekauff 1960: 65, Smith 1979: 126. This synonymy applies only to females from the Rocky Mountains and westward.
- *Sirex cyaneus* Ries, 1951: 83 (not Fabricius, 1781: 419); Middlekauff 1960: 64, Smith 1979: 127. This synonymy applies only to females from the Rocky Mountains and westward.

Diagnostic combination

Among females with a completely light reddish brown metafemur, short metatarsomere 2 (tarsomere 1.5-3.0 times as long as high), and long tarsal pad (pad 0.7–0.8 times as long as ventral length of tarsomere) [cyaneus, hispaniola, and nitidus], those of S. abietinus are recognized by the very small pits at the middle of the lancet (length 0.0-0.13 times as long as length of annulus), length of annulus 10 1.76–2.37 times as long as height of ovipositor (lance + lancet), and the lack of pits in basal 6–9 annuli of the ovipositor. Among males with a reddish brown metafemur and mainly black metatibia [cyaneus, nitidus, noctilio and varipes] those of S. abietinus are recognized by the completely light reddish brown mesotibia and mesotarsus, the generally larger pits on the gena and vertex (pit diameter 0.25–0.4 times lateral ocellus diameter), and the narrow pale spot at the base of the metatibia (spot extending slightly beyond minimum constricted portion and as long as or slightly longer than wide).

Adults of this species are extremely similar to those of *S. cyaneus*, but the range of *S. abietinus* is from the Rocky Mountains and westward.

FEMALE. Description

Color. Body, antenna and palps black with dark blue metallic reflections. Coxae black, femora, tibiae and tarsi light reddish brown (apical half of tarsomeres 5 occasionally darker but not dark brown or black, and femora black in one specimen from southern Yukon). Fore wing mainly clear, at most tinted light brown in apical third.

Head. Gena with pits 0.0–4.0 pit diameters apart; vertex especially on postocellar area with pits 0.0–2.0 pit diameters apart, and each pit diameter 0.15–0.25 times lateral ocellus diameter.

Thorax. Mesoscutum with coarse, net-like pits in median

area. Metatarsomere 2 in lateral view 2.1-3.2 times as long as high, and its length about 1.0-1.2 times length of tarsomeres 3 + 4; tarsal pad 0.8-0.9 times as long as ventral length of tarsomere. Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 0.65-1.2 times as long as median length, maximum width 1.1-1.4 times as long as median length, and median length 0.55–0.65 times cornus length (Fig. B2.87). Cornus in dorsal view usually long and thick, with edges straight and curved apically, its median length 1.2-1.4 as long as maximum width of abdomen at junction of terga 9 and 10 (Fig. B2.87). Sheath. Length 0.75-0.95 times fore wing length, basal section 0.75-1.0 times as long as apical section. Ovipositor. Lancet with 31-37 annuli (basal annuli weakly outlined); junction of basal and apical section of sheath aligned between 9th and 10th or 10th and 11th annuli, with 26–29 pits beginning with annuli 4-11 (Fig. C4.3). Pits near middle annuli or area at base of apical section of sheath 0.03-0.14 times as long as an annulus (pits gradually and markedly decreasing in size toward base), 0.15–0.4 times as high as lancet height in lateral view, and 1.0–1.7 times as long as high; annulus 10 length/ovipositor diameter (lance + lancet) 1.76-2.37 (based on 26 specimens) (Fig. B2.85). Last 4-6 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit (Fig. C3.5). Edge of apical 6-8 annuli before teeth annuli extending as ridge to ventral edge of lancet (Fig. C3.5).

MALE. Description

Color. Head thorax and coxae black with dark blue metallic reflections. Coxae, metatibia (except extreme base), and metatarsomeres 1–3 black; femora, and tibiae and tarsus of fore and middle legs light reddish brown. Fore wing tinted light yellow. Abdomen with segments 1–3 (basomedian region from tergum 4 to as many as terga 4–7) black, segments 3–7 (excluding black median spot when present) light reddish brown, and sternum 9 light reddish brown rarely with some black at side.

Thorax. Metatibia 3.9–5.5 times as long as maximum width. Metatarsomere 1 in lateral view 3.1–3.4 times as long as maximum height.

Type material

Holotype female (CNC), in perfect condition, labeled "Clearwater BC 20–VI–67" "66–6076–03 Abies lasiocarpa R'rd [reared] logs Coll [struck out]" [White label], "HOLOTYPE Sirex abietinus Goulet CNC No. 23907" [Red label]. Type locality: Canada, British Columbia, Clearwater.

Paratypes. 50 females and 10 males. **CANADA.** Alberta: Banff, 10.IX.1924 (1F, MTEC); Banff, 11,IX.1924 (1

F, MTEC). British Columbia: Atlin 22.VIII.1955 (1 F, CNC); Clearwater, 2.VIII, 3.VIII.1966, 31.V, 5.VI, 20.VI, 22.VI.1967, reared from Abies lasiocarpa (8F, 1M allotype [20.V], CNC); Forest Insect Survey 272, 6.VIII.1938 (1 F, CNC); Forest Insect Survey 393, 15.IX.1939 (1 F, CNC); Hope Mountains, 20.VIII.1931 (1 F; CNC); Lower Hazel Cr., 10.VIII (1 F, CNC); Lumberton 3.VIII.1935 (1 F, CNC); Mount Revelstoke, 6000', 12.VIII.1923 (11 F, CNC); Quam Lake (1 F, CNC); Sarita River 2.VIII. 1946, 22.VII, 30.VII, 5.VIII..1948 (3 F, 3 M, CNC); Uslika Lake 5.VII, 20VII,1967, reared from Abies lasiocarpa (2 M, CNC); Uslika Lake 20.VII.1966, reared from Abies lasiocarpa (2 M, CNC); Mi 41, Uslika Lake Rd. 18.VI.1966, reared from *Abies* lasiocarpa (1 M, CNC); Vancouver, 18.VIII.1914 (1 F, CNC); Vancouver Island (1 F, CNC); Vernon, 30.VI, 5.VII.1965, reared from Abies lasiocarpa (3 F, CNC); White Pine Cr., 26.V, 3.VII.1967, reared from Abies lasiocarpa (2 M, CNC). Yukon Territory: Lake Laberge, 1929 (1 F, CNC); Whitehorse 27.VIII.1959 (1 F, CNC). USA. California: Napa Co., Angwin, 20.IX.1968 (1 F, USNM). Colorado: no data (1 F, USNM). Montana: Gallatin Co., Bozeman, 19. VIII. 1984 (1F, MTEC); Rivali Co., Nezperce Mountain, VII.1923 (1F, MTEC). Nevada: Elko Co., Jarbidge, Hopk. U.S. 18677, 15.VIII.1929 (1 F, USNM). Oregon: Klamath Co., Crater Lake Nat. Park, Crater Springs (1 F, USNM); Sisters, 15.VII1938, reared from Abies lasiocarpa, R. L. Furniss, Hopk. U. S. 31,766-S, barcode 00105829 (1 F, OSAC). Utah: Tabionia, 25.IX.1941, R. L. Furniss, barcode 00110916 (1 F, OSAC). Washington: Clear Lake, 24.II.1955, reared from Abies amabilis, cage 26, barcode 00105775 (1 F, OSAC); Mount Rainier Nat. Park, Paradise Valley, Hopk. U.S. 4245a (1 F, USNM). Wyoming: Teton Co., Yellowstone Nat. Park, Old Faithful, 26.VIII.1925 (1 F, 2 M, USNM).

Taxonomic notes

Sirex abietinus is a Nearctic species. Adults of this species are very similar to those of *S. cyaneus*, a Nearctic species. *Sirex cyaneus* should not to be confused with the European "*S. cyaneus*", a name incorrectly used in Europe for two European species that should be called *S. torvus* M. Harris (see chapter D, Additional Notes) and *S. juvencus*. The ovipositor of *S. abietinus* has no pits in basal 0.4, a character state that does not occur in either European species. *Sirex abietinus* is the western equivalent of the more eastern *S. cyaneus*. *Sirex abietinus* females have relatively long ovipositor annuli (value calculated only for annulus between pits 9 and 10) and, commonly, a thick and long cornus, and males have completely light reddish brown apical abdominal segments. *Sirex cyaneus* females have relatively short

ovipositor annuli (value calculated only for annulus between pits 9 and 10) and a short cornus, and males (except in Alberta and perhaps Saskatchewan) have at least sterna 8 and 9 black (in most specimens, tergum 8 is completely black). The information from morphology and DNA barcoding shows a difference of 10.6% in the base pair number between *S. abietinus* and *S. cyaneus*. Clearly, the western populations (i.e., *S. abietinus*) are specifically distinct from *S. cyaneus*. The ranges of both species are allopatric. The two species have no known close relatives in Eurasia.

In western North America, this species is sympatric with *S. nitidus* and the pale femora form of *S. californicus*. In *S. abietinus* females, the pit size on the middle annuli of the ovipositor and the proportion of the length of the annulus between pits the 9 and 10 relative to the ovipositor diameter distinguish them from females of S. *nitidus*. In *S. abietinus* males (except specimens from Alberta and perhaps Saskatchewan) the middle leg color patterns distinguish them from *S. nitidus* males. *Sirex abietinus* females are easily distinguished from *S. californicus* females with pale femora by the long tarsal pad of metatarsomere 2, and the ovipositor pit size and shape at middle and base.

Though not yet within the range of *S. noctilio*, both sexes of *S. abietinus* are easily distinguished from *S. noctilio* by puncture size on the vertex, and pit development on the mesoscutum; females are easily separated by the long tarsal pad of metatarsomere 2 and the pit development near the middle of the ovipositor, and males by the reduced pale spot at the base of the metatibia.

Origin of specific epithet

This is an adjective derived from the genus name for the host tree, *Abies*, and *abietinus* means "of fir" because most specimens have been reared from fir.

Hosts and phenology

Sirex abietinus was reared mainly (83%) from *Abies* spp. (Pinaceae) (Morris 1967 [as *S. cyaneus* from *Abies lasiocarpa*]). Kirk (1975) reared 453 specimens from *Abies concolor* and *Picea engelmannii*, but we suspect that most of the specimens reared from firs are *S. abietinus* and most of the specimens reared from spruce are *S. nitidus*. Based on 68 reared and confirmed specimens, other hosts are: *Abies amabilis* (2), *A. lasiocarpa* (56) (reported by Morris (1967) under the names *S. cyaneus* and *S. juvencus*), *Picea engelmannii* (4), *P. glauca* (may not have been reared) (1), *P. sitchensis* (may not have been reared) (1), and *Tsuga heterophylla* (4). We have only one record from *Cupressus macrocarpa* (Cupressaceae).

Based on 30 field-collected specimens, the earliest and latest capture dates are July 20 and September 15. The main flight period is from late July to mid September with a peak in August.

Range

CANADA: AB, BC, YT. **USA:** CA, CO, MT, NV, OR, UT, WA, WY. *Sirex abietinus*, a western North American species, is known from southern Yukon and British Columbia south to California and Colorado (Fig. C4.4). *Sirex abietinus* has been intercepted in England (Saunt 1924). We have seen one male from New Zealand

(FRNZ).

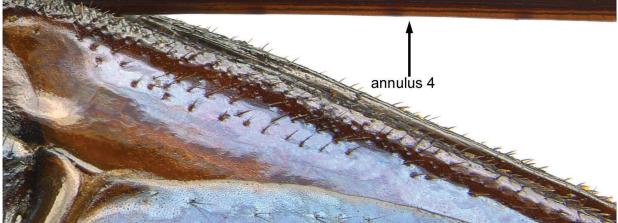
Specimens studied and included for range map: 111 females and 44 males from BYUC, CNC, DEBU, EDUM, MTEC, OSAC, PFRC, USFS–GA, and USNM.

Specimens for molecular studies: 5 specimens. See Fig. E2.5e.

CANADA. British Columbia: 2008, *CNCS 1029*, 601; 2000, *SIRCA 053*, 612; 1969, *SIRCA 064*, 583; 2000, *SIRCA 069*, 553. **USA. California**: 1999, *CBHR 103*, 658.



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C4.3: S. abietinus Q

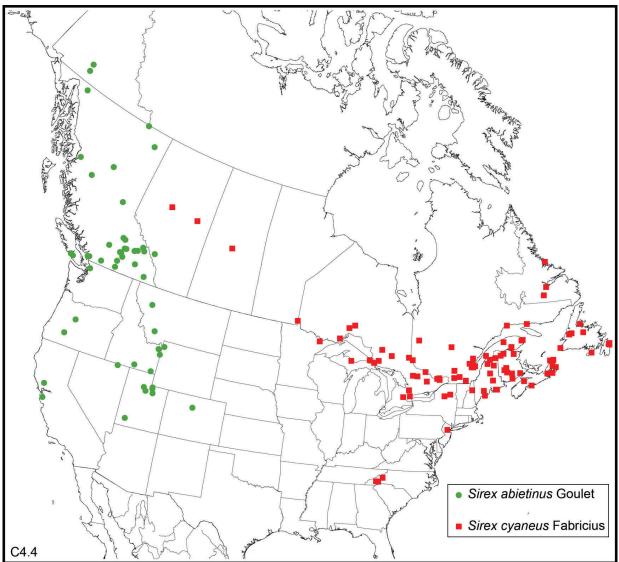


Fig. C5.1, Schiff *et al.* 2006: 20, 21 (female habitus) Fig. C5.2, Schiff *et al.* 2006: 19 (male habitus) Fig. C5.3 (map)

- *Urocerus areolatus* Cresson, 1868: 375. Holotype female (ANSP), examined by DRS; Cresson 1916: 9. Type locality: "New Mexico".
- *Sirex gracilis* Westwood, 1874: 114, pl. XXI, fig. 4. Holotype female (OXUM), images prepared by James E. Hogan and sent to HG for study. Synonym by Konow 1898: 81; accepted by Bradley 1913: 14, Ries 1951: 83, Smith 1979: 126. Type locality: "America Septentrionalis".
- *Urocerus caeruleus* Cresson, 1880: 34. Holotype female (ANSP), examined by DRS; Cresson, 1916: 10. Synonym by Konow 1898: 81; accepted by Ries 1951: 83, Smith 1979: 126. Type locality: "Vancouver's Island".
- *Urocerus gracilis*; Cresson, 1880: 51 (change in combination).
- *Sirex apicalis* Kirby, 1882: 377, pl. XV, fig. 11. Holotype male (BMNH), not examined.. Synonym by Konow 1898: 81; accepted by Baumberger 1915: 34, Ries 1951: 83, Smith 1979: 126. Type locality: "Vancouver's Island".
- *Paururus areolatus*; Konow, 1898: 90 (change in combination).
- *Sirex areolatus*; Kirby, 1882: 377 (change in combination); accepted by Bradley 1913: 13, Ries 1951: 83, Middlekauff 1960: 62, Smith 1979: 126.
- *Sirex areolatus* race *areolatus*; Bradley, 1913: 14 (change in rank). Synonym by Ries 1951: 83; accepted by Smith 1979: 126.
- *Sirex areolatus* race *caeruleus*; Bradley, 1913: 14 (change in rank). Synonym by Ries 1951: 83; accepted by Smith 1979: 126.

Diagnostic combination

Among **females** with longer tarsi (metatarsomere 2 about 5.0 times as long as high) [*longicauda*] those of *S*. *areolatus* are recognized by their completely black legs. **Males** are recognized by their completely black legs.

FEMALE. Description

Color. Body, legs, palps and antenna black with dark blue metallic reflections. Fore wing darkly to lightly tinted. **Head.** Gena with pits 1.0–5.0 pit diameters apart; vertex with pits 1.0–2.0 pit diameters apart, and each pit diameter about 0.25 times lateral ocellus.

Thorax. Mesoscutum with quite dense pits and numerous transverse ridges in median area. Metatarsomere 2 in

lateral view about 5.0 times as long as high (Fig. B2.3); tarsal pad 0.35–0.5 times as long as ventral length of tarsomere. Fore wing vein 3A present and extending along posterior margin of wing.

Abdomen. Median basin of tergum 9 with basal width 0.6–1.1 times as long as median length, maximum width about 0.9–1.3 times as long as median length, and median length about 0.55-0.7 times cornus length. Cornus in dorsal view long, attenuated in apical 0.25-0.3, and edges not angular midway; median length 1.2-1.5 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.95–1.2 times fore wing length; basal section 0.5-0.8 times as long as apical section (Fig. B2.5). Ovipositor. Lancet with 39-46 annuli (basal annuli clearly outlined); junction of basal and apical sections of sheath aligned between 10th and 11th to 12th and 13th ovipositor annuli, with 35-41 pits beginning with annulus 2 (Fig. B2.12). Pits near middle annuli or area at base of apical section of sheath about 0.15 times as long as an annulus (pits gradually decreasing in size toward base), about 0.3 times as high as lancet height in lateral view, and 1.0-1.2 times as long as high; annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last two annuli before teeth annuli with ridge on ventral edge of pit. Edge of apical 5-7 annuli before teeth annuli extending as ridge to ventral edge of lancet (Fig. B2.10).

MALE. Description

Color. Head, thorax, antenna, palps, abdominal segments 1, 2, 8, sterna 2 and 3 at side, and 8 black with dark blue metallic reflections; abdominal segments 3–7 mostly light reddish brown. Coxae and femora black (Fig. B2.93). Fore wing clear.

Thorax. Metatibia in lateral view 3.9–4.2 times as long as maximum width. Metatarsomere 1 2.8–3.1 times as long as maximum height.

Taxonomic notes

Sirex apicalis Kirby was not examined, but the description, especially the leg color pattern, perfectly matches this species.

Biological notes

Essig (1926) described adults and pupa as well as the microhabitats of the larvae and pupae. Chamberlin (1949) described pupae both in a stump and in adjacent soil.

Hosts and phenology

The host range of *S. areolatus* is very wide (Flanders 1925, Essig 1926, Middlekauff 1960, Cameron 1965, Westcott 1971). Based on 76 reared and confirmed specimens, the main hosts are Cupressaceae: *Cupressus macrocarpa* (49), *Juniperus occidentalis* (20) (from scorched trees (Westcott 1998)), *Calocedrus decurrens* (2), *Sequoia sempervirens* (first recorded by Baumberger (1915), and also from fresh cut burnt trees by De Leon (1952)), and *Taxodium distichum* (5). They are less often recorded from Pinaceae: *Pinus contorta, P. jeffreyi, P. lambertiana, P. radiata,* and *Pseudotsuga menziesii* (Chamberlin 1949).

Based on 44 field-collected specimens, the earliest and latest capture dates are late June and late November. The main flight period is from early September to early October.

Range

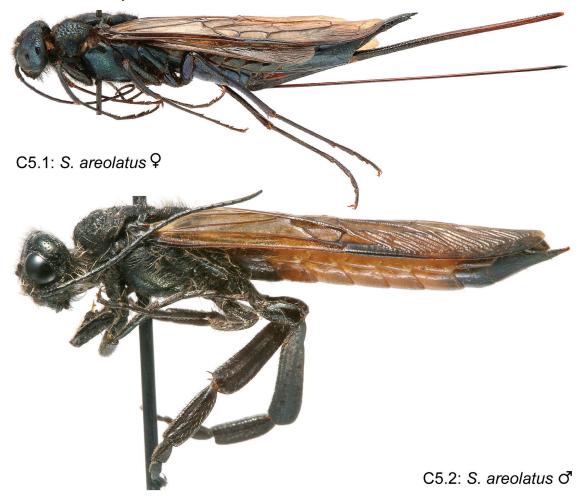
CANADA: BC, NS. **USA**: AR, AL, AZ, CA (Middlekauff 1960), CO, ID, FL, HA, NM, OR, UT, VA, WA. *Sirex areolatus* is mainly a western North American

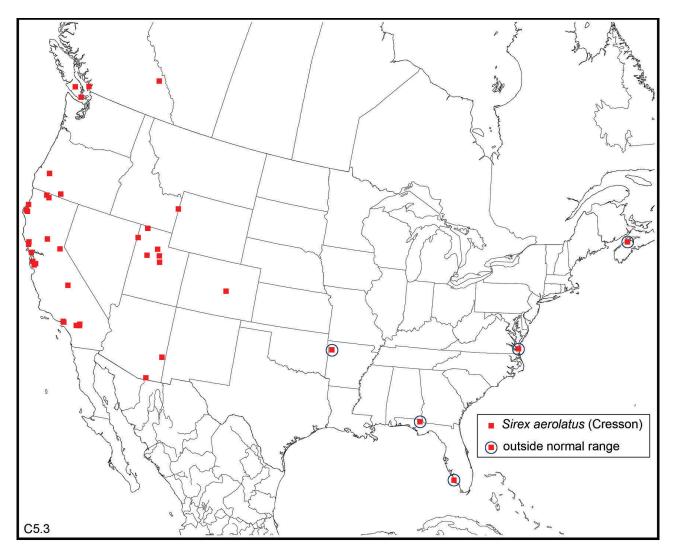
species known from British Columbia to California and New Mexico (Fig. C5.3). It is adventive in eastern North America (FL, AR, AL, NS, VA) and Hawaii (Burks, 1967) and is probably not established. The species was also intercepted in England (Benson 1940), and we have seen one female from New Zealand (PANZ). However, Smith and Schiff (2002) think that the Virginia record may suggest an establishment in wild habitats.

Specimens studied and included for range map: 50 females and 84 males from BYUC, CNC, FSCA, OSAC, PFRC, UAIC, UCRC, and USNM.

Specimens for molecular studies: 15 specimens. See Fig. E2.5a.

CANADA. British Columbia: 2008, *CNCS 1042*, 601; 2007, *CNCS 1043*, 532; 2007, *CNCS 1044*, 601; 2007, *CNCS 1045*, 607. **USA. California**: 1997, *CBHR 6*, 658; 1999, *CBHR 101*, 658; 2006, *CBHR 377*, 658; 2006, *CBHR 659*, 658; 2006, *CBHR 658*, 658; 2006, *CBHR 659*, 658; 2006, *CBHR 660*, 658; 2006, *CBHR 661*, 658; 2006, *CBHR 662*, 658; 2006, *CBHR 663*, 658; 2006, *CBHR 668*, 658.





6. Sirex behrensii (Cresson)

Fig. C6.1, Schiff *et al.* 2006: 24, 25 (female habitus) Fig. C6.2, Schiff *et al.* 2006 : 23 (male habitus) Fig. C6.4 (map)

- *Urocerus Behrensii* Cresson, 1880: 35. Holotype female (ANSP), examined by DRS; Cresson 1916: 9. Type locality: California.
- *Sirex behrensii*; Kirby, 1882: 379 (change in combination); accepted by Bradley 1913: 16, Ries 1951: 83, Middlekauff 1960, Smith 1979: 126.

Diagnostic combination

Among **females** with a black metafemur and metatibia and short metatarsomere 2 (less than 3.0 as long as high) [*californicus*, *mexicanus*, *nigricornis*, *obesus* and *xerophilus*] those of *S. behrensii* are recognized by the reddish brown tarsi and the mainly reddish brown abdomen. **Males** are recognized by the metafemur with a reddish brown ventral half and a black dorsal half, and by the brown spot on the gena behind the eye and occipital margin.

FEMALE. Description

Color. Head, antenna, palps, thorax, abdominal segments 1 and 2, lateral surface of terga 3–9 or 3–10, and lateral surface of sterna 3–7 or 4–7 black with dark blue metallic reflections; most of terga 3–9, or all of tergum 9 and 10, and most of sterna 3–7 or 4–7 reddish brown (Fig. B2.13). Coxae, femora, most of tibiae, and most of or part of tarsomere 1 of fore leg or fore and middle legs black; apex and ventral half of tibiae, tarsomeres 2–5 of fore leg, 1–5 or 2–5 of middle leg, and metatarsus reddish brown. Fore wing in apical third and basal to stigma with darkly tinted bands (Fig. C6.3).

Head. Gena with pits 4.0–8.0 diameters apart between eye and posterior head margin; very dense on vertex and postocellar area, and each pit diameter about 0.25 times

lateral ocellus. Gena with central surface with a round ridge between eye and occiput (Fig. B2.16).

Thorax. Mesoscutum with dense pits in median area; pits round, and transverse ridges moderately numerous. Metatarsomere 2 in lateral view 2.4–3.0 times as long as high; tarsal pad 0.4–0.5 times as long as ventral length of tarsomere. Fore wing vein 3A present and extending to posterior wing margin (Fig. C6.3).

Abdomen. Median basin of tergum 9 with basal width 0.8–1.0 times as long as median length, maximum width 1.1-1.7 times as long as median length, and median length 1.0–1.2 times as long as cornus length. Cornus in dorsal view short, with edges straight or slightly angular midway; its median length 1.0-1.2 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.68-0.82 times fore wing length, basal section 0.93-1.17 times as long as apical section. Ovipositor. Lancet with 31-36 annuli (basal annuli clearly outlined); junction of basal and apical section of sheath aligned between 12th and 13th annuli, with 28–32 pits beginning with annulus 2. Pits near middle annuli or area at base of apical section of sheath, about 0.2 times as long as an annulus (pits gradually decreasing in size and very small toward base), about 0.3 times as high as lancet height in lateral view, and about 1.5 times as long as high (Fig. B2.18); annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last 2-3 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 5–7 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head (except behind eye), thorax, antenna beyond flagellomere 6, palps, and abdominal segments 1 and 2 black with dark blue metallic reflections; smooth surface on gena between eye and posterior margin of occiput brown (Fig. B2.106); antennomeres 1-5, and abdominal segments 3-9 light reddish brown. Coxae, striated surface of femora of fore and middle legs, and dorsal 0.5 of metafemur black (Fig. B2.104); metatibia (except extreme base), apical 0.3-0.5 of mesotibia and mesotarsomeres 1-2, and metatarsomeres 1-3 and 5 brown to dark brown (Fig. B2.104); most of femora of fore and middle legs, ventral half of metafemur, tibiae and tarsi of fore leg, basal 0.3-0.7 of mesotibia, mesotarsomeres 3-5, metatarsomeres 4, and extreme base (spot about 0.5 times as long as minimum width of tibia at base) of metatibia light reddish brown. Fore wing clear.

Thorax. Metatibia 3.5–4.0 times as long as maximum width (Fig. B2.104). Metatarsomere 1 in lateral view

2.7–3.5 times as long as maximum height.

Taxonomic notes

Females of *S. behrensii* may be confused with the pale abdomen females of *S. nigricornis*. The clearly outlined banded wing pattern, the broad black longitudinal band along the side of the abdomen and completely reddish brown segment 10, and the presence of fore wing vein 3A should distinguish them from *S. nigricornis females*. Males are easily distinguished among New World *Sirex* by antenna and hind leg color patterns. Daly (1963) used specimens of *S. behrensii* for thoracic muscle studies.

Hosts and phenology

The host range of *S. behrensii* is moderately wide (Flanders, 1925, Essig 1926, Middlekauff 1960, Cameron 1965). All but one hosts, based on 50 reared and confirmed specimens, are Pinaceae: *Pinus Jeffreyi* (2), *P. lambertiana* (1), *P. ponderosa* (46), *P. radiata*, and *Pseudotsuga menziesii* (1). One record is on *Cupressus macrocarpa* (Cupressaceae).

Based on 30 field-collected specimens, the earliest and latest capture dates are from early June to late November. The main flight period is from late July to late October with a peak in late September.

Range

CANADA: BC. **USA:** CA (Middlekauff 1960), ID, NV, OH (probably not established), OR, WA, WV (probably not established). *Sirex behrensii*, a western North American species, is recorded from southernmost British Columbia to California and Nevada (Fig. C6.4). The specimen from Ohio was on imported lumber and is probably not established (Smith and Schiff 2002).

Specimens studied and included for range map: 32 females and 38 males from CNC, OSAC, PFRC, UCRC, and USNM.

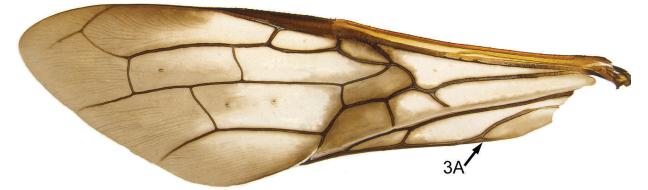
Specimens for molecular studies: 13 specimens. See Fig. E2.5a.

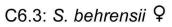
CANADA. British Columbia: 2002, *SIRCA 048*, 416; 2002, *SIRCA 050*, 407; 2002, *SIRCA 051*, 575; 2002, *SIRCA 052*, 407. **USA. California**: 2006, *CBHR 664*, 658; 2006, *CBHR 665*, 499; 2006, *CBHR 666*, 658; 2006, *CBHR 667*, 658; 2006, *CBHR 669*, 658. **Oregon**: 2006, *CBHR 1075*, 658; 2006, *CBHR 1076*, 658; 2006, *CBHR 1077*, 658. **Unknown State**: unknown year, *CBHR 171*, 658.

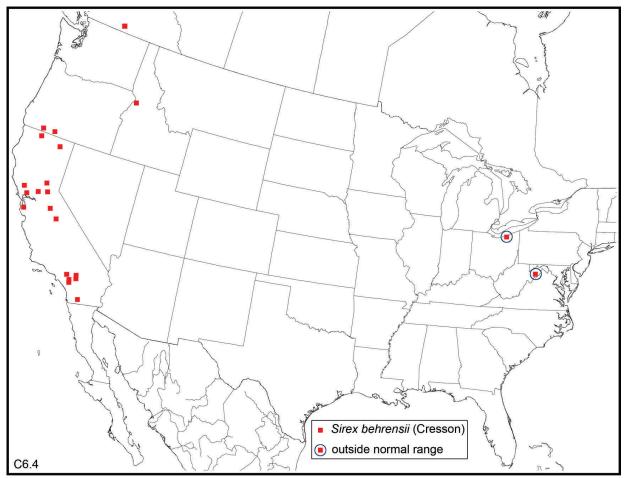


C6.1: S. behrensii Q









7. Sirex californicus (Ashmead), n. stat.

Fig. C7.1, Schiff *et al.* 2006: 36, 37 (female with dark legs, habitus)

- Fig. C7.2 (female with pale legs, habitus) Fig. C7.3, Schiff *et al.* 2006: 35 (male, habitus) Fig. C7.4 (live female with dark legs)
- Fig. C7.5 (live female with pale legs)
- Fig. C7.6 (live male)
- Fig. C7.7 (map)
- *Paururus Californicus* Ashmead, 1904: 64. Lectotype female (USNM), here designated; labeled "Sept." "Placer Co., Cal." "female Type No. 7683 U.S.N.M.", "Paururus californicus Ashm, female [handwritten] Female, type [handwritten]". Paralectotype female, here designated, from "Hoquiam, Wash."; Middlekauff 1960: 63. Type locality: California, Placer Co.
- *Sirex californicus*; Bradley, 1913: 11 (change in combination); accepted by Ries 1951: 83.
- Sirex obesus Cameron, 1967: 19 (not Bradley, 1913: 12); accepted by Smith 1979: 127.
- *Sirex juvencus* race *cyaneus* Bradley, 1913: 14 (not *S. cyaneus* Fabricius, 1781: 419); accepted as a subspecies by Ries 1951: 83, Middlekauff 1960: 65, Smith 1979: 126. This synonymy applies only to females with light reddish brown femora.
- *Sirex cyaneus* Middlekauff, 1960: 64 (not Fabricius, 1781: 419); accepted by Smith 1979: 127. This applies to the pale legged females of *S. californicus*.
- *Sirex juvencus californicus*; Benson, 1963: 252 (change in rank); accepted by Cameron 1967, Morris 1967: 60, Smith 1979: 127.

Diagnostic combination

Among females with the completely black legs, a moderately short metatarsomere 2 (about 2 times as long as high), and a completely or partly darkly tinted (dark bands behind stigma and apical third) fore wing [obesus and nigricornis], those of S. californicus are recognized by the scattered pits on the gena and part of the vertex (pits 2.0-4.0 pit diameters apart). Among females with completely pale legs beyond the coxae, a moderately short metatarsomere 2 (about 2.0 times as long as high), and a short tarsal pad on metatarsomere 2 (about 0.5 times as long as ventral tarsal length) [noctilio], those of S. californicus are recognized by the well developed pits on the vertex and the widespread net-like pits on the median 0.7 of mesoscutum. Among males with reddish brown femora, tibiae and tarsi [mexicanus and xerophilus], those of S. californicus are recognized by the light reddish brown basal five or six antennomeres.

FEMALE. Description

Color. In **dark form**, body, legs, palps, and antenna black with dark blue metallic reflections, or in **pale form**, black with dark blue metallic reflections but femora, tibiae and tarsomeres 1–4 light reddish brown. Fore wing darkly tinted (southern part of range) to clear with dark bands basal to stigma and in apical third (Fig. B2.74).

Head. Gena with pits 2.0–4.0 pit diameters apart (Fig. B2.17), vertex and postocellar area with pits 0.1–2.0 pit diameters apart, and each pit diameter about 0.15–0.2 that of lateral ocellus (Fig. B2.36).

Thorax. Mesoscutum with coarse net-like pits restricted to posterior 0.6 of median area, with transverse and longitudinal ridges in coarsely pitted area. Metatarsomere 2 in lateral view more than 2.0 times as long as high, and its length about 1.2 times length of tarsomeres 3 + 4; tarsal pad about 0.5. times as long as ventral length of tarsomere. Fore wing vein 3A absent (Fig. B2.74).

Abdomen. Median basin of tergum 9 with basal width 1.1-1.4 times as long as median length, maximum width 1.3–1.7 times as long as median length, and median length 0.6–0.8 times cornus length. Cornus in dorsal view short, either with edges straight in large specimens or clearly angular midway in small specimens, its median length 0.8-1.1 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.7-0.8 times as long as fore wing length, basal section 1.05–1.35 times as long as apical section. Ovipositor. Lancet with 28-38 annuli (edge of basal annuli difficult to see); junction of basal and apical section of sheath aligned between 12th and 13th to 15th and 16th annuli, with 24–34 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1 (Fig. B2.25). Pits near middle annuli (Fig. B2.19) or area at base of apical section of sheath 0.3–0.35 times as long as an annulus (pits clearly decreased at base to about 0.2), about 0.4–0.6 times as high as lancet height in lateral view, and about 1.6-2.2 times as long as high (Fig. B2.38, middle); length of lancet annulus/ovipositor diameter (lance + lancet) for annulus 2 1.43-2.07, for annulus 5 1.46-2.14, for annulus 10 1.3-1.8, and for annulus 13 1.40-1.66 (7 specimens). Last 4 or 5 annuli before teeth annuli and as well as first tooth annulus with ridge on ventral edge of pit (Fig. C1.15). Edge of apical 4-5 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head. Head, apical 0.7 of antenna, palps, thorax, abdominal segments 1, median area of tergum 2 or 1 and 2, and median area of tergum 3 black with dark blue metallic reflections; abdominal segments 3–10, and antennomeres 1–5 light reddish brown (Fig. B2.113). Legs reddish brown, but black on coxae (Fig. B2.107).

Fore wing clear with a very light yellow tint in some specimens (Fig. B2.115).

Thorax. Metatibia 3.8–4.3 times as long as maximum width. Metatarsomere 1 in lateral view 2.7–3.1 times as long as maximum height (Fig. B2.107).

Taxonomic notes

Benson (1963) ranked S. californicus as a subspecies of the European S. juvencus. The two populations differ in color pattern in both sexes (the color pattern of males was unknown to Benson at the time); in females of S. californicus, the tarsal pad of metatarsomere 2 is short (long in S. juvencus) and the ovipositor pits are long and large medially and about twice as long as high (short and small medially and a little longer than high in *S. juvencus*). The main hosts of S. californicus are various species of Pinus; for S. juvencus they are various species of Picea. The range of S. californicus extends from southernmost British Columbia and southwestern Alberta to California, Colorado and South Dakota; a Holarctic species would not have such a range in the Nearctic region. Therefore, S. californicus is clearly and specifically distinct from S. juvencus.

Females of *S. californicus* exist in two discrete color forms. The legs are either all black or they are light reddish brown beyond the coxae. Dark-legged females are the most common form seen over the range. Pale-legged females are known from southern British Columbia and the northern half of western United States as far east as the Black Hills of South Dakota.

Females of *S. californicus* with black legs are similar to three other western species: *S. obesus, S. mexicanus,* and *S. xerophilus.* They are distinguished from them by the less dense pits on the vertex. They are also distinguished from *S. mexicanus* and *S. xerophilus* by the partial or complete dark tinted wings and differences in the pit development on the ovipositor, and from the very similar *S. obesus* by the more slender metatarsomere 2. Females of *S. californicus* may also be confused with females of the black abdomen form of *S. nigricornis* (if the British Columbia record for this species is correct). The ovipositor pits are longer and the pit density on the vertex is clearly less in *S. californicus* than in *S. nigricornis.*

Females of *S. californicus* with pale legs may be confused with similarly colored species associated with firs and spruces (e.g., *S. abietinus, S. cyaneus, S. nitidus,* and very few specimens of *S. varipes*). Pits on the head of *S. californicus* are clearly larger and the tarsal pad on metatarsomere 2 shorter than in the above four species. Females of the pale form of *S. californicus* may be confused with those of *S. noctilio* with short tarsal pads on metatarsomere 2, but they are easily distinguished by

the much larger and denser pits on the vertex.

Males of *S. californicus* from westernmost Nevada were first associated with females and described by Cameron (1967), and are easily distinguished from males of the three other species with a reddish brown metafemur.

Biological notes

Cameron (1967) reported 216–804 eggs in female ovaries of *S. californicus*, with the highest number of eggs associated with the largest females. Eggs that are going through the ovipositor become 2.5 times as long as those within the ovaries (Cameron 1967). *Megarhyssa nortoni nortoni* (Cresson), an important parasitoid, was often observed ovipositing in logs of *Pinus jeffreyi* containing larvae of *S. californicus* (Cameron, 1967).

Hosts and phenology

The host range of *S. californicus* is wide (Essig 1926, Middlekauff 1960, Cameron 1965, Cameron 1967, Morris 1967, Kirk 1975 [some of the reared specimens could be *S. obesus*]). The most commonly seen hosts belong to *Pinus* (99% of reared specimens). Based on 128 reared and confirmed specimens, all hosts are Pinaceae: *Larix occidentalis* (1), *Pinus albicaulis* (1), *P. contorta* (107) (pale legged females reported as *S. juvencus* by Morris (1967)), *P. coulteri* (1), *P. jeffreyi* (3), *P. lambertiana* (11), *P. monticola* (1), *P. ponderosa* (336) (large emergence reported by Cameron (1968) and Kirk (1975)), *P. sylvestris* (2), and *Pseudotsuga menziesii* (1). We have only one record from *Cupressus macrocarpa* (Cupressaceae).

Based on 74 field-collected specimens, the earliest and latest capture dates are July 17 and September 11. The main flight period is from second half of July to second half of September with a peak in late August (Cameron 1967).

Range

CANADA: AB, BC. **Mexico:** Intercepted specimen from Mexico at United States border in southern California. **USA:** CA (Middlekauff 1960), CO, ID, MT, NV, OR, SD, UT, WA, WY. *Sirex californicus* is found from the Rocky Mountains of southern British Columbia to California, Colorado and South Dakota (Fig. C7.7). We have seen one intercepted female from New Zealand.

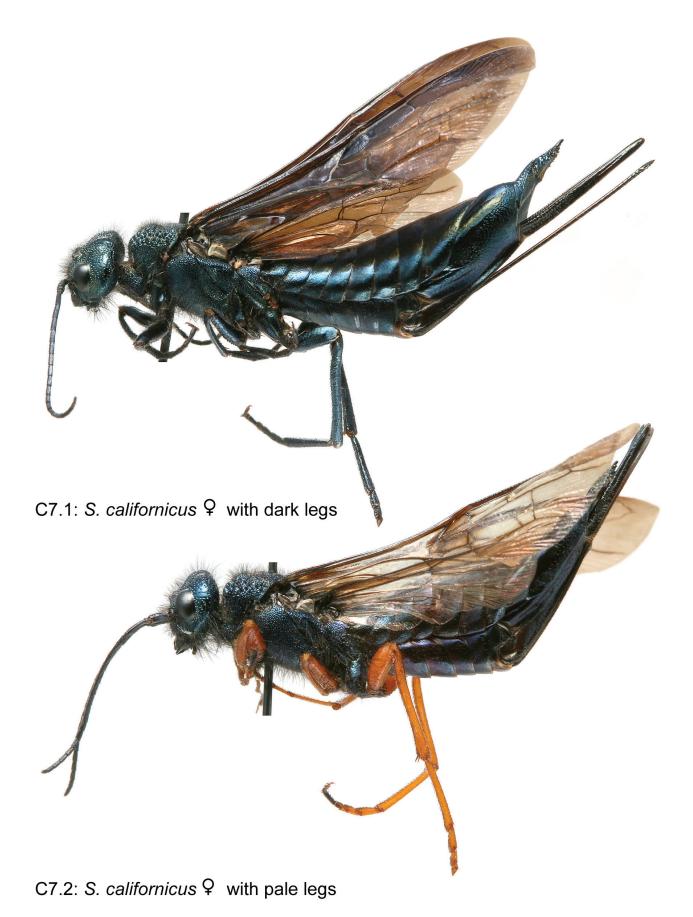
Specimens studied and included for range map: 384 females and 91 males from BDUC, BYUC, CFIA, CNC, MTEC, NFRC, OSAC, PFRC, USFS–GA, and USNM.

Specimens of *S. californicus* for molecular studies: 52 specimens. See Fig. E2.5f.

CANADA. British Columbia: 2006, CBHR 415, 658; 2006, CBHR 416, 658; 2006, CBHR 417, 658; 2006, *CBHR 421*, 601; 2006, *CBHR 422*, 624; 2006, *CBHR 424*, 658; 2006, CBHR 426, 621; 2006, CBHR 427, 658; 2006, CBHR 428, 658; 2006, CBHR 429, 658; 2006, CBHR 430, 658; 2006, CBHR 431, 658; 2006, CBHR 432, 658; 2006, CBHR 434, 617; 2006, CBHR 435, 658; 2006, CBHR 436, 658; 2006, CBHR 437, 658; 2006, CBHR 447, 658; 2006, CBHR 473, 658; 2000, SIRCA 075, 587; 2000, SIRCA 077, 636.. USA. California: 2007, CNCS 1020, 590. Colorado: 2005, CBHR 191, 658; 2006, CBHR 407, 607. Idaho: 2008, CBHR 1355, 624; 2008, CBHR 1359, 658. Montana: 2004, CBHR 207, 658; 2007, CNCS 1001, 609; 2007, CNCS 1002, 603; 2007, CNCS 1003, 557; 2007, CNCS 1004, 610; 2007, CNCS 1009, 604; 2007, CNCS 1010, 611. Oregon: 2004, CBHR 521, 658. Washington: 2005, CBHR 233, 602; 2007, CBHR 1184, 658; 2007, CBHR 1185, 658; 2007, CBHR 1186, 658; 2007, CBHR 1187, 658; 2007, CBHR 1243, 658; 2008, CBHR 1340, 580; 2008, CBHR 1341, 643; 2008, CBHR 1343, 658; 2008, CBHR 1344, 624; 2008, CBHR 1347, 630; 2008, CBHR 1349, 514; 2008, CBHR 1350, 658; 2008, CBHR 1970, 658. Unknown state: 2006, CBHR 402, 658; 2006, CBHR 403, 658; 2006, CBHR 404, 601; 2006, CBHR 405, 630; 2006, CBHR 406, 658.

Specimens of *S.* sp. near *californicus* for molecular studies: 9 specimens. See Fig. E2.5f.

USA. Colorado: 2007, CNCS 1006, 585; 2007, CNCS 1007, 605; 2007, CNCS 1008, 609; 2007, CNCS 1013, 588; 2007, CNCS 1014, 619; 2007, CNCS 1015, 603; 2007, CNCS 1016, 584; 2007, CNCS 1018, 608; 2007, CNCS 1019, 608.





C7.3: S. californicus o



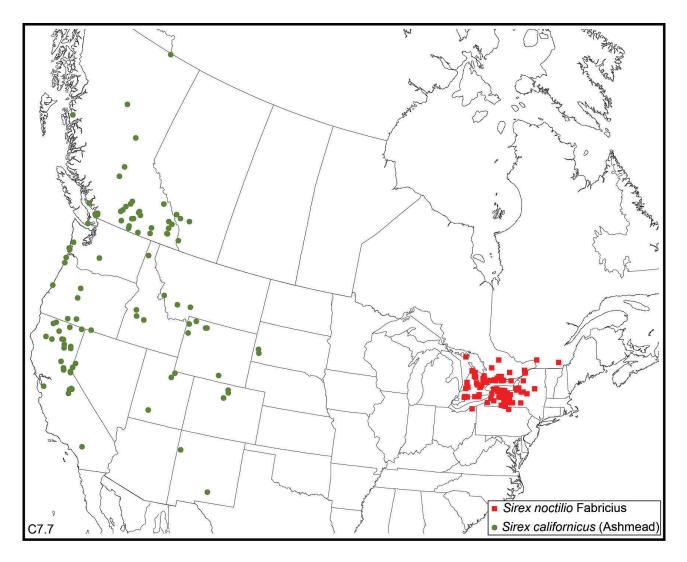
C7.4: S. californicus Q with dark legs



C7.5: *S. californicus* Q with pale legs



C7.6: S. californicus o



8. Sirex cyaneus Fabricius

Fig. C8.1 (female habitus) Fig. C8.2 (male habitus) Fig. C4.4 (map)

- *Sirex cyaneus* Fabricius, 1781: 419. Type female (HMUG), dissection and images of ovipositor prepared by Geoff Hancock and sent to HG for study. Type locality: "America boreali".
- *Urocerus cyaneus*; Norton, 1869: 357 (change in combination); accepted by Provancher 1879: 230 and 1883: 241.
- Sirex abbotii Kirby, 1882: 378, pl. XV, fig. 8. Holotype male (BMNH), examined by HG. Synonym by Bradley 1913: 14; accepted by Smith 1979: 126. Until recently, no one knew the whereabouts of the *S. cyaneus* type. The synonymy by Bradley 1913: 14 was thus applied correctly by chance. Type locality: Georgia.
- *Sirex hirsutus* Bradley, 1913: 14 (not Kirby, 1882: 380); accepted by Ries 1951: 83, Smith 1979: 126. See

"Additional notes"

Sirex juvencus cyaneus; Bradley, 1913: 14 (change in rank); accepted by Hedicke 1938: 19.

Diagnostic combination

Among **females** with a completely light reddish brown metafemur, short metatarsomere 2 (tarsomere 1.5–3.0 times as long as high), black abdomen, and long tarsal pad (length of pad 0.7–0.8 as long as ventral length of tarsomere) [*abietinus*, *nitidus*, and *varipes*], those of *S. cyaneus* are recognized by the much very small pits at the middle of the lancet (pit length 0.0–0.13 times as long as length of annulus), length of annulus 10 1.33– 1.82 as long as height of ovipositor (lance + lancet) at this annulus, and the lack of pits in basal 6–9 annuli of the ovipositor. Among **males** with a reddish brown metafemur and mainly black metatibia [*abietinus*, *nitidus*, *noctilio* and *varipes*], those of *S. cyaneus* are recognized by the completely light reddish brown mesotibia and mesotarsus, the moderately large pits on the gena and the vertex (diameter of pit 0.25–0.4 that of lateral ocellus), and the narrow pale base of the metatibia (spot extending slightly beyond minimum constricted portion and as long as or slightly longer than wide).

Adults of *S. cyaneus* are extremely similar to those of *S. abietinus*. If the male is from east of the Rocky Mountains within the range of *Abies balsamea*, it is likely this species, but outside this range it will likely be those of *S. nitidus*.

FEMALE. Description

Color. Body, antenna (less than 3% of specimens with flagellomeres 1 or 1 and 2 brown; only one specimen with flagellomeres 1–4 light reddish brown), and palps black with dark blue metallic reflections. Coxae black; femora (except brown base), tibiae, and tarsi (apical half of tarsomere 5 usually darker but not dark brown or black (as in Fig. B2.60)) light reddish brown. Fore wing mainly clear, at most light yellowish brown behind stigma.

Head. Gena with pits 2.0–6.0 pit diameters apart and mainly absent centrally behind eye; vertex and postocellar area with pits 0.0–2.0 pit diameters apart (as in Fig. B2.62), and each pit diameter 0.15–0.2 that of lateral ocellus.

Thorax. Mesoscutum with coarse, net like–pits in posteror 0.6 of median area (as in Fig. B2.65). Metatarsomere 2 in lateral view 2.3-2.8 times as long as high, and length 1.1-1.2 times length of tarsomeres 3 + 4; tarsal pad 0.8-0.9 times as long as ventral length of tarsomere (as in Fig. B2.67). Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 0.9–1.3 times as long as median length, maximum width 1.1-1.5 times as long as median length, and median length 0.55-0.65 times as long as cornus length (Fig. B2.88). Cornus in dorsal view short, with edges straight to slightly angular midway; its median length 1.05–1.3 times as long as maximum width of abdomen at junction of terga 9 and 10 (Fig. B2.88). Sheath. Length 0.7-0.87 times fore wing length, basal section 0.87-1.12 times as long as apical section. Ovipositor. Lancet with 29-33 annuli (basal annuli hardly outlined and very difficult to see); junction of basal and apical section of sheath aligned between 9th and 10th or 10th and 11th annuli, with 16-20 pits beginning with annuli 8-10 (Fig. B2.84, base). Pits near middle annuli or area at base of apical section of sheath 0.0-0.12 times as long as an annulus (pits gradually and markedly decreasing in size toward base and disappearing before any of annuli 7-11), 0.07-0.25 times as high as lancet height in lateral view, and about 1.0–1.6 times as long as high (Fig. B2.86); annulus 10 length/ovipositor diameter (lance + lancet) 1.33-1.82 (based on 29 specimens) (Fig. B2.86). Last 3-4 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit . Edge of apical 5–7 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head and thorax black with dark blue metallic reflections. Coxae, metatibia (except extreme base), and metatarsomeres 1–3 black; femora, tibiae, and tarsus of fore and middle legs light reddish brown (Fig. B2.132). Fore wing clear. Abdomen with segments 1 and 2 or 1–3 black, segments 3–7 or 4–7 light reddish brown, and segment 8 black, rarely light reddish brown (Fig. B2.133); sternum 8 and 9 black or completely reddish brown (only specimens from Alberta).

Thorax. Metatibia 4.2–4.6 times as long as maximum width. Metatarsomere 1 in lateral view 3.2–3.6 times as long as maximum height.

Taxonomic notes

Much of the North American literature under *S. cyaneus* or *S. juvencus* is very confusing because up to five species fall under these traditional names (Slosson 1895, Blackman and Stage 1918, Essig 1926, Rohwer 1928, Middlekauff 1960, Benson 1963, Cameron 1965, Okutani 1965, Smith and Schiff 2002, Schiff *et al.* 2006).

Females of S. cyaneus have commonly been confused with females of the European "S. cyaneus" (identified here as S. torvus M. Harris, see Chapter D. Additional Notes) and S. juvencus because the whereabouts of the Fabricius type of *S. cyaneus* was unknown. Its discovery in HMUG clarifies the name used for several European and American species. Sirex cyaneus is distinguished from all European species (S. juvencus, S. torvus, and S. atricornis) by the absence of pits and annuli in the basal 0.4 of the ovipositor. The following character states also distinguish S. cyaneus from S. torvus: in both sexes of S. cyaneus the pits on the gena and vertex are moderate in size (smaller in S. torvus); in females of S. cyaneus there are no pits in the basal annuli of the ovipositor (pits start on ovipositor annulus 2 in S. torvus) and, on average, the apical section the sheath is equal to the basal section (apical section longer than basal section in S. torvus); in males of S. cyaneus (except in Alberta) the abdominal apex is black (reddish brown in S. torvus) and (except in a very few specimens from Alberta) the mesotibia and mesotarsus are completely light reddish brown (widely black mesotibia, except at base, and mesotarsomeres 1-3 in S. torvus). Sirex cyaneus has even been considered as a subspecies of S. juvencus. Adults of S. juvencus are easily distinguished from those of S. cyaneus by antennal color pattern and ovipositor pit development.

Sirex abbotii and S. hirsutus have been assigned traditionally to S. cyaneus. The holotype male (from coastal Georgia or southeastern USA) of S. abbotii matches males of S. cyaneus in color pattern. In the southern Appalachian Mountains, Abies fraseri is the only host for S. cyaneus. Abies fraseri grows only at high elevations. The holotype could have arrived in coastal Georgia (where A. fraseri is absent) with logs harvested in the Appalachian Mountains in westernmost Georgia or South Carolina. The holotype of S. hirsutus is not a Nearctic species as it is a typical specimen of S. juvencus (see Chapter D. Additional Notes about its synonymy). So the holotype is probably an intercepted specimen from Europe.

Where the ranges overlap, females of *S. cyaneus* could be confused only with *S. nitidus* and *S. noctilio* females. Ovipositor pit development distinguishes *S. cyaneus* from these two species. In addition, both sexes of *S. cyaneus* are easily distinguished from those of *S. noctilio* on puncture size on the vertex and pit development on the mesoscutum, and females of *S. cyaneus* are distinguished by the long tarsal pad of metatarsomere 2 and very small pits near the middle of the ovipositor.

Outside its range S. cyaneus could be confused with S. abietinus, a species found from the Rocky Mountains and westward. The S. cyaneus range extends as far as west of Lesser Slave Lake, Alberta. The two species are probably allopatric like their main hosts, various species of Abies. There is a gap between A. balsamea, an eastern species, and A. lasiocarpa, a western species, in western Alberta. In S. cyaneus, females have annulus 10 relatively short compared to ovipositor diameter, and, commonly, a relatively thin, short cornus (relatively long annulus and a thick cornus in S. abietinus); males (only those at least from Manitoba and eastward) have black sterna 8 and 9 (in most specimens tergum 8 is completely black) (completely light reddish brown apical abdominal segments in S. abietinus). The information from morphology and DNA barcoding shows a difference of 10.6% in base pairs between S. cyaneus and S. abietinus. Despite their great similarity, the two taxa are considered as specifically distinct.

Biological notes

Stillwell (1966) published a fine study on the biology *S. cyaneus* (under the name *S. juvencus* – 800 specimens of this study are in CNC and all are *S. cyaneus*). Adults were reared from weakened *Abies balsamea* collected throughout New Brunswick and Nova Scotia.

Females oviposit in dead and dying firs, but they could be induced to oviposit in healthy logs. Males emerge first, but continue to emerge throughout the summer. On the day of emergence, females start to oviposit. Oviposition

lasts from 4–20 minutes (most last 8–10 minutes). The ovipositor penetrates at about right angle to the surface to a depth of 2-10 mm. Generally, each female lays one to three eggs as the ovipositor is withdrawn. The eggs are about 1 mm long and usually overwinter or hatch in late summer. Larvae overwinter in the first or second instar. The first instar is usually within the oviposition hole, but the second instar larva bores at about a right angle to the oviposition hole. Larvae molt 5-11 times, based on exuviae that are packed in the frass at intervals within each gallery. Most larvae stay within the first 4 cm of the log surface and the length of the galleries vary from 5-15 cm. The pupae are in a chamber usually 2 cm below the surface. The prepupa lasts 4–6 weeks and the pupal stage 2-3 weeks. Most life cycles last two years, but some may last three years. Unmated females produce males only, mated females produce both sexes.

A mycangium is a special organ that carries oidia (a kind of fungal conidia). Two mycangia are found at the base of the ovipositor. In most instances oidia are carried in them. Several kinds of fungi grow in a log, but only one, Amylostereum chailletii (in Stillwell's paper, this species is under the genus Stereum) is carried by females of S. cyaneus. The oidia are deposited on the end of each egg at oviposition time and are also found along the oviposition hole. The larva at hatching time has plenty of this fungus to eat. Without the fungus the larva dies at the first instar. Female larvae carry the fungus in a paired organ called the hypopleural organ. This organ is found in the fold between the first and the second abdominal segments. Following a molt, the fungal oidia remain in the exuvia and the female larvae must pick the fungus again to fill the new hypopleural organ. The female prepupae enclose the fungal oidia in wax-like plates.

Hosts and phenology

The host range of *S. cyaneus* is mainly restricted to species of *Abies* (99% of the reared specimens). Based on 1103 reared and confirmed specimens, all recorded hosts are Pinaceae: *Abies* sp. (38), *Abies balsamea* (932), *A. fraseri* (16, Kirk 1974), *Larix* sp. (5), *Picea glauca* (10), *P. mariana* (1), and *Pinus strobus* (1). *P. elliottii* (Kirk (1974) under *S. abbotii* (see *S. cyaneus* synonymy) is record of a specimen taken outside the range of *S. cyaneus*. Verified published records: (Stillwell 1966, Stillwell 1966, Kirk 1972).

Based on 675 field-collected and reared (under natural conditions) specimens, the earliest and latest capture dates are July 2 and October 3. The main flight period is from the second half of July to the first half of September with a peak in second half of August.

Range

CANADA: AB, MB, NB, NL, NS, ON, QC, SK. **USA:** ME, MI, MN, NC, NH, WV. *Sirex cyaneus* is recorded from western Alberta to Newfoundland south to the Great Smoky Mountains (Fig. C4.4). We have seen many intercepted specimens from New Zealand (FRNZ).

Specimens studied and included for range map: 484 females and 933 males from CASS, CNC, CUIC, DEBU, FRLC, GLFC, LECQ, LEMQ, NFRC, NFRN, and USNM.

Specimens for molecular studies: 11 specimens. See Fig. E2.5d.

CANADA. Alberta: 2008, *CNCS 1030*, 598; 2008, *CNCS 1031*, 575; 2008, *CNCS 1032*, 575; 2008, *CNCS 1033*, 580; 2008, *CNCS 1034*, 580; 2008, *CNCS 1035*, 577; 2008, *CNCS 1036*, 587. **New Brunswick**: year unknown, *SIRCA 043*, 594; 2007, *SIRCA 044*, 613. **USA. New York**: 2006, CBHR 610, 658. **Washington**: 2007, CBHR 1327, 628.



9. Sirex hispaniola Goulet, n. sp.

Fig. C9.1 (female habitus). Fig. C9.2 (female dorsal habitus). Fig. C9.6 (map)

Diagnostic combination

Among **females** with completely reddish brown abdomen beyond the 2^{nd} segment [pale form of *nigricornis*], that of *S. hispaniola* is recognized by the short metatarsomere 2 in lateral view (1.7 times as long as high), the long tarsal pad on metatarsomere 2 (0.8 times as long as ventral length of tarsomere). **Both sexes** probably (male unknown) are recognized by crater-like pits on most of median half of the mesoscutum, and the very dense pits on the gena and most of the vertex (pits on gena 0.0–1.0 and on the vertex 0.0–0.5 pit diameters apart).

FEMALE. Description

Color. Head, thorax, antenna, palps, coxae, apical section of sheath, margin of tergum 9, ventral surface of tergum 10 at base and in anterior half, and all of tarsomeres 5 black with dark blue metallic reflections. Legs after coxae (except tarsomere 5), legs reddish brown. Both wings darkly tinted. Abdomen basal segments 1 and 2 and side of tergum 3 black, remaining terga including cornus light reddish brown.

Head. Gena with pits 0.0–0.5 pit diameters apart (Fig. B2.55); vertex and postocellar area with pits 0.0–0.5 pit diameters apart (Fig. B2.57), and each pit diameter about 0.3–0.4 that of lateral ocellus.

Thorax. Mesoscutum with coarsely, net-like pits over most of median area. Metatarsomere 2 in lateral view 1.7 times as long as high and as long as length of tarsomeres 3 + 4 (Fig. 2.59); tarsal pad 0.8 times as long as ventral length of tarsomere (Fig. C9.3). Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 1.3 times as long as median length, maximum width 1.7 times as long as median length, and median length 0.75 times as long as cornus length. Cornus in dorsal view short, with edges clearly angular midway, its median length 0.7 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.57 times fore wing length, basal section 1.4 times as long as length of apical section (Fig. B2.53). Ovipositor. Lancet with 32 annuli (basal annuli not clearly outlined); junction of basal and apical section of sheath aligned between 15th and 16th annuli, with 29 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1 (Fig. C9.4). Pits near middle annuli (see A, B, C & D in Fig. C9.5) or area at base of apical section of sheath, 0.5 times as long as an annulus (pits scarcely decreasing in

size toward base) (A), about 0.65 times as high as lancet height in lateral view (B), and about 1.5 times as long as high (2.0 times as long on annulus 3) (C); annulus 10 length/ovipositor diameter (lance + lancet) 1.25 (D) (Fig. C9.5). Last 4–5 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 4–5 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Unknown.

Type material.

Holotype female (MHND), in good condition except right metatarsus missing and left metatarsus glued on a point; labeled [white label] "REP. DOM.: Prov. La Vega, La Sal, Res. Ebano Verde (19°4'101"N 70°34'89"W), 1043 m, 11–12 July 2002, coll. D. Perez, B. Hiero, R. Bastardo" [red label] "HOLOTYPE Sirex hispaniola Goulet". Type locality: Dominican Republic, La Vega, Reserva Ebano Verde.

Taxonomic notes

This is the first species of Sirex recorded from the Greater Antilles. The female was captured at high elevation (1040 m, at the lower reaches of pine forests). Hispaniola has three isolated, high mountain ranges. Each could have different species of Siricidae. The same could be said of the three isolated mountain ranges of Cuba. Sirex hispaniola is found in the Cordillera Central in the Dominican Republic. It is most similar to the eastern North American S. nigricornis. Both have very dense pits on the head and mesoscutum, a short angular cornus, and the unusual basal black transversal band on the ventral surface of segment 10. These two species differ in several characters: the proportions in lateral view and the relative length of the tarsal pad of metatarsomere 2, ovipositor annulus number at the junction of the apical and basal sheath sections, and the long and deep second annulus pit. These differences suggest a rather long period of isolation between the species from continental North America and Hispaniola.

Origin of specific epithet

The name, *hispaniola*, is a noun in apposition and refers to the island that includes Haiti and the Dominican Republic. Julio A. Genaro found an unexpected specimen of *Sirex* while examining the insect collection in Santo Domingo. The discovery is significant and similar discoveries in coniferous forests of other high mountain ranges of Hispaniola and Cuba may be expected. Julio

proposed most appropriately that we use the name *hispaniola* for the new species to emphasize its origin.

Hosts and phenology

Hosts are unknown, but are most likely *Pinus* spp. This is supported by the short apical section of the sheath and the trough development of the pit on annulus 2, a character shared by all New World species of *Sirex*

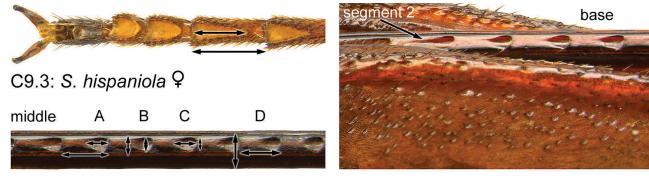
associated with pines. The single female was captured in mid July.

Range

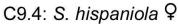
Sirex hispaniola is known from a single female captured in the Cordillera Central of Hispaniola (Fig. C9.6).

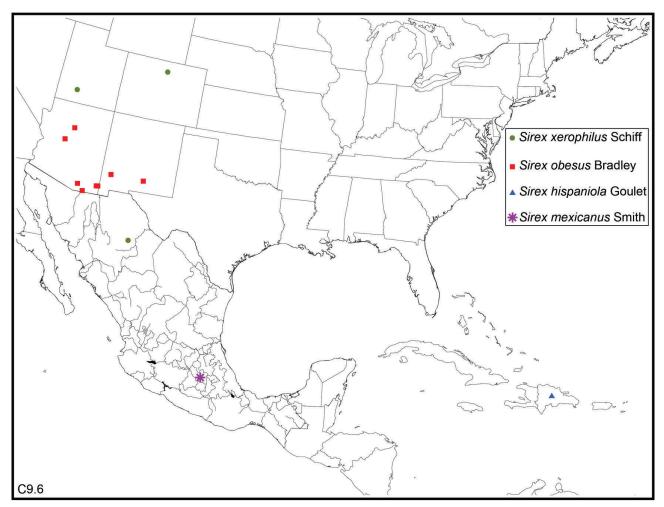


C9.2: S. hispaniola Q



C9.5: S. hispaniola Q





10. Sirex longicauda Middlekauff

Fig. C10.1, Schiff *et al.* 2006 : 44 (female habitus) Fig. C10.2, Schiff *et al.* 2006 : 43 (male habitus) Fig. C10.4 (map)

Sirex longicauda Middlekauff, 1948: 189. Holotype, female (CASC), not examined; Middlekauff 1960: 65, Middlekauff 1962: 31 (male), Burks 1958: 16, Burks 1967: 26, Smith 1979: 127. Type locality: Berkeley, California.

Diagnostic combination

Among **females** with long (4.0–6.0 times as long as high) metatarsomere 2 [*areolatus*], those of *S. longicauda* are recognized by the reddish brown tibiae and tarsi. Among **males** with black metafemur and gena [*areolatus*, dark form of *S. nigricornis*, and dark legged form of *nitidus*], those of *S. longicauda* are recognized by the reddish brown protibia and protarsus, the finely pitted vertex, and the widely reddish brown base of the metatibia (brown area about 2.0 times as long as minimum width at base).

FEMALE. Description

Color. Body, antenna, and palps black with dark blue or green metallic reflections. Coxae and femora (except apex) black; tibiae and tarsi reddish brown (Fig. B2.7). Fore wing clear.

Head. Gena with pits 2.0–8.0 pit diameters apart, vertex with pits 2.0–4.0 pit diameters apart, and each pit diameter about 0.16 times lateral ocellus.

Thorax. Mesoscutum with dense pits, each pit round but in median area with numerous transverse ridges. Metatarsomere 2 in lateral view 4.0–5.0 times as long as high; tarsal pad about 0.4 times as long as ventral length of tarsomere. Fore wing vein 3A present and clearly extending along posterior margin of wing.

Abdomen. Median basin of tergum 9 with basal width about 0.72 times as long as median length, maximum width about 0.86 times as long as median length, and median length about 0.63 times as long as cornus length. Cornus in dorsal view long, attenuated in apical 0.25– 0.3, and edges not angular midway, its median length 1.42 times as long as maximum width of abdomen at junction of terga 9 and 10. *Sheath*. Length 1.1–1.4 times fore wing length, basal section 0.4–0.6 times as long as length of apical section. *Ovipositor*. Lancet with 40–47 annuli (outline of edge of basal annuli difficult to see (Fig. B2.11)); junction of basal and apical section of sheath aligned between 7th and 8th, or 8th and 9th annuli, with about 22 pits beginning near annulus 18. Pits near middle annuli or area at base of apical section of sheath about 0.25 times as long as an annulus (pits gradually decreasing in size toward base), about 0.5 times as high as lancet height in lateral view, and about 1.2 times as long as high; annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last annulus before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit (Fig. C10.3). Edge of apical 9–16 annuli before teeth annuli extending as ridge to ventral edge of lancet (Fig. B2.9).

MALE. Description

Color. Head, thorax, antenna, palps, abdominal segments 1, 2, 8, sterna 2, 3 and 4 laterally, and 8 black with dark blue metallic reflections; abdominal segments 3–7 (except for black spot laterally on segments 3 and 4) light reddish brown. Coxae, femora, metatibia (except base), and metatarsomeres 1–3 black (Fig. B2.99); tibiae, and tarsi of fore and middle legs, and metatarsomeres 4 and 5 reddish brown (Fig. B2.101); reddish brown spot at base of metatibia large (spot about 2.0 times as long as minimum width of tibia at base) (Fig. B2.99). Fore wing clear.

Thorax. Metatibia 5.5 times as long as maximum width. Metatarsomere in lateral view 1 4.4 times as long as maximum height.

Taxonomic notes

The type of *Sirex longicauda* was not examined, but the female description and especially the length of the ovipositor sheath and the long and narrow cornus fits our concept of this species perfectly.

Hosts and phenology

The host range of *Sirex longicauda* is moderately wide (Middlekauff 1960, Wickman 1964b, Cameron 1965). The most preferred hosts (96%) are various species of *Abies*. Based on 134 reared and confirmed specimens all hosts are Pinaceae: *Abies* sp. (2), *Abies concolor* (127) (most records from Kirk (1975)), *A. magnifica* (1), *A. balsamea* (1), *Pinus* sp. (1), *P. albicaulis*, *P. ponderosa*, *P. strobus* (1), and *Pseudotsuga menziesii* (1).

Based on 29 field-collected and reared (under natural conditions) specimens, the earliest and latest capture dates are from early June to mid October. The main flight period is in late September.

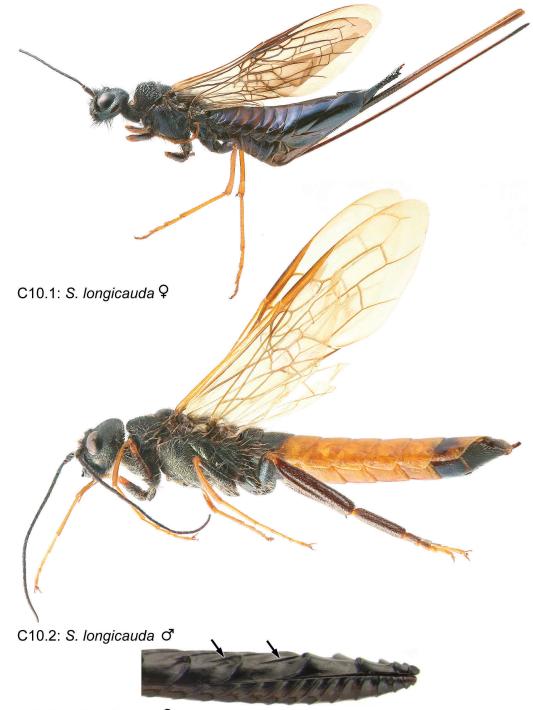
Range

CANADA: BC. **USA:** CA (Middlekauff 1960), CO, ID, GA, HI, KS (from west coast lumber), NE, NM, OH (from *Pinus strobus*), OR, UT, VA, WA.

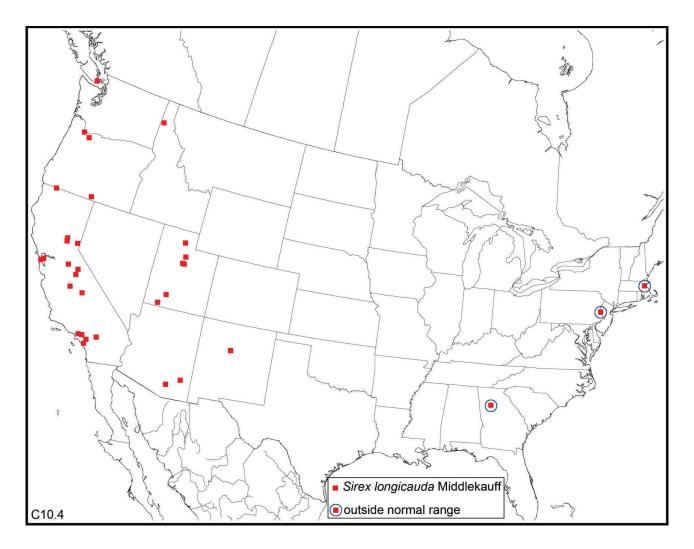
Sirex longicauda, a western species, is recorded from southwestern British Columbia to forested regions of California and New Mexico (Fig. C10.4). The four eastern specimens (GA, KS, NE and OH) are probably adventive (Burks 1967, Smith and Schiff 2002).

Specimens studied and included for range map: 46 females and 16 males from BYUC, CNC, OSAC, PFRC, UAIC, UCRC, and USNM. Specimens for molecular studies: 6 specimens. See Fig. E2.5a.

CANADA. British Columbia: 1982, *SIRCA 066*, 307. **USA. Colorado**: 2006, *CBHR 914*, 658; 2006, *CBHR 915*, 658; 2006, *CBHR 916*, 658; 2006, *CBHR 917*, 658; 2006, *CBHR 918*, 658.



C10.3: S. longicauda Q



11. Sirex mexicanus Smith, n. sp.

Fig. C11.1 (female habitus) Fig. C11.2 (male habitus) Fig. C9.6 (map)

Diagnostic combination

Among **females** with metatarsomere 2, 2.0–3.0 times as long as high, and completely black body, legs and a clear fore wing [*xerophilus*], those of *S. mexicanus* are recognized by the few transverse ridges on the posterior half of the mesoscutum. Among **males** with brown femora, tibiae, and tarsi [*californicus*, *obesus*, and *xerophilus*], those of *S. mexicanus* are recognized by light reddish brown antenna (apical antennomeres may be a little darker) and coxae, and the clear fore wing.

FEMALE. Description

Color. Body, legs, palps, and antenna black with dark blue metallic reflections. Fore wing clear.

Head. Gena with pits 0.0–0.5 pit diameters apart (Fig. C11.3), vertex and postocellar area with pits 0.0–0.5 pit diameters apart (Fig. B2.119), and each pit diameter about 0.25–0.3 that of lateral ocellus.

Thorax. Mesoscutum with few transverse ridges in posterior half of median area; pits large but not net-like (Fig. B2.46). Metatarsomere 2 in lateral view 3.0 times as long as high, and its length about 1.2 times as long as tarsomeres 3 + 4; tarsal pad 0.3 times as long as ventral length of tarsomere. Fore wing vein 3A present and clearly outlined (Fig. B2.48).

Abdomen. Median basin of tergum 9 with basal width as long as median length, maximum width 1.2 times as long as median length, and median length 0.8 times as long as cornus length. Cornus in dorsal view short, with edges straight, its median length 0.88 times as long as maximum width of abdomen at junction of terga 9 and 10. *Sheath*. Length 0.65 times fore wing length, and basal section 1.25 times as long as length of apical section. *Ovipositor*. Lancet with 32 annuli (basal annuli clearly outlined (Fig. B2.52)); junction of basal and apical section of sheath aligned between 15^{th} and 16^{th} annuli, with 28 pits beginning with annulus 2; pit present from annulus 2; pit of annulus 2 only extending to edge of annulus 1 (Fig. B2.52, base). Pits near middle annuli (Fig. B2.50) or area at base of apical section of sheath 0.5 times as long as an annulus (pits slightly decreasing in size toward base), 0.5 times as high as lancet height in lateral view, and 1.4 times as long as high (Fig. B2.52, middle); annulus 2 length/ovipositor diameter 1.35, for annulus 5 1.18, and for annulus 13 1.12 (1 specimen). Last 4 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 5 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Body, head, palps, thorax, and abdominal segments 1 or 1 and 2 black with dark blue metallic reflections; remaining abdominal segments and antenna (a little darker apically) (Fig. B2.117) light reddish brown. Legs and coxae reddish brown (Fig. B2.121). Fore wing clear. **Thorax.** Metatibia 3.4–3.8 times as long as maximum width (Fig. B2.121). Metatarsomere 1 in lateral view 2.7–3.2 times as long as maximum height.

Type material

Holotype female (FSCA), in perfect condition; labeled [White] "Mexico, D.F. 22 June 1980 Woodpile: Garage D. J. Pletsch" [White with red frame] "HOLOTYPE Sirex mexicanus Smith". Type locality: Mexico, Distrito Federal.

Paratypes. 1 female and 4 males. **MEXICO**. Distrito Federal: 22.VI.1980, woodpile, garage D. J. Pletsch (3M, 1M allotype, FSCA). USA. Texas: Brownsville (Port of Entry), pallets, 20.VI.2005, M. A. Garcia (1 F, USNM).

Origin of specific epithet

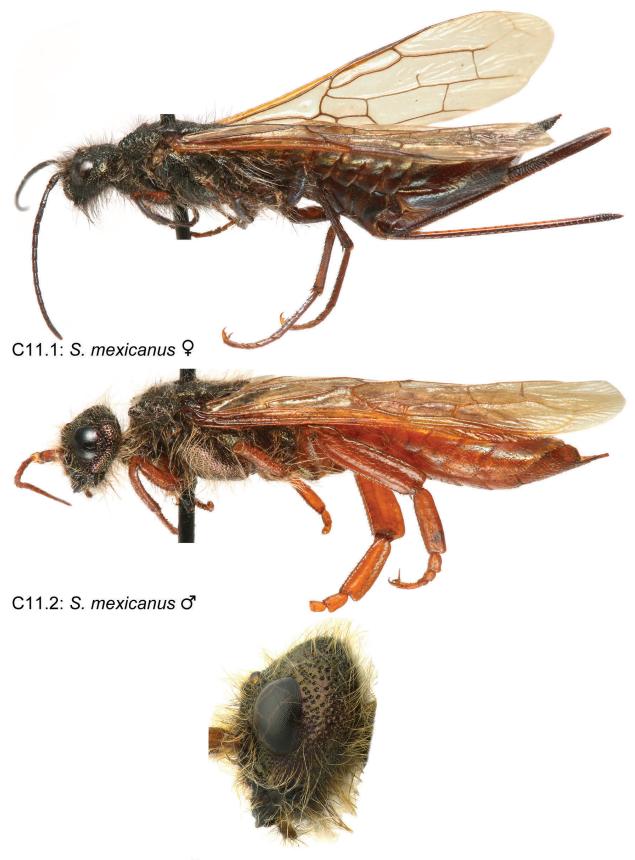
The name *mexicanus* is an adjective derived from the country and capital name – most specimens were collected in the vicinity of Mexico City. This species may be the first of many to be discovered in Mexico.

Hosts and phenology

The host of *S. mexicanus* is unknown; it may be on various species of *Pinus* because *S. mexicanus* is related to *S. californicus*, with a short apical sheath section, and annulus 2 with a trough. The type specimens were captured on June 20 and July 22.

Range

Mexico: Distrito Federal, and northern Mexico intercepted at Brownsville, TX. *Sirex mexicanus* is probably widespread as it is found from the vicinity of Mexico City to the port of entry at Brownsville in, southern Texas (Fig. C9.6).



C11.3: S. mexicanus d

12. Sirex nigricornis Fabricius

Fig. C12.1, Schiff *et al.* 2006: 32, 33 (female with black abdomen, habitus)

Fig. C12.2, Schiff *et al.* 2006: 46, 47 (female with mainly reddish brown abdomen, habitus)

Fig. C12.3, Schiff *et al.* 2006: 31(male with dark abdomen, habitus)

Fig. C7.4, Schiff *et al.* 2006: 45 (male with pale abdomen, habitus)

Fig. C12.5 (live female with mainly reddish brown abdomen)

Fig. C12.6 (live male with dark abdomen) Fig. C12.7 (live male with pale abdomen)

Fig. C12.10 (map)

- *Sirex nigricornis* Fabricius, 1781: 418. Type, female (HUMG) not examined; Bradley 1913: 16, Ries 1951: 83, Smith 1979: 127. Type locality: "America boreali".
- *Urocerus Edwardsii* Brullé, 1846: 645, pl. 45, fig. 1. Holotype, female (probably MNHN), not examined; Bradley 1913: 11, Ries 1951: 83, Smith 1979: 126. NEW SYNONYM. Type locality: "l'Amérique septentrionale".
- *Urocerus zonatus* Norton, 1869: 357. Lectotype male (ANSP) designated by Cresson (1928), examined by DRS; Cresson 1928: 11. Previously synonymized under *S. edwardsii* by Konow 1898: 81; accepted by Bradley 1913: 11, Ries 1951: 83, Smith 1979: 126. NEW SYNONYM. Type locality: "New York".
- *Sirex* (*Urocerus*) *Edwardsii*; Brullé, 1846: 15 (combination in figure legend).
- *Sirex Edwardsii*; Brullé, 1846: pl. 45, fig. 1 (combination engraved on plate).
- *Urocerus nigricornis*; Norton, 1869: 359 (change in combination).
- Sirex fulvocinctus Westwood, 1874: 114, pl. XXI, fig. 1. Holotype female (OXUM), images prepared by James E. Hogan and sent to HG for study. Previously synonymized under S. edwardsii by Konow 1898: 81; accepted by Cresson 1880: 67, Bradley 1913: 11, Ries 1951: 83, Smith 1979: 126. NEW SYNONYM. Type locality: "America Septentrionalis".
- Sirex abaddon Westwood, 1874: 115, pl. XXI, fig. 7. Syntype females (all in OXUM), images of one female prepared by James E. Hogan and sent to HG for study. Species described from "2 larger and 2 smaller specimens". Previously synonymized under S. edwardsii by Cresson 1880: 67; accepted by Bradley 1913: 11, Ries 1951: 83, Smith 1979: 126. NEW SYNONYM. Type locality: "America Septentrionalis".
- Sirex morio Westwood, 1874: 115, pl. XXI, fig. 6. Holotype female (OXUM), images prepared by James E. Hogan and sent to HG for study. Synonym by Cresson 1880: 67; accepted by Bradley 1913: 11, Ries

1951: 83, Smith 1979: 126. Type locality: "America Septentrionalis".

- *Paururus pinicolus* Ashmead, 1898: 179. Lectotype female (USNM), here designated and labeled "Washington, D.C.", "Paururus pinicolus Ashm. Female, type [handwritten]". Number of specimens not stated, but described from "Jacksonville, Fla.; Washington, D.C., and Morgantown W. Va.". A specimen labeled "Kanawha Sta., W.V." is labeled "type", but this was not mentioned in the original description. Synonym by Konow 1898: 270; accepted by Ries 1951: 83, Smith 1979: 126. Type locality: "Washington, D.C.".
- Paururus Hopkinsi Ashmead, 1904: 64. Lectotype female (USNM), here designated and labeled "Fiske Colr., Oct. 8, Tryon, N.C,". "Pinus," "Female Type No. 7684 U.S.N.M.," "Paururus Hopkinsi, Ash. [handwritten]". Described from "many specimens" reared from dead pines from "Tryon, N.C. and Kanawha, W. Va.". Although "many specimens" are from this locality, only three have red type labels. Konow 1905a: 7. Previously synonymized under *S. edwardsii* by Bradley 1913: 11; accepted by Ries 1951: 83, Smith 1979: 126. NEW SYNONYM. Type locality: "Tryon, N.C.".
- *Sirex nigricornis pinicola*; Bradley 1913: 16 (change in rank).

Diagnostic combination

Among females with a completely black body and legs and fore wing either darkly tinted or with dark bands near middle and apex [californicus and obesus], those of S. nigricornis are recognized by the long metatarsomere 2 (2.7–3.3 times as long as high, and dorsal length clearly longer than metatarsomeres 3 + 4), the crater-like pits on most of median half of the mesoscutum, and the very dense pits on the gena and most of the vertex (pits on gena 0.0-1.0 and on the vertex 0.0-0.5 pit diameters apart). Among **females** with mainly reddish brown abdomen [behrensii], those of S. nigricornis are recognized by the black edge of the cornus. Among males with black metafemur and reddish brown tibiae and tarsi of the fore and mid legs [longicauda and nitidus], those of S. nigricornis are recognized by the very dense pits on the gena and most of the vertex (pits on the gena 0.0-1.0 and on the vertex 0.0–0.5 pit diameters apart).

FEMALE. Description

Color. Head thorax, antenna, palps, coxae, and femora (except apex in some specimens) black with dark blue metallic reflections. Legs in **black form** completely black, in **pale form** as follows: coxae and femora black, and tibiae and tarsi completely black to completely reddish brown (Figs. B2.28 & as in B2.27). Both wings

lightly to darkly tinted (northern localities) (Fig. B2.31b) to darkly tinted (southern localities) (Fig. B2.31a). Abdomen in **dark form** completely black, in **pale form** as follows: basal segments 1 and 2 to as many as 1–4 black, remaining terga light reddish brown (except laterally in some specimens), remaining sterna completely reddish brown to black, basal section of sheath light reddish brown, apical section black at least in basal half (Fig. B2.15), lateral surface of tergum 9 broadly black, ventral surface of tergum 10 black at base and in anterior half (Fig. B2.15), and cornus dorsally at apex and laterally and widely ventrally black.

Head. Gena with pits 0.0–1.0 pit diameters apart (Fig. B2.33), vertex and postocellar area with pits 0.0–0.5 pit diameters apart (Fig. B2.35), and each pit diameter about 0.3–0.4 that of lateral ocellus.

Thorax. Mesoscutum with coarse, net-like pits over most of median area (Figs. B2.42, close–up C12.8). Metatarsomere 2 in lateral view 2.7–3.3 times as long as high, and its length 1.1–1.3 times length of tarsomeres 3 + 4 (Fig. B2.28); tarsal pad 0.3–0.4 times as long as ventral length of tarsomere. Fore wing vein 3A absent (Fig. B2.31b).

Abdomen. Median basin of tergum 9 with basal width 0.9–1.2 times as long as median length, maximum width 1.1-1.4 times as long as median length, and median length 0.7–0.9 times as long as cornus length. Cornus in dorsal view short, with edges clearly angular midway, its median length 0.8-0.9 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.57-0.69 times fore wing length, basal section 1.08-1.45 times as long as apical section. Ovipositor. Lancet with 30-35 annuli (basal annuli not clearly outlined); junction of basal and apical section of sheath aligned between 10th and 11th to 13th and 14th annuli, with 26-31 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1 (Fig. B2.37, base). Pits near middle annuli (Fig. B2.44) or area at base of apical section of sheath 0.35-0.45 times as long as an annulus (pits scarcely decreasing in size toward base), 0.55–0.65 times as high as lancet height in lateral view, and 1.3–1.5 times as long as high (Fig. B2.37, middle); annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last 4–5 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 5-6 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head, thorax, antenna (flagellomeres 1 and 2 black to light reddish brown), palps, coxae, and femora (except apex on fore and middle legs in many specimens) black with dark blue metallic reflections. Tibiae, and

tarsi of fore and middle legs light reddish brown (except for brown or black spot on tibia and tarsomeres 1 or 1 and 2 of middle leg in many specimens (Fig. B2.94)); Metatibia and metatarsus black (except metatarsomere 4 usually reddish brown); reddish brown spot at base of metatibia narrow, about as long as minimum width of tibia at base (Fig. C12.9). Fore wing light yellow tinted. Abdomen in **pale form** black on segments 1 and 2 to as many as 1–4, light reddish brown on terga 3–8 or 5–8, and black on sterna 3–9 or 6–9; in **dark form** abdomen black on segments 1–4 and on segments 7 and 8 (including sternum 9).

Thorax. Metatibia 4.3–4.6 times as long as maximum width (Fig. C12.9). Metatarsomere 1 in lateral view 3.2–3.5 times as long as maximum height.

Taxonomic notes

Until this study, pale specimens of S. nigricornis were assigned to S. nigricornis whereas dark specimens were assigned to S. edwardsii. The two color forms have an unusually similar flight period (two periods, clearly separated), the same range, and adults may emerge from the same pine trunk. In addition, the proportions between the length of lancet annuli 2, 5 and 10 relative to the diameter of the ovipositor are similar for both color forms (based on 10 specimens for each color form). For both color forms combined (20 specimens), the annulus length/ovipositor diameter (lance + lancet) for annulus 2 1.6-2.1 (mean = 1.8), for annulus 5 1.1-1.6 (mean = 1.4), annulus $10 \, 1.1 - 1.5$ (mean = 1.3). Finally, the information from morphology and DNA barcoding confirms that the two populations are the same. Therefore, we regard these as two discrete color forms of a single species.

Two types were not examined: *S. nigricornis* Fabricius (pale form) and *S. Edwardsii* Brullé (dark form), but the original description and illustration for both species were adequate to allow us to match them with our concept of *S. nigricornis*, the oldest name.

Females of *S. nigricornis* with a pale abdomen could be confused with those of *S. behrensii*. In **both sexes** of *S. nigricornis* the banded pattern is absent in the fore wing, and fore wing vein 3A is absent (banded pattern clearly present in the fore wing, and fore wing vein 3A present in *S. behrensii*). Females of *S. nigricornis* lack the broad black longitudinal band along the side of the abdomen, the ventral surface of tergum 10 is black basally and at the side in anterior half, and the cornus is partly black (broad black longitudinal band along the side of the abdomen present, dorsal and ventral surfaces of tergum 10 without black spots, and cornus completely reddish brown in *S. behrensii*). Males of the two species are easily distinguished on antennal and hind leg color patterns.

Geographical variation

The two color forms are not equally distributed. For instance in Ontario only 23% of trapped adults are the dark body form. The next significant sample is from Indian Head, Saskatchewan, and there 60% of 47 specimens belong to the dark body form. Father west at Lac La Biche in eastern Alberta, all eight specimens are black. So, a gradual increase westward occurs in the proportion of the dark body form.

Hosts and phenology

Sirex nigricornis has a wide host range. Most rearing records are from various species of *Pinus* (94%) (Johnson 1928, Cameron 1965, Kirk 1974). Based on 229 reared and confirmed specimens all hosts are Pinaceae: *Picea* sp. (12), *P. abies* (1), *Pinus* sp. (16), *P. banksiana* (58), *P. clausa, P. echinata* (68), *P. elliottii, P. palustris, P. resinosa* (21), *P. rigida, P. strobus* (42), *P. sylvestris* (8), *P. taeda* (1), and *P. virginiana* (2). Records from the *Populus* sp. (Salicaceae) (4) and *Quercus* sp. (Fagaceae) (1) are most likely incorrect.

Based on 893 field-collected specimens, the earliest and latest capture dates are from late July to early October. There are two flight periods, a small one in the second half of July and a major one from mid August to late September with a peak in the second half of September.

Range

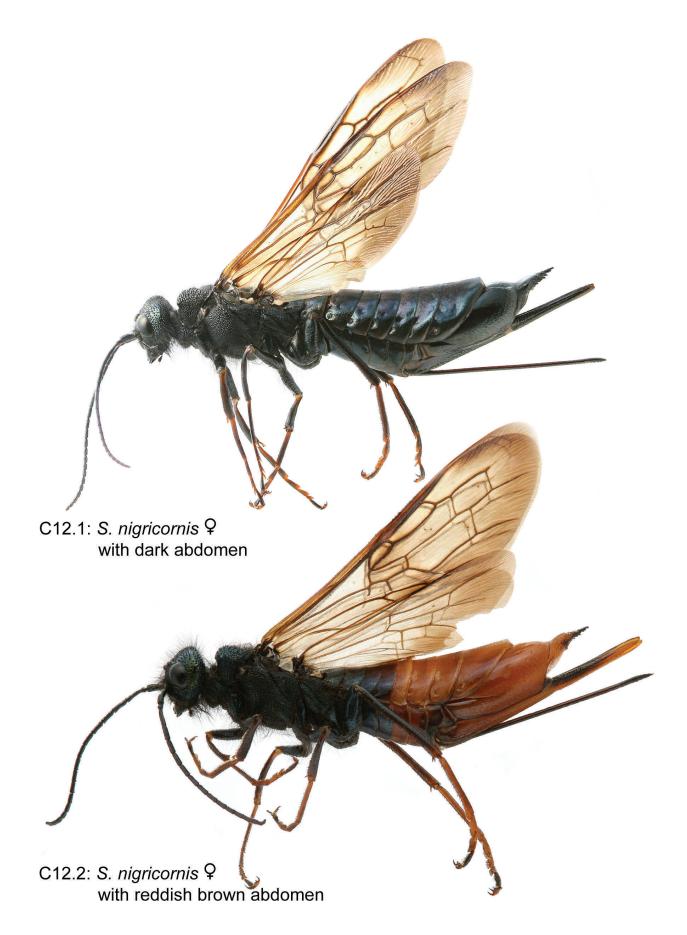
CANADA: AB, BC (probably mislabeled), ON, QC, SK. **USA:** AL, AR, DC, FL, GA, LA, MD, MS, NC, NY, OH, PA, TN, TX, VA, WI, WV. If the possibly mislabeled record from British Columbia and one specimen (probably *S. obesus*) from Arizona reported by Cameron (1965) are ignored, *S. nigricornis* has an eastern range

extending from Alberta to Quebec south to Louisiana and northern Florida (Webster 1895, Johnson 1928, Rohwer 1928, Ries 1951, Burks 1958, Burks 1967, Smith 1979, Chapin and Oliver 1986) (Fig. C12.10).

Specimens studied and included for range map: 1406 females and 1561 males from BYUC, CASS, CNC, CUCC, CUIC, DEBU, EDUM, FSCA, GLFC, MRNQ, NFRN, USFS–GA, and USNM.

Specimens for molecular studies: 53 specimens. See Fig. E2.5b.

CANADA. Ontario: 2007, SIRCA 002, 658; 2007, SIRCA 003, 557; 2007, SIRCA 004, 632; 2007, SIRCA 005, 619; 2007, SIRCA 014, 617; 2007, SIRCA 015, 629; 2007, SIRCA 016, 628; 2007, SIRCA 017, 624; 2006, CBHR 597, 658; 2006, CBHR 598, 658. USA. Georgia: 2006, CBHR 513, 658; 2006, CBHR 514, 658; 2006, CBHR 516, 658; 2006, CBHR 518, 658; 2006, CBHR 519, 658; 2006, CBHR 520, 658; 2006, CBHR 571, 658; 2006, CBHR 572, 658; 2006, CBHR 574, 658; 2006, CBHR 575, 658; 2006, CBHR 576, 658; 2006, CBHR 577, 658; 2006, CBHR 587, 658; 2006, CBHR 588, 658; 2006. Illinois: 2006, CBHR 170, 658. Indiana: 2005, CBHR 172, 658; 2005, CBHR 173, 658; 2005, CBHR 174, 658; 2005, CBHR 175, 658; 2005, CBHR 177, 658; 2005, CBHR 178, 658; 2005, CBHR 179, 658; 2005, CBHR 180, 658; 2005, CBHR 181, 658; 2005, CBHR 182, 658. Louisiana: 2005, CBHR 243, 658; 2005, CBHR 256, 658. Minnesota: 2008, CBHR 1384, 658; 2008, CBHR 1460, 658. Mississippi: 2001, CBHR 30, 658; 2001, CBHR 32, 658; 2001, CBHR 152, 658; 2001, CBHR 153, 658; 2001, CBHR 154, 658; 2001, CBHR 155, 658; 2001, CBHR 156, 658. New York: 2005, CBHR 205, 658; 2005, CBHR 206, 658. South Carolina: 2006, CBHR 512, 658; 2006, CBHR 894, 658. Unknown state: 2005, CBHR 120, 658; 2005, CBHR 121, 658.



C12.3: S. nigricornis of with dark abdomen

C12.4: S. nigricornis of with pale abdomen



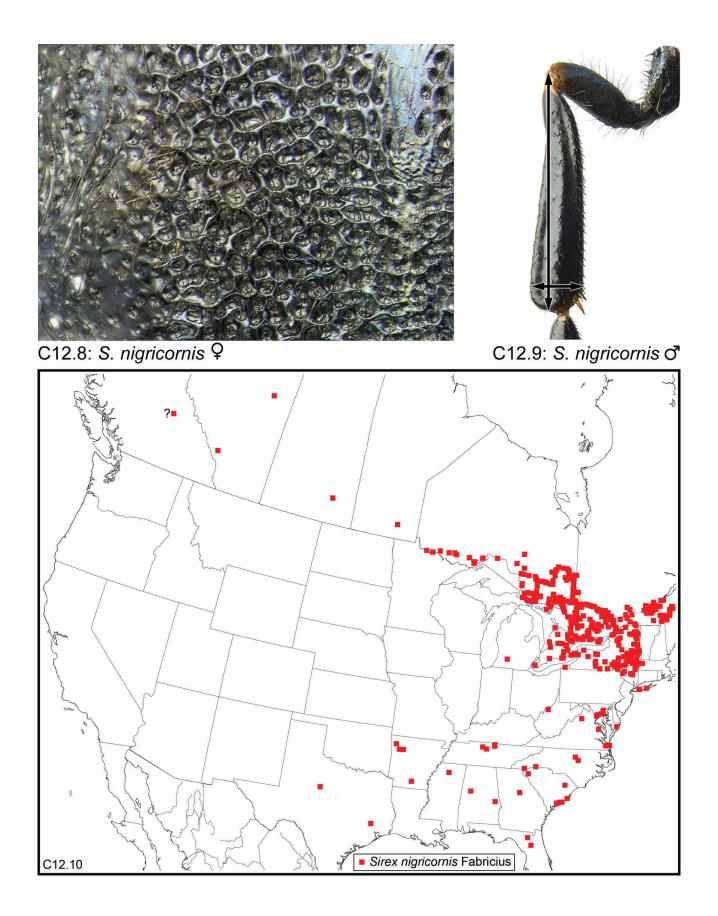
C12.5: S. nigricornis Q with reddish brown abdomen



C12.6: S. nigricornis of with dark abdomen



C12.7: S. nigricornis of with pale abdomen



13. Sirex nitidus (T. W. Harris), comb n. and sp. rev.

Fig. C13.1 (female with pale femora, habitus)

Fig. C13.2 (females with dark femora, habitus)

Fig. C13.3 (male with pale femora and dark abdominal apex, habitus)

Fig. C13.4 (male with pale femora and light abdominal apex, habitus)

Fig. C13.5 (male with black femora and light abdominal apex, habitus)

Fig. C13.6 (male with black femora and black abdomen, habitus)

Fig. C3.1 (live female with pale femora) Fig. C13.8 (map)

- *Urocerus nitidus* T. W. Harris, 1841: 391. Holotype female (MCZC) with abdomen missing, examined by DRS and image examined by HG. Type locality: Massachusetts.
- Sirex juvencus juvencus Smith, 1979: 127 (not Linnaeus, 1758: 560).

Sirex juvencus cyaneus Bradley, 1913: 14 (not Fabricius, 1781: 419).

Sirex cyaneus Ries, 1951: 83 (not Fabricius 1781: 419); Smith 1979: 126.

Sirex californicus Bradley, 1913: 14 (not Ashmead, 1904: 64); Ries 1951: 83, Middlekauff 1960: 62. This misidentification applies only to pale legged females of *S. californicus*.

Diagnostic combination

Specimens with reddish brown femora. Among females with black abdomen, completely light reddish brown tibiae, and a long tarsal pad (pad length 0.7-0.8 as long as ventral length of tarsomere) [cyaneus, abietinus], those of S. nitidus are recognized by the larger pits at the middle of the lancet (length 0.18-0.25 times as long as length of annulus). Among **males** with mainly black metatibia and with net-like pits on median 0.5-0.7 of mesoscutum [abietinus, cyaneus, and varipes], those of S. nitidus are recognized by the black or brown spot on at least part of the dorsal surface of the mesotibia and mesotarsomere 1 (it may include mesotarsomeres 2 and 3), the generally fine pits on the gena and vertex (diameter of pit 0.1-0.2 that of lateral ocellus), and the narrow pale base of the metatibia (only the area of minimum constriction reddish brown).

Specimens with black or mainly black femora (AK, YT, northern BC and northern half of AB). **Females** of *S. nitidus* are recognized by the long tarsal pad (length 0.7–0.8 times ventral length of tarsomere), short metatarsomere 2 (2.0–3.0 times as long as high), dark blue abdomen, and larger pits at the middle of the

lancet (length 0.18-0.25 times length of annulus). Males of *S. nitidus* are recognized by the light reddish brown protibia and protarsus, moderately fine pits on the head, and narrow light reddish brown transverse band at the base of the metatibia.

FEMALE. Description

Color. Body, antenna (less than 1% of specimens with flagellomeres 1 or 1 and 2 brown; only one specimen with flagellomeres 1–4 light reddish brown), and palps black with dark blue metallic reflections. Coxae black, femora (except brown base), tibiae and tarsi (apical half of metatarsomeres 5 usually darker but not dark brown or black) light reddish brown (Fig. B2.2), or in Alaska, Yukon, and northern British Columbia and northern Alberta some specimens with metafemur black (usually pro– and mesofemur also, and in some specimens the dorsal surface of the metatibia black as in *S. varipes* and in one specimen the tibiae and tarsi are completely black). Fore wing mainly clear, at most light yellowish brown behind stigma (Fig. B2.75).

Head. Gena with pits 2.0–4.0 pit diameters apart and mainly absent centrally behind eye (Fig. B2.56), vertex and postocellar area with pits 2.0–4.0 pit diameters apart (Fig. B2.62), and each pit diameter about 0.1–0.2 that of lateral ocellus.

Thorax. Mesoscutum with coarse, net-like pits over most of median surface (Fig. B2.65). Metatarsomere 2 in lateral view 2.0–2.2 times as long as high, and its length about 1.0–1.1 times length of tarsomeres 3 + 4) (Fig. B2.60); tarsal pad 0.7–0.9 times as long as ventral length of tarsomere (Fig. B2.67). Fore wing vein 3A absent (Fig. B2.75).

Abdomen. Median basin of tergum 9 with basal width 0.9–1.1 times as long as median length, maximum width 1.3–1.4 times as long as median length, and median length 0.5–0.6 times as long as cornus length (as in Fig. B2.88). Cornus in dorsal view quite short, with edges straight, its median length 1.0-1.2 times as long as maximum width of abdomen at junction of terga 9 and 10 (as in Fig. B2.88). Sheath. Length 0.65-0.8 times fore wing length, basal section 0.91–1.17 times as long as length of apical section (Fig. A3.26). Ovipositor. Lancet with 29-35 annuli (basal annuli clearly outlined); junction of basal and apical section of sheath aligned between 10th and 11th or 11th and 12th annuli, with 25-30 pits beginning with annulus 2. Pits near middle annuli or area at base of apical section of sheath, 0.18–0.3 times as long as an annulus (pits gradually and markedly decreasing in size toward base (Fig. B2.83)), 0.4–0.6 times as high as lancet height in lateral view, and about 1.1-1.4 times as long as high (Fig. B2.83); annulus 10 length/ovipositor diameter (lance + lancet) 1.29-1.81 (based on 32 specimens).

Last three annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit (Fig. C13.7). Edge of apical 5–6 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head, thorax and coxae black with dark blue metallic reflections. Pale form with coxae, mesotibia (part of dorsal surface), mesotarsomere 1 (often mesotarsomere 2) (Fig. B2.135), metatibia (except extreme base), and metatarsomeres 1-3 black; femora, protibia and protarsus, most of mesotibia, mesotarsomeres 2-5, base of metatibia (spot extended slightly beyond minimum constricted portion and about as long as wide (Fig. B2.91)), ventral and part of dorsal surfaces of mesotarsomere 1, and metatarsomeres 4 and 5 light reddish brown (Fig. B2.135). Black form (from Alaska commonly, and Yukon to Newfoundland occasionally) with at least metafemur (pro- and mesofemur ranging from partly to completely black) black. Fore wing clear, lightly yellowish brown in apical 0.25. Abdomen segments 1 and 2 or 1-3 black (rarely abdomen completely black, and a few specimens with intermediate pattern seen); segments 3-9 or 4-9 light reddish brown (dominant pattern in the Prairies and western regions) (Fig. B2.140), or segments 3–7 or 4–7 light reddish brown and segment 8 (including sternum 9) black (common pattern east of the Prairie region) (Fig. B2.139).

Thorax. Metatibia 3.8–4.3 times as long as maximum width (Fig. B2.91). Metatarsomere 1 in lateral view 2.7–3.4 times as long as maximum height.

Taxonomic notes

One type female of *Urocerus nitidus* exists, but the abdomen (and, therefore, the ovipositor, which has the only diagnostic characters) is missing so this type specimen cannot be assigned unequivocally to this species. The type is from a region in eastern North America where both *Picea* and *Abies* occur. Therefore, based on the type locality, the holotype could be either the species associated with *Picea*, or the species associated with *Abies*, namely *S. cyaneus*. We decided to assign the T. W. Harris name, *S. nitidus*, to the species associated with *Picea*, rather than describing it as new.

Specimens of *S. nitidus*, as well as those of *S. varipes*, *S. abietinus*, *S. cyaneus*, and pale specimens of *S. californicus* and *S. varipes* have been variously assigned to *S. juvencus* or *S. cyaneus* (Essig 1926, Bedard 1938, Middlekauff 1960, Cameron 1965, Morris 1967). Published information is not meaningful without voucher specimens.

Both sexes of S. nitidus differ from those of the

European S. juvencus. Females of S. nitidus have the five basal flagellomeres almost always (99%) black or brown (light reddish brown in *S. juvencus*), the most basal annuli (2 or 3) of the ovipositor have very small pits relative to those near the middle (quite similar in size at the base and the middle in S. juvencus), and the junction of the basal and apical sections of the sheath is aligned between the 10th and 11th annuli of the ovipositor (between the 12th and 13th annuli in S. juvencus) (Viitasaari 1984, Viitasaari and Midtgaard 1989). Almost all males of S. *nitidus* have a brown or black spot on the dorsal surface of the mesotibia, and/or a brown spot on mesotarsomere 1 or 1 and 2 (completely light reddish brown in S. juvencus). Therefore, S. nitidus is specifically distinct from S. juvencus. Sirex juvencus is only known from interceptions at American and Canadian ports but has not established in North America because in most ports its host plants, Picea spp., are absent.

Sirex nitidus is very similar to the European S. torvus M. Harris, known as S. cyaneus in Europe (see "taxonomic notes" under S. cyaneus and Chapter D. Additional Notes). Sirex torvus is found in central Europe. Females share the same type of ovipositor and color pattern and are almost undistinguishable from S. nitidus. However, in S. nitidus, the gena is clearly pitted and the pits are scattered, but in S. torvus the pits are few and very fine. In addition, we compared the distances between lancet annuli 2, 5 and 10 relative to the ovipositor diameter of S. nitidus (32 females from Laniel, Quebec) against the same measurements taken from Viitasaari and Midtgaard (1989) based on 5 females of S. torvus. In females of S. nitidus the annulus length/ ovipositor diameter (lance + lancet) for annulus 2 is 2.0-2.7 (mean = 2.3) [2.6–2.7 (mean = 2.65) in *S. torvus*], for annulus 5 1.5–2.2 (mean = 1.9) [2.25–2.35 (mean = 2.3) in S. torvus], and for annulus 10 1.3-1.8 (mean = 1.5) [values not available in Viitasaari and Midtgaard, (1989) for S. torvus]. We measured 26 specimens of S. torvus for the above parameters of annulus 10, and the values vary from 1.39-1.90. Except for a small difference in annulus 5 between the two species there were no differences in the other proportions. Males of S. nitidus have the mid leg (except for males from Alaska) usually less darkly colored (mesotibia and/or mesotarsomere 1 each with a brown or black spot on the dorsal surface) [more darkly colored in S. torvus: most of the mesotibia dorsal, lateral and most or all of ventral surface and almost all of mesotarsomere 1 black]. In eastern North America, the apex of the abdomen of most specimens of S. nitidus is black whereas the apex is reddish brown westward (apex of abdomen is completely reddish brown in S. torvus). Sirex nitidus is close to S. torvus, but is not exactly the same. The main hosts of S. torvus are Abies spp., but for S. nitidus are Picea spp. The differences in

color pattern of the middle leg, the geographical change in color of the apex of the abdomen, and the differences in host preferences preclude an accidental introduction of *S. torvus* into North America. Because of differences in genal pits size and density, color pattern in males and host preferences, we recognize *S. nitidus* as specifically distinct from the *S. torvus*.

Sirex nitidus is also very similar to the little known European species, S. atricornis Kjellander. The species is subarctic in northern Scandinavia, Finland and Russia. It may extend to eastern Russia. In Scandinavia, the larvae of this species probably develop only on Pinus spp. as no other conifers are recorded from that region of northern Europe. The only difference seen in the two females (DABH) of S. atricornis studied by Viitasaari (1984) is the shape of the second annulus before the apical teeth annuli. The ridge of this annulus is straight in *S. atricornis* (very slightly curved in S. nitidus). This very subtle difference may vary geographically. Females of S. nitidus have wings that are lightly darkened near middle and apical 0.25 (completely clear in S. atricornis). In addition, we compared the distances between lancet annuli 2, 5 and 10 relative to the ovipositor diameter of each annulus (32 females from Laniel, Quebec) of S. nitidus against the same measurements based on 15 females of S. atricornis studied by Viitasaari and Midtgaard (1989). In females of S. nitidus the annulus length/ovipositor diameter (lance + lancet) for annulus 2 is 2.0–2.7 (mean = 2.3) [2.5–2.6 (mean = 2.55) in *S. torvus*], for annulus 5 1.5–2.2 (mean = 1.9) [2.1–2.2 (mean = 2.15) in *S. atricornis*], and for annulus 10 1.3-1.8 (mean = 1.5) [values not available for S. atricornis]. The S. atricornis proportions are within the range of the S. nitidus proportions, but the means for S. nitidus are clearly lower than those for S. atricornis. It seems that the coefficient of variation is much lower for S. atricornis than for S. nitidus (8% and 9% in the latter). At this point, we do not see any difference between S. *nitidus* and *S. atricornis*. As pointed out by Viitasaari and Midtgaard (1989), S. atricornis may be part of a species complex in the Palaearctic. We think that S. torvus and S. nitidus are also part of this complex.

In North America, females of *S. nitidus* may be confused with North American *S. cyaneus* and *S. abietinus* females. They are distinguished from the latter two species by a pit on annulus 2. Females of *S. nitidus* may be confused with *S. noctilio* and the pale legged form of *S. californicus*. They are distinguished from the latter two species by the length of the tarsal pad on metatarsomere 2, and pit development on the vertex and ovipositor.

Geographical variation

Adults of S. nitidus show great variation in color

pattern. The patterns are not random but change along geographical lines. Specimens with intermediate color patterns have been seen. Therefore, the color forms are not discrete. The most striking variation is in femur color. Femora may be black or light reddish brown. The pale femora pattern is seen in all regions, but females with black femora are centered in Alaska and are recorded from northernmost British Columbia, Yukon, and as far south as central Alberta. In males the pattern is similar but a few males with black femora have been recorded across Canada as far as Newfoundland in the boreal zones. The black femora form is not recorded in the southern boreal zone and further south. The next significant character in males is the color pattern at the apex of the abdomen. The apical segments may vary from black to reddish brown. From Manitoba and westward the apex is completely reddish brown. From Manitoba and eastward, most specimens have a black abdominal apex. A rare color variation is recorded in males with completely black abdomen in southern Yukon, and northernmost and southern British Columbia. All the above color variation patterns change gradually and subspecific segregation is not justifiable.

Hosts and phenology

Long series of carefully reared and identified specimens of *S. nitidus* are mainly from *Picea* spp. (88%). A few specimens were associated with *Abies*, *Larix*, *Pseudotsuga*, *Tsuga*, *Pinus*, and *Thuja*. Based on 253 reared and confirmed specimens all but one hosts are Pinaceae: *Abies balsamea* (14) (Johnson 1930 – no voucher specimens seen, they could be *S. cyaneus*), *A. lasiocarpa* (2), *Larix laricina* (7), *Picea* sp. (2), *P. engelmannii* (34), *P. glauca* (107) (reported as *S. cyaneus* by Morris (1967)), *P. mariana* (63), *P. rubens* (6), *Pinus contorta* (1), *P. ponderosa* (6), *Pseudotsuga menziesii* (7), and *Tsuga heterophylla* (2). We have only two records from *Thuja plicata* (2), a Cupressaceae. The record on *Populus* (1) is probably incorrect.

Based on 244 field-collected specimens, the earliest and latest capture dates are July 10 and September 25. The main flight period is from the first half of July to early October with a peak in September. Harrington (1882a) reported later capture dates, up to October 18.

Range

CANADA: AB, BC, MB, NB, NF, NS, NT, NU, QC, ON, SK, YT. **USA:** AK, CO, ID, MT, NH, NY, OR, UT, WA, WY. *Sirex nitidus* is a widespread species that occurs transcontinentally from Newfoundland to Alaska anywhere spruces grow in boreal, cold temperate, and mountain zones (Fig. C13.8). We have seen several

intercepted specimens from New Zealand (FRNZ and PANZ).

Specimens studied and included for distribution map: 658 females and 203 males from BDUC, BYUC, CASS, CNC, CUCC, CUIC, DEBU, EDUM, FRLC, GLFC, LECQ, LEMQ, MNRQ, MTEC, NFRC, NFRN, OSAC, PFRC, UAIC, UAM, UASM, USFS–AK, and USNM.

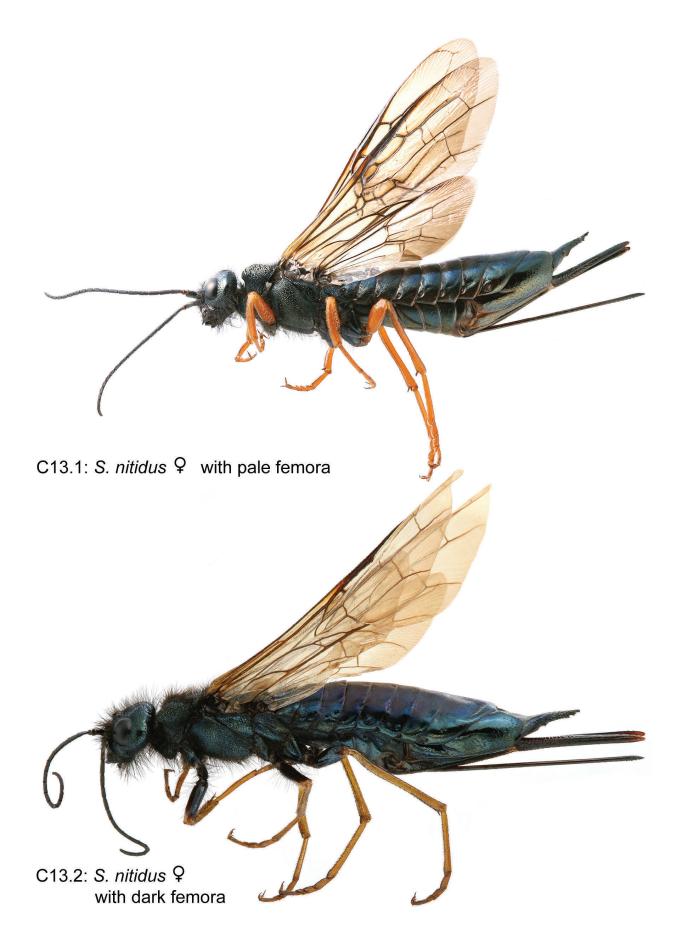
Specimens of *S. nitidus* for molecular studies: 47 specimens. See Fig. E2.5d.

CANADA. British Colombia: 2002, *SIRCA 056*, 393; 2002, *SIRCA 057*, 605; 2001, *SIRCA 058*, 613; 1999, *SIRCA 059*, 612; 2002, *SIRCA 060*, 604; 2001, *SIRCA 067*, 604; 2004, *SIRCA 090*, 639. **Nova Scotia**: 2005, *CBHR 292*, 658; 2005, *CBHR 293*, 658. **Ontario** : 2006, *CBHR 1096*, 658; 2006, *CBHR 1097*, 658; 2006, *CBHR 1098*, 658; 2006, *CBHR 1099*, 611; 2006, *CBHR 1191*, 658; 2006, *CBHR 1192*, 658; 2006, *CBHR 1193*, 658; 2006, *CBHR 1195*, 658; 2006, *CBHR 1196*, 658; 2006, *CBHR 1198*, 658; 2007, *SIRCA 006*, 630; 2007, 2

SIRCA 007, 595; 2007, *SIRCA 008*, 612; 2007, *SIRCA 009*, 604; 2007, *SIRCA 010*, 613; 2007, *SIRCA 011*, 613. **USA. Minnesota**: 2008, *CBHR 1378*, 658. **Montana**: 2004, *CBHR 255*, 658; 2006, *CBHR 331*, 658; 2006, *CBHR 368*, 658. **New York**: 2006, *CBHR 599*, 658; 2006, *CBHR 608*, 658; 2006, *CBHR 615*, 658; 2006, *CBHR 640*, 658; 2006, *CBHR 644*, 658; 2006, *CBHR 740*, 658. **Oregon**: 2005, *CBHR 1057*, 658; 2006, *CBHR 1079*, 658; 2006, *CBHR 1083*, 658; 2006, *CBHR 1079*, 658; 2006, *CBHR 1083*, 658; 2006, *CBHR 1056*, 658; 2007, *CBHR 1276*, 658; 2008, *CBHR 1964*, 658; 2008, *CBHR 1967*, 658; 2008, *CBHR 1964*, 658; 2008, *CBHR 1967*, 658; 2008, *CBHR 1968*, 658.

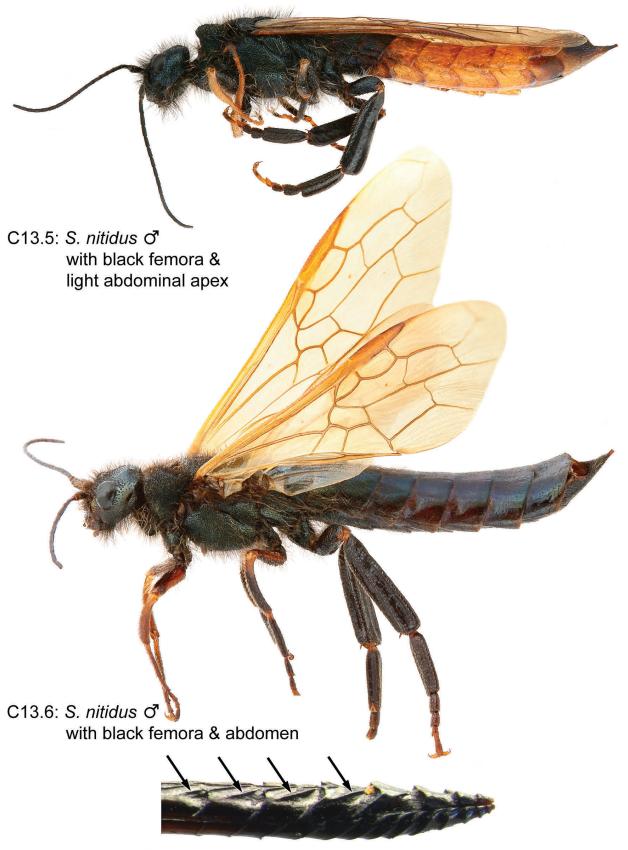
Specimens of *S*. sp. near *nitidus* for molecular studies: 6 specimens. See Fig. E2.5d.

USA. Colorado: 2005, CBHR 194, 658; 2005, CBHR 554, 658; 2005, CBHR 555, 658; 2005, CBHR 556, 658; 2005, CBHR 557, 658; 2005, CBHR 558, 658.

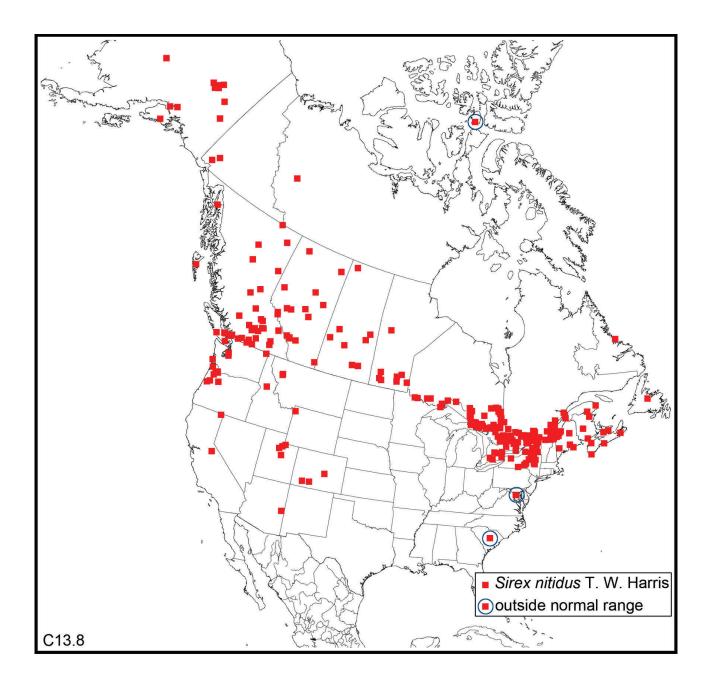


C13.3: S. *nitidus* σ with pale femora & dark abdominal apex

C13.4: S. nitidus O^{*} with pale femora & light abdominal apex



C13.7: S. nitidus Q



14. Sirex noctilio Fabricius

Fig. C14.1, Schiff *et al.* 2006: 50, 51 (female habitus) Fig. C14.2, Schiff *et al.* 2006: 49 (male habitus) Fig. C14.3 (live female) Fig. C14.4 (live male) Fig. C14.5 (live male checking a female) Fig. C14.6 (live mating pair) Fig. C14.7 (male moving away)

Fig. C7.7 (map)

Sirex noctilio Fabricius, 1793: 130. Holotype, male, not examined. Type depository unknown (Viitasaari and Midtgaard 1989); but supposedly in the "Sehested" collection, ZMUC; Benson 1943: 36, Burks 1958: 16, Smith 1979: 127. Type locality: "Germania".

Sirex melanocerus Thomson, 1871: 328. Taeger et al. 2010.

Paururus atlantidis Ghiji, 1909: 163-170. Taeger et al. 2010.

Diagnostic combination

Among **females** with a light reddish brown metafemur and black abdomen [*abietinus*, pale legged form of *californicus*, *cyaneus*, *nitidus*, and *varipes*], those of *S. noctilio* are recognized by the large median pits on the lancet of the ovipositor (pit 0.5–0.75 times as long as annulus) and the short tarsal pads (tarsal pad of metatarsomere 2 0.2–0.4 times as long as ventral length of tarsomere 2). Among **males** with a reddish brown metafemur and a mainly black metatibia and metatarsomere 1 [*abietinus*, *cyaneus*, *nitidus* and *varipes*], those of *S. noctilio* are recognized by the wide reddish brown base of the metatibia (reddish brown area 2.0–3.0 times as long as minimum width of tibia at base).

FEMALE. Description

Color. Body, antenna and palps black with dark blue metallic reflections. Coxae and apical tarsomeres black (Fig. B2.66); femora (except brown base), tibiae and tarsi light reddish brown (some specimens from the Mediterranean region have black femora, but this color pattern has not been seen in North America). Fore wing basically clear except for brownish yellow spot behind stigma (spot black with dark purple reflections on live specimens).

Head. Gena with pits very fine and 4.0-10.0 pit diameters apart, vertex and postocellar area with pits 2.0-8.0 pit diameters apart (maybe much denser in some specimens) (Fig. B2.61), and each pit diameter about 0.1-0.2 times

lateral ocellus diameter.

Thorax. Mesoscutum mostly with round pits in median area (Figs. B2.63 & B2.64), pits commonly with toothlike process behind, and teeth rarely fused transversally (Fig. B2.64). Metatarsomere 2 in lateral view 2.9–3.5 times as long as high, and its length about 1.1-1.4 times tarsomeres 3 + 4) (Fig. C14.8); tarsal pad 0.3–0.4 times as long as ventral length of tarsomere (Fig. B2.66). Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 0.9–1.1 times as long as median length, maximum width 1.1-1.3 times as long as median length, and median length 0.5–0.7 times as long as cornus length. Cornus in dorsal view short, with edges straight, its median length 1.0-1.2 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.6–0.75 times fore wing length, basal section 1.05–1.28 times as long as length of apical section. Ovipositor. Lancet with 33-37 annuli (basal annuli clearly outlined); junction of basal and apical section of sheath aligned between 14th and 15th to 16th and 17th annuli, with 29-33 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1. Pits near middle annuli (Fig. B2.68) or area at base of apical section of sheath 0.55-0.75 times as long as an annulus (pits at base a little smaller: about 0.7 times as high as middle pits), about 0.6-0.75 times as high as lancet height in lateral view, and about 1.4–2.0 times as long as high; annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last 4-5 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 3-5 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head, thorax, antenna (flagellomeres 1 and 2 sometimes brown), palps, and coxae black with dark blue metallic reflections. Femora (except brown base), tibiae and tarsi of fore and middle legs light reddish brown; metatibia and metatarsus black (except metatarsomere 4 and at least base of 5 reddish brown); reddish brown spot at base of metatibia 2.0–3.0 times as long as minimum width of tibia at base (Fig. B2.124). Fore wing light yellowish brown. Abdomen black on segments 1–2 and on segment 8 (including sternum 9).

Thorax. Metatibia 3.8–4.2 times as long as maximum width (Fig. B2.124). Metatarsomere 1 in lateral view 2.7–3.8 times as long as maximum height.

Taxonomic notes

Viitasaari and Midtgaard (1989) mentioned that there were no type specimens of *S. noctilio* in the Fabricius collection (ZMUC). We were also able to confirm

that the type is not in ZMUC (Vilhelmsen, personal communication). However, in the Linnean Collection (LSUK), there are 3 males of *S. noctilio*. One of the specimens, labelled "*S. noctilio* Fab.", was collected by "Cromer Mrs Kett." four years after Fabricius' description and matches it perfectly. Though this specimen is not the type, it gives us a good idea that Linnaeus considered his *Ichneumon juvencus* (images of lectotypes in the Linnean Collection seen by HG) distinct from *Sirex noctilio*.

The original description is rather informative. First, Fabricius (1793) had a male (number of specimens not indicated) because both in his brief and long descriptions he clearly stated that the abdomen was reddish brown on the middle segments and blue on the basal and apical segments. Second, he wrote that the antennae are black, and the legs other than the hind legs (coxa, tibia and tarsus) are reddish brown. In Germany, only three species of *Sirex* are known: *S. noctilio, S. juvencus* and *S. torvus*. It is not *S. juvencus* based on antennal and abdominal color patterns. It is not the European *S. torvus* based on abdominal and mid leg color patterns. So, the present day concept of *S. noctilio* seems to fit perfectly with Fabricius' description.

Geographical variation

Most specimens of S. noctilio have light reddish brown femora and in females clear wings. However, we discovered 20 specimens (USNM, all intercepted at American ports) with black femora and in females dark tinted wings. Pale legged specimens are found all over Europe, but dark legged ones are recorded from southern Europe only. Moreover, it seems that there are no specimens with intermediate color patterns (Figs. C14.9 & C14.10). All structures and color patterns other than the femoral and wing color patterns are the same between the two color forms. Therefore, the dark legged color form is considered as a discrete color form of the common and widespread pale legged S. noctilio. Specimens with dark femora are recorded from the Azores (see Ghigi 1909: 163 under Paururus atlantidis), Portugal, Spain, Italy, and Turkey. The pale form is seen everywhere in Europe. In North and South America only the form with light reddish brown femora is recorded.

Biological notes.

Hoebeke *et al.* (2005) briefly summarized the biology of *S. noctilio*. Females attack *Pinus* spp. in Europe as well as in North America. Development requires one or two years. Adults live one or two weeks and do not feed. Females lay one to three eggs at each oviposition hole. During oviposition, they introduce a toxic mucus with the spores (oidia) of *Amylostereum areolatum* (Fries: Fries). Larvae can develop only on this fungus. A female can use the same oviposition hole to drill one or more lateral holes to oviposit (Viitasaari 1984). Females may lay 75–400 eggs. The largest batch of eggs comes from the largest females (Chrystal 1928, Rawlings 1953, Coutts 1965). Adults dig themselves out and leave exit holes from 3–7 mm in diameter (dependant on adults size (9–35 mm). Adults are able to fly several kilometers.

Hosts and phenology

Based on over 100 reared and confirmed specimens in North America, the hosts of *S. noctilio* are various *Pinus* spp. (Pinaceae). We have seen specimens reared from *P. resinosa*, *P. sylvestris*, and *P. strobus*. In addition *S. noctilio* has been recorded from *P. caribaea*, *P. contorta*, *P. echinata*, *P. elliottii*, *P. kesiya*, *P. nigra*, *P. palustris*, *P. patula*, *P. pinaster*, *P. pinea*, *P. radiata*, and *P. taeda*. In Europe, *S. noctilio* has been reared from *Pseudotsuga menziesii* and in New Zealand and Australia on *Pinus radiata*. The wider host range recorded from Europe may be due to accumulated information from misidentified specimens of other species of *Sirex*.

Based on 66 field-collected specimens, the main flight period is from early July to first half of October with a peak in the second half of July and the first half of August.

Range

ARGENTINA: Rio Negro, Entre Rios, Corrientes, Misiones, Buenos Aires, Cordoba Jujuy (Allard 2008a). BRAZIL: Paraná, General Carniero. CANADA: MB, ON, QC. CHILE: IX and X regions (Allard 2008b), Patagonia, Dina Huapi (Villacide 2010). USA: MI, NY, OH, PA, VT. URUGUAY. Though the range of S. noctilio is originally from Europe to Siberia, it became accidentally established in Australia (Gilbert and Miller 1952), New Zealand (Gourlay 1951, Rawlings 1955), and South Africa (Taylor 1962, Tribe 1995, Tribe 1997). The species was also introduced into South America (Haugen and Hoebeke 2005) and recently into the Great Lake region of North America (Fig. C7.7). The earliest record in North America is a specimen (BMNH) from the Albany River, Ontario, Canada, which ends at James Bay (Benson 1943). It was collected in the early 1800s. Despite some collecting in northern Ontario and intensive collecting in northern Manitoba, no other specimen has been found. It may be an intercepted specimen if it was originally collected near Fort Albany. Sirex noctilio became established around Lake Ontario (Ontario and New York) in early 2000 (Hoebeke et al. 2005).

Specimens studied and included for distribution map: 313 females and 114 males from CFIA, CNC, CUIC, FRNZ, GLFC, ICCM, NZAC, PANZ, USFS–GA, and

USNM.

Specimens for molecular studies: 127 specimens. See Fig. E2.5c.

ARGENTINA: 2005, *CBHR 48*, 658; 2005, *CBHR 49*, 658; 2005, *CBHR 52*, 658; 2005, *CBHR 53*, 658;

AUSTRALIA: year unknown, *CBHR 15*, 658; year unknown, *CBHR 16*, 658; year unknown, *CBHR 17*, 658; year unknown, *CBHR 39*, 658.

CANADA. Ontario: year unknown, *CBHR 286*, 658; 2007, *SIRCA 18*, 615; 2007, *SIRCA 19*, 616; 2007, *SIRCA 20*, 620; 2007, *SIRCA 21*, 628; 2007, *SIRCA 22*, 606; 2007, *SIRCA 45*, 612; 2007, *SIRCA 46*, 658; 2007, *SIRCA 47*, 620.

SOUTH AFRICA: 2007, 2007, CBHR 1085, 658.

USA. New York: 2005, CBHR 20, 658; 2005, CBHR 21, 658; 2005, CBHR 22, 658; 2005, CBHR 23, 658; 2005, CBHR 24, 658; 2005, CBHR 25, 658; 2005, CBHR 26, 658; 2005, CBHR 27, 658; 2007, CBHR 805, 658; 2007, CBHR 807, 658; 2007, CBHR 810, 658; 2007, CBHR 811, 658; 2007, CBHR 814, 658; 2007, CBHR 815, 658; 2007, CBHR 817, 658; 2007, CBHR 819, 658; 2007, CBHR 824, 658; 2007, CBHR 826, 658; 2007, CBHR 827, 658; 2007, CBHR 828, 595; 2007, CBHR 829, 658; 2007, CBHR 834, 658; 2007, CBHR 836, 658; 2007, CBHR 837, 611; 2007, CBHR 1011, 658; 2007, CBHR 1012, 658; 2007, CBHR 1013, 658; 2007, CBHR 1014, 658; 2007, CBHR 1015, 658; 2007, CBHR 1016, 658; 2007, CBHR 1017, 658; 2007, CBHR 1018, 658; 2007, CBHR 1019, 658; 2007, CBHR 1020, 658; 2007, CBHR 1021, 658; 2007, CBHR 1103, 658; 2007, CBHR 1104, 658; 2007, CBHR 1105, 658; 2007, CBHR 1106, 658; 2007, CBHR 1107, 658; 2007, CBHR 1108, 658; 2007, CBHR 1109, 658; 2007, CBHR 1110, 658; 2007, CBHR 1111, 658; 2007, CBHR 1112, 658; 2007, CBHR 1113, 658; 2007, CBHR 1114, 658; 2007, CBHR 1115, 658; 2007, CBHR 1116, 658; 2007, CBHR 1117, 658; 2007, CBHR 1118, 658; 2007, CBHR 1119, 658; 2007, CBHR 1124, 658; 2007, CBHR 1125, 658; 2007, CBHR 1126, 658; 2007, CBHR 1127, 658; 2007, CBHR 1128, 658; 2007, CBHR 1129, 658; 2007, CBHR 1130, 658; 2007, CBHR 1131, 658; 2007, CBHR 1132, 658; 2007, CBHR 1133, 658; 2007, CBHR 1134, 658; 2007, CBHR 1135, 658; 2007, CBHR 1136, 658; 2007, CBHR 1137, 658; 2007, CBHR 1138, 658; 2007, CBHR 1139, 658; 2007, CBHR 1140, 658; 2007, CBHR 1141, 658; 2007, CBHR 1142, 658; 2007, CBHR 1143, 658; 2007, CBHR 1144, 658; 2007, CBHR 1145, 658; 2007, CBHR 1146, 658; 2007, CBHR 1147, 658; 2007, CBHR 1148, 658; 2007, CBHR 1149, 658; 2007, CBHR 1150, 658; 2007, CBHR 1151, 658; 2007, CBHR 1152, 658; 2007, CBHR 1153, 658; 2007, CBHR 1154, 658; 2007, CBHR 1155, 658; 2007, CBHR 1156, 658; 2007, CBHR 1158, 658; 2007, CBHR 1159, 658; 2007, CBHR 1160, 658; 2007, CBHR 1161, 658; 2007, CBHR 1162, 658; 2007, CBHR 1163, 658; 2007, CBHR 1164, 658; 2007, CBHR 1165, 658; 2007, CBHR 1166, 658; 2007, CBHR 1167, 658; 2007, CBHR 1168, 658; 2007, CBHR 1169, 658; 2007, CBHR 1170, 658; 2007, CBHR 1171, 658; 2007, CBHR 1172, 658; 2007, CBHR 1173, 658; 2007, CBHR 1174, 658; 2007, CBHR 1175, 658; 2007, CBHR 1176, 658; 2007, CBHR 1177, 658. Pennsylvania: 2007, CBHR 992, 658; 2007, CBHR 993, 658; 2007, CBHR 994, 658; 2007, CBHR 995, 658.



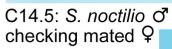


C14.3: S. noctilio ♀



C14.4: S. noctilio o





C14.6: *S. noctilio* ♂ mating with virgin ♀



C14.7: S. noctilio of bypassing mated Q



C14.8: S. noctilio♀



C14.10: *S. noctilio d* with black femora

Fig. C15.1 (female habitus) Fig. C15.2 (male habitus) Fig. C9.6 (map)

- *Sirex obesus* Bradley, 1913: 12. Holotype female (ANSP), examined by HG and DRS. Cresson 1928: 11. Middlekauff 1960: 65. Type locality: Arizona.
- *Sirex juvencus californicus*; Cameron, 1967: 19 (not Ashmead, 1904: 64); accepted by Smith 1979: 127.

Diagnostic combination

Among **females** with completely black legs and darkly tinted fore wing [*areolatus* and dark legged form of *californicus*], those of *S. obesus* are recognized by the short metatarsomere 2 (1.5 times as long as high) in lateral view and the dense pits on the gena and on most of the vertex (pits 0.0–1.0 pit diameter apart). Among **males** with reddish brown femora, tibiae and tarsi [*californicus*, *mexicanus* and *xerophilus*], those of *S. obesus* are recognized by the black antenna (flagellomeres 1 or 1 and 2 may be reddish brown) and the yellow tinted fore wing.

FEMALE. Description

Color. Body, legs, palps, and antenna black with dark blue metallic reflections. Fore wing darkly tinted.

Head. Gena, vertex and postocellar area with pits 0.0–0.5 pit diameter apart (Fig. C15.3), and each pit diameter about 0.3–0.4 times lateral ocellus diameter.

Thorax. Mesoscutum with some transverse ridges in median area; pits quite large but not coarse or net-like (Fig. B2.41). Metatarsomere 2 in lateral view 1.5 times as long as high, and its length as long as or shorter than length of metatarsomeres 3 + 4 (Fig. B2.39); tarsal pad 0.6 times as long as ventral length of tarsomere. Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 1.1 times as long as median length, maximum width 1.4 times as long as median length, and median length 0.6 times as long as cornus length. Cornus in dorsal view short, with edges slightly angular midway, its median length 0.95 as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.7 times fore wing length, basal section 1.15 times as long as length of apical section. Ovipositor. Lancet with 32 annuli (basal annuli clearly outlined); junction of basal and apical section of sheath aligned between 12th and 13th annuli, with 28 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1 (as in Fig. B2.52, base). Pits near middle annuli (Fig. B2.43) or area at base of apical section of sheath 0.35 times as long as an annulus (pits not or hardly decreasing in size toward base), about 0.6–0.7 times as high as lancet height in lateral view, and about 1.3 times as long as high (as in Fig. B2.52, middle); length/ovipositor diameter (lance + lancet) for annulus 2 1.76, for annulus 5 1.53, for annulus 10 1.4, and for annulus 13 1.37 (based on one specimen). Last four annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical five annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head, thorax, antenna (flagellomere 1 or 1 and 2 may be reddish brown) (Fig. B2.112), palps, thorax, and abdominal segments1 or 1 and 2 black with dark blue metallic reflections; remaining abdominal segments light reddish brown. Reddish brown, but black on coxae. Fore wing clearly yellow tinted (B2.114).

Thorax. Metatibia 3.7–4.1 times as long as maximum width. Metatarsomere 1 in lateral view 2.5–3.1 times as long as maximum height.

Taxonomic notes

Adults of *S. obesus* are very similar to those of *S. californicus*, but **both sexes** are distinguished from *S. californicus* by the pit density dorsally on the head, in **females** by a short metatarsomere 2, and in **males** by color pattern of the flagellum.

Females of *Sirex obesus* and dark winged females of *S. californicus* have been confused in the literature. Many females of *S. californicus* and all of those of *S. obesus* have very darkly tinted wings, so wing base tint is not diagnostic. Therefore, published information under *S. obesus* needs confirmation with voucher specimens (Middlekauff 1960, Cameron 1965).

Host and phenology

One specimen of *S. obesus* was reared from *Pinus ponderosa*. Based on 15 field-collected specimens, the earliest and latest capture dates are July 30 to September 23. Thirteen males were caught at hill tops on August 12 (1), August 24 (1), September 20 (4) and September 23 (7).

Range

MEXICO. USA: AZ, NM. Mexico. *Sirex obesus* is known from forested regions of southwestern United States (Fig. C9.6) and has been intercepted from Mexico at Nogales, Arizona and Brownsville, Texas.

Specimens studied and included on range map: 11 females and 14 males from CNC, OSAC, UAIC, and

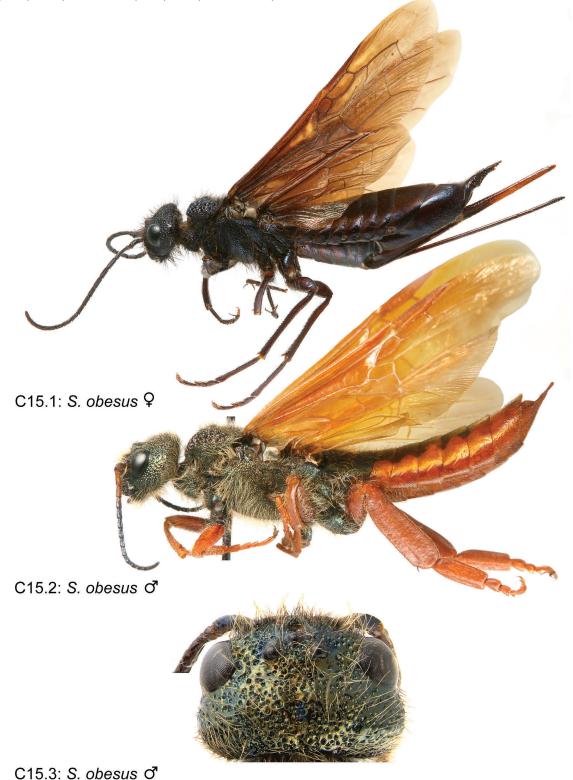
USNM.

Specimens for molecular studies: 10 specimens. See Fig. E2.5f.

USA. Arizona: 2008, *CNCS 1037*, 599; 2008, *CNCS 1038*, 578; 2008, *CNCS 1039*, 606; 2008, *CNCS 1040*,

593; 2007, CNCS 1041, 599.

New Mexico: 2004, *CNCS 1091*, 597; 2004, *CNCS 1092*, 597; 2004, *CNCS 1093*, 593; 2004, *CNCS 1094*, 584; 2004, *CNCS 1095*, 594.



16. Sirex varipes Walker

Fig. C16.1, Schiff *et al.* 2006: 54, 55 (female habitus) Fig. C16.2, Schiff *et al.* 2006: 53 (male habitus) Fig. C16.3 (map)

- *Sirex varipes* Walker, 1866: 342. Holotype, female (BMNH, according to Kirby, 1882), not examined. Walker 1873: 78. Burks 1958: 16, Smith 1979: 128. Type locality: Vancouver Island, British Columbia.
- *Sirex variipes*; Dalla Torre, 1894: 393 (unjustified emendation).
- *Sirex juvencus cyaneus*; Konow, 1898: 17, 81, 90, (not Fabricius, 1781: 419).
- *Sirex cyaneus*; Bradley, 1913: 14, (not Fabricius, 1781: 419); accepted by Ries 1951: 83.
- *Sirex juvencus juvencus x juvencus californicus*; Benson, 1962: 252.

Diagnostic combination

Among **females** with a light reddish brown metafemur, black abdomen, and long tarsal pad (pad length 0.7–0.8 as long as ventral length of tarsomere) [*abietinus*, *cyaneus* and *nitidus*], almost all those of *S. varipes* are recognized by the black (with dark blue metallic reflections) longitudinal band along part of or most of the dorsal surface of the metatibia, and usually black on dorsal surface of the protibia and mesotibia. Among **males** with a reddish brown metafemur and mainly black metatibia [*abietinus*, *cyaneus*, *nitidus* and *noctilio*], those of *S. varipes* are recognized by the black surface of most of the mesotibia and almost all of mesotarsomere 1 (often mesotarsomeres 2 and 3 as well) and the very narrow pale base of metatibia (length of pale area shorter than minimum width of tibia at base).

FEMALE. Description

Color. Body, antenna and palps black with dark blue metallic reflections. Coxae and usually tarsomeres 5 black; femora (except brown base) and tarsomeres 1–4 light reddish brown; protibia and mesotibia usually mostly black with dark blue metallic reflections (Fig. B2.72), but in some specimens completely light reddish brown, and metatibia light reddish brown with a dark blue metallic longitudinal band along dorsal surface (black longitudinal band absent in the palest specimens) (Fig. B2.72). Fore wing clear, at most light yellowish brown behind stigma.

Head. Gena with pits 0.0–4.0 pit diameters apart; vertex and postocellar area with pits 0.0–3.0 pit diameters apart, and each pit diameter about 0.1–0.2 that of lateral ocellus. **Thorax.** Mesoscutum with few coarse, net-like pits in median area. Metatarsomere 2 in lateral view 3.0–3.6

times as long as high, and its length about 1.1-1.3 times length of tarsomeres 3 + 4; tarsal pad 0.7-0.8 times as long as ventral length of tarsomere. Fore wing vein 3A absent.

Abdomen. Median basin of tergum 9 with basal width 0.9–1.2 times as long as median length, maximum width 1.2-1.5 times as long as median length, and median length 0.55–0.7 times as long as cornus length. Cornus in dorsal view short, with edges straight or slightly rounded in apical third, its median length 0.9-1.3 times as long as maximum width of abdomen at junction of terga 9 and 10. Sheath. Length 0.7-0.85 times as long as fore wing length, basal section 0.9-1.05 times as long as length of apical section. Ovipositor. Lancet with 35-38 annuli (basal 2-4 annuli difficult to see); junction of basal and apical section of sheath aligned between 10th and 11th to 12th and 13th annuli, with 27–31 pits beginning with annuli 3-5. Pits near middle annuli or area at base of apical section of sheath 0.3-0.5 times as long as an annulus (pits gradually and markedly decreasing in size toward base), about 0.5–0.6 times as high as lancet height in lateral view, and 1.5-2.3 times as long as high (Fig. B2.71); annulus 10 length/ovipositor diameter (lance + lancet) not measured. Last 3-5 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 6-8 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head and thorax black with dark blue metallic reflections. Coxae, mesotibia (at least most of dorsal surface), mesotarsomere 1 (usually mesotarsomeres 2 and 3) (Fig. B2.136), metatibia (except extreme base), and metatarsomeres 1–3 black (Fig. B2.138); femora, protibia and protarsus, at least base of mesotibia, ventral surface of mesotarsomere 1 (in some specimen mesotarsomeres 2 and 3), metatarsomere 4, extreme base of metatibia (spot restricted to minimum constricted portion and less long than wide) (B2.138), and metatarsomere 4 light reddish brown. Fore wing lightly yellowish brown. Abdominal segments 1, 2, and in some specimens basomedian area of terga 3 up to a maximum of terga 3–8 black, remaining segments light reddish brown (Fig. B2.141).

Thorax. Metatibia 3.8–4.5 times as long as maximum width (Fig. B2.138). Metatarsomere 1 in lateral view 2.9–3.8 times as long as maximum height.

Taxonomic notes

We did not examine the type of *Sirex varipes*, but the description of the leg color pattern of the female type perfectly matches our concept of this species.

Sirex varipes has been confused with the European

S. juvencus (Benson, 1962) and *S. torvus*. Females of *Sirex varipes* are easily distinguished from the latter two species by the size and proportions of pits at the middle and base of the ovipositor. Males of *Sirex varipes* are easily separated from *S. juvencus* by the color pattern of the middle leg, but are very similar in color to males of *S. torvus*.

Almost all females of *Sirex varipes* examined could be correctly identified by metatibial color pattern. However, three females had completely pale metatibia. Such females may be confused with *S. cyaneus*, *S. abietinus* and *S. nitidus*. All four species share a long tarsal pad on metatarsomere 2. However in *S. varipes*, the ovipositor pit development in apical 0.25 is distinctive and consists of large and long pits.

Hosts and phenology

Sirex varipes has a wide host range. Based on 27 reared and confirmed specimens, all hosts are Pinaceae: Abies amabilis (10), A. concolor (3), A. grandis (1), A. magnifica (1), A. lasiocarpa (2), Picea englemannii, P. sitchensis (2), Pinus ponderosa (1), Pseudotsuga menziesii (6), and Tsuga heterophylla (1).

Based on 15 field-collected specimens, the main flight period is from early July to early October with a peak in August and September.

Range

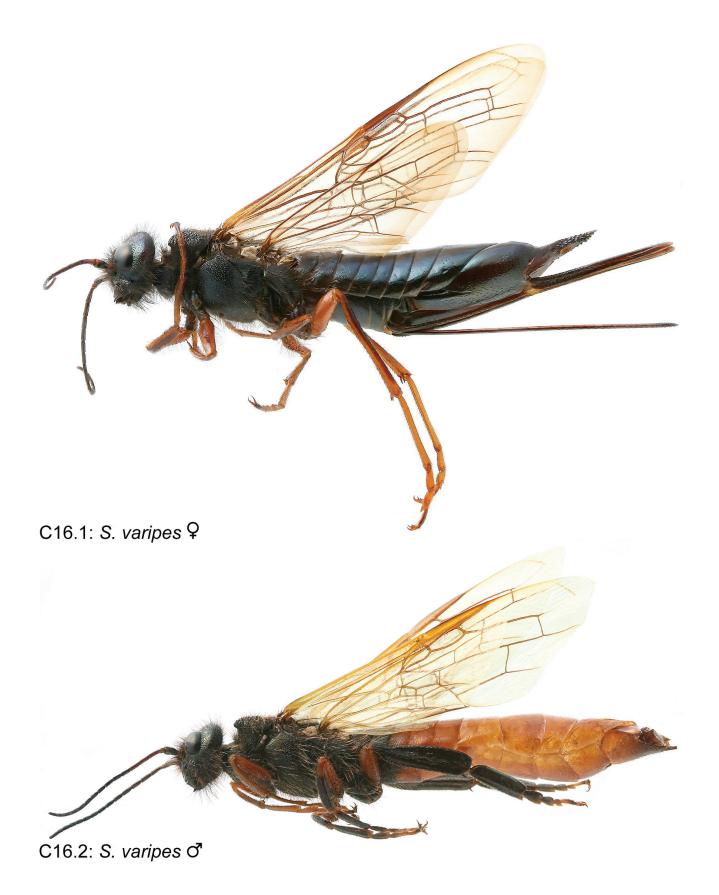
CANADA: AB, BC, NS (emerged from western lumber).**USA:** CA, MT, NV, IA (wood bed frame), OH (wall probably associated with western lumber), NJ (from wood in home), OR, WA. *Sirex varipes*, a western species, known from southern British Columbia and southwestern Alberta south to California and Arizona (Fig. C16.3). There are a few records of adventive specimens emerged from lumber in eastern North America (IA, OH, NJ and NS) and Britain (Burks 1967), and we have seen one intercepted specimen from New Zealand (FRNZ). None have become established.

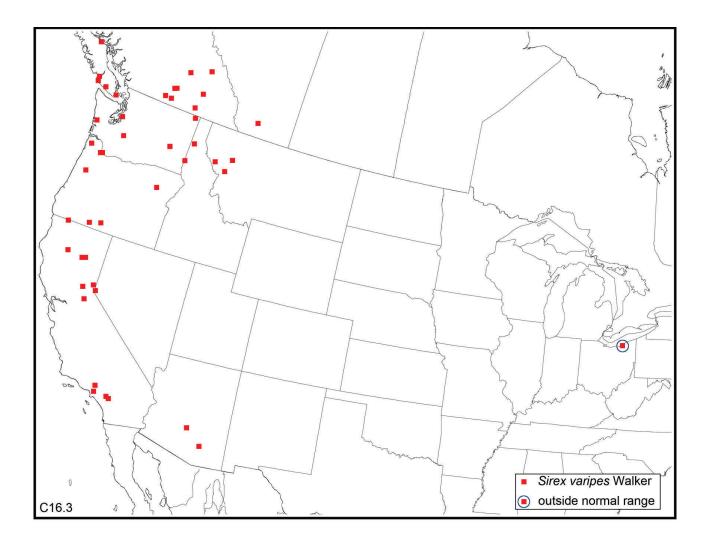
Specimens studied and included for the distribution map: 94 females and 46 males from CNC, MTEC, NFRC, OSAC, PFRC, UAIC, UCRC, and USNM.

Specimens for molecular studies: 20 specimens. See Fig. E2.5e.

CANADA. British Columbia: 2007, *CNCS 1046*, 621; 2002, *SIRCA 054*, 639; 2002, *SIRCA 055*, 630; 1999, *SIRCA 068*, 384; 1992, *SIRCA 070*, 348.

USA. California: 2005, *CBHR 96*, 658; 1999, *CBHR* 102, 658; 1999, *CBHR 104*, 658. **Idaho**: 2008, *CBHR* 1450, 658. **Oregon**: 2004, *CBHR 223*, 658; 2004, *CBHR* 244, 658; 2001, *CBHR 1363*, 658; 2001, *CBHR 1364*, 658. **Unknown state**: year unknown, *CBHR 117*, 658; year unknown, *CBHR 410*, 658; year unknown, *CBHR* 411, 658; year unknown, *CBHR 412*, 658; year unknown, *CBHR 413*, 658. **Washington**: 2005, *CBHR 213*, 658; 2005, *CBHR 247*, 658.





17. Sirex xerophilus Schiff, n. sp.

Fig. C17.1 (female habitus) Fig. C17.2 (male habitus) Fig. C9.6 (map)

Diagnostic combination

Among **females** with completely black legs and abdomen, and a clear fore wing [*mexicanus*], those of *S. xerophilus* are recognized by the coarse and crater-like pits over most of the median half of the mesoscutum. Among **males** with a reddish brown hind leg beyond the coxa [*californicus* and *obesus*], those of *S. xerophilus* are recognized by the completely reddish brown antenna and black coxae.

FEMALE. Description

Color. Body, legs, palps, and antenna black with dark blue metallic reflections. Fore wing lightly tinted (Fig. B.2.32).

Head. Gena with pits (except centrally) 0.0–1.5 pit diameters apart; vertex and postocellar area with pits 0.0–1.0 pit diameters apart; and each pit diameter about 0.2–0.45 that of lateral ocellus.

Thorax. Mesoscutum widely covered with net-like pits in median area (Fig. B2.45). Metatarsomere 2 in lateral view 2.2–2.6 times as long as high, and its length about 1.2 times length of tarsomeres 3 + 4; tarsal pad 0.3–0.5 times as long as ventral length of tarsomere. Fore wing vein 3A absent (Fig. B2.47).

Abdomen. Median basin of tergum 9 with basal width 1.0–1.3 times as long as median length, maximum width 1.2–1.6 times as long as median length, and median length about 0.7 times as long as cornus length. Cornus in dorsal view short, with edges angularly rounded or very angular midway, its median length 0.9–1.2 as long as maximum width of abdomen at junction of terga 9 and 10. *Sheath*. Length 0.7–0.9 times fore wing length, basal section 1.1–1.2 times as long as length of apical section. *Ovipositor*. Lancet with 33–36 annuli (basal annuli clearly outlined); junction of basal and apical section of

sheath aligned between 11^{th} and 12^{th} to 13^{th} and 14^{th} annuli, with 29–32 pits beginning with annulus 2; pit of annulus 2 only extending to edge of annulus 1 (Fig. B2.51, base). Pits near middle annuli (Fig. B2.51) or area at base of apical section of sheath 0.7–0.8 times as long as annulus (pits slightly decreasing in size toward base, and about 0.6 times as high as lancet height in lateral view, with posterior edge hardly outlined, and 2.5–3.4 times as long as high (Fig. B2.51, middle); length/ovipositor diameter (lance + lancet) for annulus 2 is 1.9–2.35, for annulus 5 1.5–2.00, for annulus 10 1.4–1.7, and for annulus 13 1.40–1.60 (7 specimens). Last 4–5 annuli before teeth annuli as well as first tooth annulus with ridge on ventral edge of pit. Edge of apical 4–5 annuli before teeth annuli extending as ridge to ventral edge of lancet.

MALE. Description

Color. Head, palps, thorax, and abdominal segments 1 or 1 and 2 black with dark blue metallic reflections; remaining abdominal segments and antenna (a little darker apically) light reddish brown. Coxae black, remaining articles of legs reddish brown. Fore wing clear.

Thorax. Metatibia 4.0 times as long as maximum width. Metatarsomere 1 in lateral view 3.3 times as long as maximum height.

Type material

Holotype female (USNM) in perfect condition; labeled [White with red frame] [White] "Panguitch Utah" "Hopk. U.S. 4533j" "H. E. Burke Collector" "Pinus ponderosa"; [Red] "HOLOTYPE Sirex xerophilus N.M. Schiff, 2011". Type locality: Panguitch, Garfield Co., UT.

Paratypes. 11 females and 1 male. **MEXICO. Chihuahua:** Intercepted at El Paso, Texas (#51422),

28.IX.1948, pine lumber (#48–16199) (2F, USNM); [no locality] madera [lumber] pine, J. A. Backer (2F, USNM). **USA. Colorado:** *Larimer Co.*, Big Elk Fire, 40°17'02"N 105°22'59"W, 16.IX.2005, S. M. McElway (5 F, CNC). **Utah:** *Garfield Co.*, Panguitch, Hopk. U.S. 4533j, H. E. Burke, *Pinus ponderosa* (1F, 1M, USNM).

Origin of specific epithet

The name *xerophilus* is an adjective derived from two Greek words meaning "dry loving" because the species is found in dry ecosystems where its only recorded host, *Pinus ponderosa*, occurs.

Host and phenology

Specimens of *S. xerophilus* have been reared from *Pinus ponderosa* in Utah. They were also collected on pine lumber in Mexico.

One specimen was captured on September 16, three on September 17, two on September 28 and two on November 26.

Range

Mexico: (northern region). **United States:** CO, UT. *Sirex xerophilus* is known from southern Utah and northern Colorado south to northern Mexico (Fig. C9.6).

Specimens studied and included for the distribution map: 11 females and 1 male from CNC and USNM.

Specimens for molecular studies: 5 specimens. See Fig. E2.5b.

USA. Colorado: 2005, *CBHR 538*, 658; 2005, *CBHR 541*, 658; 2005, *CBHR 542*, 658; 2005, *CBHR 544*, 658; 2005, *CBHR 545*, 658.



C17.1: S. xerophilus Q



C17.2: S. xerophilus o



C18.1: S. flammeus of

18. Genus Sirotremex Smith

Fig. C18.1 (male lateral habitus)

Sirotremex Smith, 1988: 244. Type species: *Sirotremex flammeus* Smith; monotypic.

Diagnostic combination

Both sexes of *Sirotremex* probably (female unknown) are recognized by the fore wing with a broadly rounded apex and a short 3R1 cell (2.2 times as wide as long), and the flagellum with 10 or 11 short flagellomeres (middle flagellomeres 1.5 times as long as wide).

Description

Color. Surfaces dark brown and without metallic reflections.

Head. Antennal sockets with distance between their inner edges 2.5 times distance between inner edge of eye and outer socket edge (Fig. C18.2, in black). Distance between inner edges of lateral ocelli 1.1 times as long as distance between outer edge of lateral ocellus and nearest edge of eye (Fig. C18.2, in white). Maximum distance between outer edges of eyes longer than maximum width of head (thus, in frontal view, genal edge intersected by outer edges of eyes) or slightly shorter (Figs. C1.18, C18.2). Minimum distance between inner edges of eyes 1.6 times maximum eye height (Fig. C18.2, in red). Gena without ridge behind eye and without white spot, with large pits, each pit not elevated along posterior edge as

low tooth. Head with setae sharp at apex. Antenna with 10 or 11 flagellomeres, and middle flagellomeres in dorsal view 1.5 times as long as high; middle flagellomeres with sensory pits on ventral surface, and apical 5 or 6 flagellomeres each with sensory pits on inner surface only, but without oval impression on inner dorsal and inner ventral surfaces.

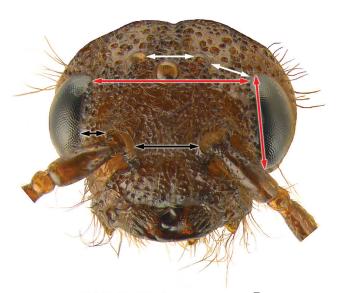
Thorax. Pronotum smooth or pitted over less than 0.5 of anterior vertical surface. Mesoscutum densely pitted over median 0.5–0.7 only. Mesotarsomere 1 in lateral view enlarged, its dorsal and ventral edges quite divergent in basal half and base of tarsomere about 0.5 times its maximum width. Metatibia with two apical spurs, in **male** in lateral view metatibia 3.7–4.1 times as long as maximum width. Metatarsomere 2 length and height not described as female unknown. Metatarsomere 5 shorter than metatarsomeres 2 + 3. Fore wing with apex broadly rounded (Fig. B1.49), with vein 2r–m joined to cell 2M (as in Fig. B1.51), with vein 2r–m present, with cell 1Rs2

about as wide as long (as in Fig. B1.71), with cell 3R1 2.2 times as long as wide (Fig. B1.53), with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even distal to junction with vein 2r-rs (as in Fig. B1.25), with vein Cu1 usually present, with vein 1cu–a joining vein Cu about mid way between veins 1m–cu and M, with vein 2A extending along posterior edge of wing for 0.4 times length of cell 1A length (as in Fig. A3.30), and with vein 3A absent. Hind wing with anal cell.

Abdomen. Cornus, median basin, sheath, and ovipositor not described as female unknown.

Diversity and distribution

One species, known only from two males, is recorded from northwestern Mexico (Smith 1978; Taeger and Blank 2011, Taeger *et al.* 2010).



C18.2: S. flammeus of

19. Sirotremex flammeus Smith

Fig. C18.1 (male lateral habitus) Fig. C19.1 (male dorsal habitus) Fig. C32.3 (map)

Sirotremex flammeus Smith, 1988:244. Holotype male (CNC), with right flagellomeres 6–11 and left metatibia and metatarsus missing, labeled [White] "8 mi.E.El Salto Dgo.MEX. 8,200' 25 June 1964 L.A. Kelton"; [White red border] "HOLOTYPE Sirotremex flammeus D. R. Smith"; [Red] "HOLOTYPE Sirotremex flammeus Smith CNC No 20266". Type locality: Mexico, Durango, 8 miles E. El Salto.

Diagnostic combination

Both sexes probably (female unknown) are recognized by the broadly rounded apex of the fore wing.

FEMALE. Unknown.

MALE. Description

Most character states except color of body and microsculpture of sternum 9 should apply to both sexes. **Color.** Body, antenna, palps, mandible and legs dark brown and without metallic reflections. Both wings yellow tinted, with extreme apex tinted black (Fig. B1.49).

Head. Median furrow behind ocelli well outlined. Flagellum with 10–11 flagellomeres, and in lateral view middle flagellomeres about 1.5 times as long as high (Fig. B1.55). Head smooth between pits. Gena and lateral area of vertex with pits 0.3–0.5 diameter of lateral ocellus and usually 1.0 pit diameter apart; frons, median section of vertex, and lateral 0.3 of mesoscutellum with pits 0.2–0.3 diameter of lateral ocellus and mainly touching; clypeus with pits 0.2–0.3 diameter of lateral ocellus, generally shallow, and small. Head with long setae.

Thorax. Thorax smooth between pits. Pits about 0.3 diameter of lateral ocellus and less than one pit apart on mesepisternum and metepisternum, net-like on median section of mesoscutum and all of mesoscutellum, and denser laterally on tergum 1. Pronotum with long setae. Abdomen. Abdomen with pits 0.2–0.3 diameter of lateral ocellus, shallow, and small. Setae on tergum 1 long medially and laterally, on tergum 2 long laterally, on terga 3-8 short and scattered laterally, and on disc of terga 2-8 and sterna 2-9 less dense than elsewhere. Meshes of microsculpture outlined over all terga and sterna of abdomen; posterior 0.5 excluding lateral area of terga 2-8 with pitted sculpticells, followed by clearly raised scale-like sculpticells on most of posterior 0.5 of terga 2–7 and less of tergum 8; terga 1, 2–8 laterally and extreme apex, and sterna 2-9 with flat sculpticells forming weak scales.

Taxonomic notes

It is not clear what a female of this species will look like, but the following characters should help to recognize it when it is eventually discovered: the fore wing shape and the proportion of cell 3R1, and the narrow gena intersected or almost intersected by the outer eye edge in frontal view.

Host and phenology.

The host of *S. flammeus* is unknown. The species may be close to *Sirex* and likely is associated with conifers.

Range.

Mexico: Durango (Fig. C32.3).

Specimens studied and included for the distribution map: 2 males from CNC.





C20.1: U. albicornis Q

20. Genus Urocerus Geoffroy

Fig. C20.1 (live female)

Urocerus Geoffroy, 1785: 363. Type species: *Ichneumon gigas* Linnaeus; monotypic.

Xanthosirex Semenov 1921: 86. Type species: *Xanthosirex phantasma* Semenov; original designation. Gussakovskij 1935: 340, Benson 1943: 24.

Diagnostic combination

Among genera with antennal sockets quite close (inner edges of antennal sockets 1.5–2.0 times as long as distance between inner edge of eye and outer edge of socket) [*Sirex, Sirotremex, Xeris,* and *Xoanon*], **both sexes** of *Urocerus* are recognized by the mesoscutum with dense pits on the lateral third, pronotum with anterior vertical surface densely pitted, the gena mainly smooth with a white spot dorsally, and the lack of a ridge behind the eye.

Description

Color. Black portions of body without metallic reflections. **Head.** Antennal sockets with distance between their inner edges 1.5–2.0 times distance between inner edge of

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eye and outer edge of socket (as in Fig. B1.4). Distance between inner edges of lateral ocelli about as long as distance between outer edge of lateral ocellus and nearest edge of eye (Fig. B4.13). Maximum distance between outer edges of eyes less than maximum width of head (thus, in frontal view, genal edges completely visible and not intersected by outer edges of eyes). Minimum distance between inner edges of eyes about 1.3-1.6 times as long as maximum eye height (as in Fig. B1.2). Gena without ridge behind eye and almost always with white spot in dorsal half (Figs. B1.42 & B1.69), with large pits, each with posterior edge not raised as a low tooth. Head with setae sharp at apex. Antenna with 13 or more flagellomeres (the smallest specimens have the lowest number), and middle flagellomeres in dorsal view 2.0-3.5 times as long as wide; in female, middle and apical flagellomeres with sensory pits over all except outer surface, and apical 5-10 flagellomeres with sensory oval impression on dorsal and ventral surfaces; in male, with sensory pits on inner surface to almost all or all surfaces, and apical flagellomeres without sensory oval impressions.

Thorax. Pronotum densely pitted over most of anterior vertical surface (Fig. B1.73). Mesoscutum entirely and densely pitted (including lateral third). Mesotarsomere 1 in lateral view not enlarged, its dorsal and ventral

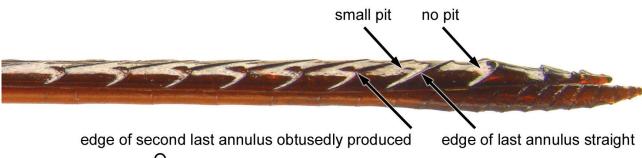
edges almost parallel and base of tarsomere at most 0.7 times its maximum width. Metatibia with two apical spurs, in male, metatibia in lateral view 5.5–9.0 times as long as maximum width. In female, metatarsomere 2 in lateral view 1.5–3.0 times as long as maximum height. Metatarsomere 5 as long as metatarsomere 2 or shorter than metatarsomeres 2 + 3. Fore wing with apex acutely and angularly rounded, with vein 2r-m joined to cell 2M (Fig. B1.71), with vein 2r-m present, with cell 1Rs2 clearly wider than long, with cell 3R1 3.5-4.5 times as wide as long, with cell 2R1 about 0.5 times as wide as cell 3R1, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even distal to junction with vein 2r-rs (as in Fig. B1.25), with vein Cu1 absent, very rarely a short stub, with vein 1cu-a joining vein Cu about mid way between veins 1m-cu and M, with vein 2A extending along wing posterior edge for about 0.4 times cell length (Fig. B1.71), and with vein 3A absent (Fig. B1.71). Hind wing with anal cell 1A (Fig. B1.44); hamuli clearly present both basal and apical to junction of veins R1 and C (as in Fig. B1.11).

Abdomen. Female. Cornus in dorsal view long, narrow, and lateral edges usually constricted at base or (in a few Asiatic species) not constricted (Fig. B1.75). Tergum 9 with median basin with lateral edges markedly divergent and straight then rounded near lateral angle and sharply outlined for about 0.5 times median length of basin, and with basin base (outlined by black furrows laterally) 1.1–1.5 times as wide as median length (Fig. B1.75). Cercus present but very small and wart-like. *Sheath.* Length

of basal section 0.6–0.8 times as long as apical section; apical section without longitudinal lateral ridge, with teeth (absent in a few species of *Urocerus* from China) in apical third of dorsal margin and each tooth with bristle near apex (as in Fig. C1.19). *Ovipositor*. Lancet with any of annuli 3–9 aligned with junction of basal and apical sections of sheath; first tooth annulus without pit; annuli anterior to first annulus before teeth annuli with small pit, and edge of last and preceding annuli above pit and before teeth annuli obtusely produced or sometimes straight (Fig. C20.2).

Diversity and distribution

Urocerus is very diverse, with 33 species restricted to the Northern Hemisphere. Taeger and Blank (2011) and Taeger *et al.* (2010) recorded 32, but we raised *U. flavicornis* to species level. There are 28 known Palaearctic species mostly in Asia (Taeger and Blank 2011, Taeger *et al.* 2010) but only 7 New World species. One introduced species is recorded from Chile; the remaining species (one introduced and five native) are recorded from Mexico north to the tree line in North America. Because we studied only 11 Palaearctic species in addition to the Nearctic ones our generic concept may be incomplete and one should expect that some Asiatic species may not fit one or more character states described above.



C20.2: U. californicus Q

21. Urocerus albicornis (Fabricius)

Fig. C21.1, Schiff *et al.* 2006: 60, 61 (female habitus) Fig. C21.2, Schiff *et al.* 2006: 59 (male habitus) Fig. C20.1 (live female) Fig. C21.3 (live male) Fig. C21.4 (map)

- *Sirex albicornis* Fabricius, 1781: 419. Type female (HMUG), not examined; Fitch 1858a: 45. Type locality: "America boreali".
- *Sirex abdominalis* T.W. Harris, 1833: 586. Not available. Nomen nudum.
- *Sirex magus*; Stephens, 1835: 116 (not Fabricius 1787:257). Specimen probably intercepted.
- *Urocerus abdominalis* T. W. Harris, 1841: 392. Holotype male (MCZC), images from MCZ type database examined by HG. Synonymy by Konow 1898: 77; accepted by Ries 1951: 84, Smith 1979: 128. Type locality: Massachusetts.
- *Urocerus albicornis*; T. W. Harris, 1841: 391 (change in combination); accepted by Walker 1873: 78, Townsend 1878: 93, Bradley 1913: 19, Ries 1951: 84, Middlekauff 1960: 66, Smith 1979: 128. Harrington 1882a.
- *Sirex latifasciatus* Westwood, 1874: 114, pl. XXI, fig. 2. Holotype male (OXUM), images prepared by James E. Hogan and examined by HG. NEW SYNONYM. Type locality: "America Septentrionalis".
- *Urocerus latifasciatus*; Cresson, 1880: 50 (change in combination).
- Sirex Stephensii Kirby, 1882: 375, pl. XVI, fig. 6. According to S. M. Blank (pers. comm.), this name is not a replacement name but a name given for a misinterpretation of *S. magus* Fabricius, *sensu* Stephens (1835). Therefore, it is an original description by Kirby (1882). Accordingly, material identified as *S. magus* in the Stephen's collection should be regarded as the type or syntypes). Synonym by Konow 1898: 77; accepted by Bradley 1913: 19, Ries 1951: 84, Smith 1979: 128. *Sirex stephensi*; Bradley, 1913: 18 (misspelling); Ries, 1951: 84.

Diagnostic combination

Among **females** with a completely or almost completely black abdomen, including the cornus [*californicus*], those of *U. albicornis* are recognized by the wide white central portion of the flagellum with black or brown flagellomeres at the base and apex. Among **males** with black abdominal segments 7–9 and with head mainly black [*flavicornis* and *gigas*], almost all those of *U. albicornis* are recognized by the gena partly reddish brown near the mandible, and the anterolateral angle of the pronotum, and metatarsomere 1 relatively short (4.0–5.2 times as long as high).

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FEMALE. Description

Color. Head black except for white spot behind eye. Maxillary palp and mandible black. Scape and pedicel black; flagellomere 1 usually 2 in part, rarely 3 and 4 in part black or mainly so, apical flagellomeres 3–8 brown to black, and central flagellomeres white or yellowish (Fig. B4.30). Thorax black. Legs black but white on basal 0.25–0.6 of tibiae and tarsomeres 1 (Fig. B4.5). Fore and hind wings darkly tinted (Fig. B4.32). Abdomen black, or many specimens black with a white spot laterally on tergum 8 (Fig. B4.19).

Head. Vertex densely pitted between the white genal spots (as in Fig. B4.47).

Thorax. Metatarsomere 2 in lateral view about 2.5 times as long as high (Fig. B4.34), and its tarsal pad about 0.8 times as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 1.7 times as wide as median length, with maximum width of basin 1.6–1.8 times as wide as median length, and with median length 0.35 times cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction 0.7 times maximum width subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) with clearly impressed meshes, and sculpticells flat and hardly elevated posteriorly (Fig. B4.36); tergum 9 with dorsal surface lateral to median basin smooth and without meshes, and ventral surface with meshes and sculpticells flat and hardly elevated posteriorly. Sheath. Length 0.7-0.9 times length of fore wing, apical section 1.18-1.67 times as long as basal section. Ovipositor. Lancet with 24-30 annuli (annuli in basal half of lancet outlined but difficult to see); junction of basal and apical section of sheath aligned between 5th and 6th or 6th and 7th annuli; apical part of lancet with 8–14 pits. Pits 0.12–0.15 times as long as an annulus, becoming gradually very small, and disappearing in basal 0.5 of apical section of sheath. Edge of last 6-9 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head capsule in ventral third reddish brown or paler at least above mandible to as much as above mandible and clypeus combined, rarely completely black (Fig. B4.50). Scape and pedicel black; flagellum usually pale in basal half, gradually shifting to brown in apical half (Fig. B4.52), occasionally all brown (Fig. B4.53), and rarely completely yellowish. Pronotum light reddish brown at least near anterolateral angle to as much as most of dorsal surface, rarely completely black.

Meso- and metathorax black. Coxae, femora, part of pro- and mesotibia in many specimens, apical 0.25–0.3 of metatibia, and most of metatarsomeres 1–3 black; pro- and mesotibia, pro- and mesotarsus, and metatarsomeres 4 and 5 light reddish brown to reddish brown (Fig. B4.63, hind leg). Fore and hind wings clear and slightly dark tinted in apical half of fore wing. Abdomen with terga 3–6 reddish brown, terga 1, 2, 7 and 8 black, side of terga 3–6 often black, and sterna 2–9 mainly black or brown (Fig. B4.66).

Head. Vertex densely pitted between the white genal spots.

Thorax. Metatibia 5.5–7.0 times as long as maximum width (Fig. B4.44). Metatarsomere 1 in lateral view 4.0–5.2 as long as maximum height (Fig. B4.63).

Taxonomic notes

The types of *S. albicornis* and *S. magus* were not examined, but the descriptions (especially those of the antenna and abdomen) match our concept of this species.

Biological notes

Adults of *U. albicornis* are evidently strong fliers; specimens have been caught in the alpine zone of Mount Washington, NH (Slosson 1895). Damage by larvae was described by Thomas (1881) and Champlain (1922). Females prefer to attack recently killed or weakened trees (Blackman and Stage 1918).

Hosts and phenology

The host range of *U. albicornis* is very wide (T. W. Harris 1841, Thomas 1881, Felt 1906, Blackman and Stage 1918, Essig 1926, Bedard 1938, Reeks and Smith 1945, Belyea 1952, Stillwell 1960, Middlekauff 1960, Morris 1967, Smith, 1979: 128). Based on 131 reared and confirmed specimens, all but one host records are Pinaceae: *Abies amabilis* (1), *A. balsamea* (14), *A. grandis* (1), *A. fraseri, A. lasiocarpa* (1) (Morris 1967), *A. nobilis* (Benson, 1945), *Larix laricina* (18), *L. occidentalis* (11), *Picea* sp. (1), *Picea engelmannii, P. glauca* (33), *P. mariana* (11), *P. sitchensis, Pinus banksiana* (2), *P. contorta* (2), *P. resinosa* (3), *P. strobus* (12), *Pseudotsuga menziesii* (6) (Morris 1967), *Tsuga heterophylla* (14), and *Tsuga canadensis* (Felt 1906). One specimen was

recorded from Thuja plicata (Cupressaceae).

Based on 356 field-collected specimens, the earliest and latest capture dates are June 7 and October 4. The main flight period is from the second half of June to the first half of September with a peak from early July to late August.

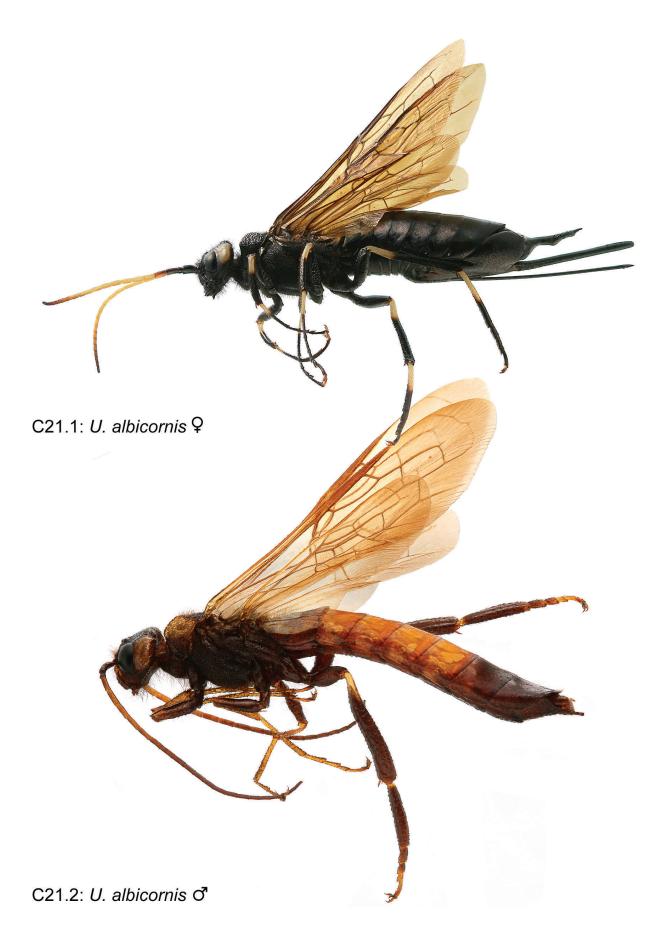
Range

CANADA: AB, BC, MB, NB, NF, NS, ON, PI, QC, SK. **USA:** CA (Middlekauff 1960), DC, GA(?), ID, IL, IN, LA, MA, ME, MI, MO, MT, NC, NJ, NY, OR, PA, RI, VA, VT, WA, WV. *Urocerus albicornis*, a widespread species in forested regions, occurs from southern boreal regions of Canada south to California, New Mexico, Missouri, and North Carolina (Lintner 1898, Blackman and Stage 1918, Rohwer 1928, Smith 1979) (Fig. C21.4). It has been reported as an interception in the United Kingdom (Lintner 1898, Cameron 1890, Benson 1945).

Specimens studied and included for the distribution map: 763 females and 242 males from BYUC, CASS, CFIA, CNC, CUCC, CUIC, DEBU, EDUM, FRLC, GFLC, LECQ, LEMQ, MNRQ, NFRC, NFRN, OSAC, PFRC, USFS–GA, and USNM.

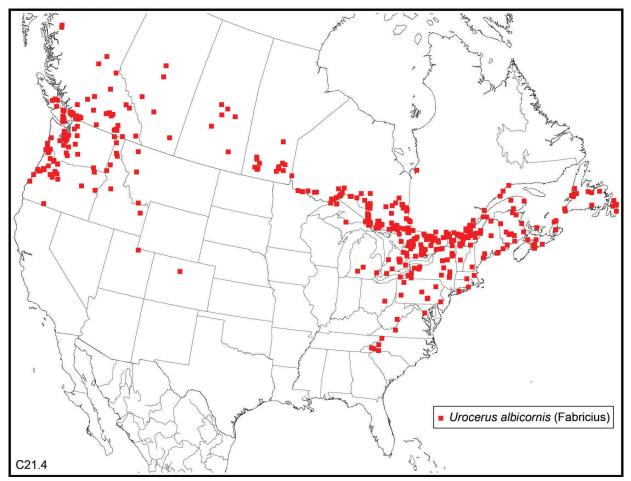
Specimens for molecular studies: 39 specimens. See Fig. E2.4a.

CANADA. British Columbia: 2006, CBHR 451, 658; 2006, CBHR 452, 658; 2006, CBHR 454, 658; 2006, CBHR 455, 658; 2006, CBHR 456, 658; 2006, CBHR 457, 658; 2006, CBHR 458, 658; 2006, CBHR 459, 658; 2006, CBHR 461, 658; 2006, CBHR 463, 658; 2006, CBHR 464, 658; 2006, CBHR 465, 658; 2006, CBHR 467, 658; 2006, CBHR 468, 658; 2006, CBHR 469, 658; 2006, CBHR 470, 658; 2006, CBHR 471, 658; 2006, CBHR 472, 658; 2009, SIRCA 087, 595. Nova Scotia: 2006, CBHR 295, 658; 2006, CBHR 298, 658. Ontario: 2009, CNCS 1072, 608; 2009, CNCS 1073, 591; 2009, SIRCA 029, 616; 2009, SIRCA 030, 614; 2009, SIRCA 031, 615; 2009, SIRCA 032, 619; 2009, SIRCA 033, 615. USA. Minnesota: 2008, CBHR 1372, 658; 2008, CBHR 1463, 658; 2008, CBHR 1472, 658; 2008, CBHR 1473, 658. Montana: 2006, CBHR 327, 658; 2006, CBHR 328, 658; 2006, CBHR 329, 658. New York: 2005, CBHR 199, 658; 2005, CBHR 202, 658. Washington: 2005, CBHR 240, 658; 2005, CBHR 251, 658.





C21.3: U. albicornis o



22. Urocerus californicus Norton

Fig. C22.1, Schiff *et al.* 2006: 64, 65 (female habitus) Fig. C22.2, Schiff *et al.* 2006: 63 (male habitus) Fig. C22.6 (map)

- Urocerus albicornis var. californicus Norton, 1869: 360, Ries 1951: 84, Smith 1979: 128. Norton described a female as this variety of *U. albicornis*, but gives no locality or number of specimens. California is not listed in the distribution of *U. albicornis* and no specimens were located (the name is not mentioned in Cresson 1928: 10, 11). Type locality: perhaps California. There is no evidence that the name was either subspecific or infrasubspecific in the original text. The name, *californicus*, suggests a geographical variant of the species. The description is also clearly diagnostic. Therefore, we consider this name as subspecific and valid.
- *Urocerus fulvus* Cresson, 1880: 35. Lectotype male (ANSP) designated by Cresson 1916, seen by DRS; Cresson, 1916: 10. Synonym by Bradley 1913: 20; accepted by Ries 1951: 84, Smith 1979: 128, Smith 1988: 242. Type locality: Colorado.
- *Sirex flavipennis* Kirby, 1882: 380, pl. XV, fig. 10. Holotype female (BMNH), not examined. Synonym by Bradley 1913: 20; accepted by Ries 1951: 84, Smith 1979: 128, Smith 1988: 242. Type locality: "Vancouver's Island".

Sirex fulvus; Kirby, 1882: 379 (change in combination).

Urocerus californicus; Bradley, 1913: 20 (change in rank); accepted by Ries 1951: 84, Smith 1979: 128, Smith 1988: 242.

Diagnostic combination

Among **females** with a completely or almost completely black abdomen, including cornus [*albicornis*], those of *U. californicus* are recognized by the completely white flagellum and clearly yellow tinted wings. **Males** of *U. californicus* are recognized by the almost completely light reddish brown body and the brown or reddish brown legs.

FEMALE. Description

Color. Head black except for white spot behind eye. Maxillary palp and mandible black. Scape black or brown (rarely as pale as flagellum), and pedicel as pale as flagellum or a little darker; flagellum white or yellowish (Fig. B4.29). Thorax black. Legs black but white on basal 0.25–0.6 of tibiae (usually more on protibia than on metatibia) and on tarsomeres 1. Fore and hind wings clearly yellow tinted (Fig. B4.31). Abdomen black, or a few specimens with a white spot laterally on tergum 8 (as in Fig. B4.19).

Head. Vertex densely pitted between the white genal spots (as in Fig. B4.47).

Thorax. Metatarsomere 2 in lateral view about 4.0 times as long as high (Fig. B4.33), and its tarsal pad about 0.8 as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 1.7 times as wide as median length, with maximum width 1.6-1.8 times as wide as median length, and with median length 0.3–0.4 times as long as cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction 0.7-0.9 times as wide as maximum width subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) smooth and without meshes (except near spiracle); tergum 9 with dorsal surface lateral to median basin smooth and without meshes, ventral surface with meshes, and sculpticells flat and hardly elevated posteriorly. Sheath. Length 0.8-1.0 time length of fore wing; apical section 1.25-1.67 times as long as basal section. Ovipositor. Lancet with 25-32 annuli (annuli in basal 0.5 of lancet outlined but difficult to see (Fig. C22.3)); junction of basal and apical sections of sheath aligned between 5th and 6th or 6th and 7th annuli (Fig. C22.4); apical part of lancet with 13–19 pits. Pits 0.2–0.3 times as long as an annulus, becoming gradually small, and disappearing in basal 0.15-0.4 of apical section of sheath; edge of last 8-12 annuli before teeth annuli extending as ridge to ventral margin of lancet (Fig. C22.5).

MALE. Description

Color. Body mainly light reddish brown (Fig. B4.61 abdomen). Gena from lowest edge of eye to postocellar furrow white (Fig. B4.57). Legs light reddish brown, but brown on coxae, femora, apical 0.7 of mesotibia, metatibia, and most of meso- and metatarsomeres 1–3 (Fig. B4.59, hind leg). Fore and hind wings clearly yellow tinted.

Head. Vertex densely pitted between the white genal spots (Fig. B4.55).

Thorax. Metatibia 4.4–6.2 times as long as maximum width. Metatarsomere 1 in lateral view 4.0–5.0 as long as maximum height (Fig. B4.59).

Taxonomic notes

The types of *Urocerus albicornis* var. *californicus* and *Urocerus flavipennis* were not examined, but their descriptions (especially the fore wing color pattern) match our concept of this species.

The females of this species and U. albicornis are

similarly colored, but both species occur sympatrically in southern British Columbia and nearby Washington, without any intermediate specimens. Adults are easily distinguished as outlined in the diagnostic combination.

Hosts and phenology

The host range of *U. californicus* is very wide (Essig 1926, Bedard 1938, Benson 1945, Middlekauff 1960, Cameron 1965, Morris 1967, Kirk 1975, Smith, 1979: 128). Based on 109 reared and confirmed specimens, all hosts are Pinaceae: *Abies balsamea, A. concolor* (104), *A. lasiocarpa, A. magnifica, A. nobilis, Larix occidentalis, Calocedrus decurrens, Picea engelmanni, P. sitchensis, Pinus sp.* (1), *P. contorta, P. lambertiana, P. monticola, P. ponderosa, Pseudotsuga menziesii* (3), and *Tsuga heterophylla* (Morris 1967).

Based on 25 field-collected specimens, the earliest and latest capture dates are April 30 and early November. The main flight period is from the second half of July to the end of September with a peak in August.

Range

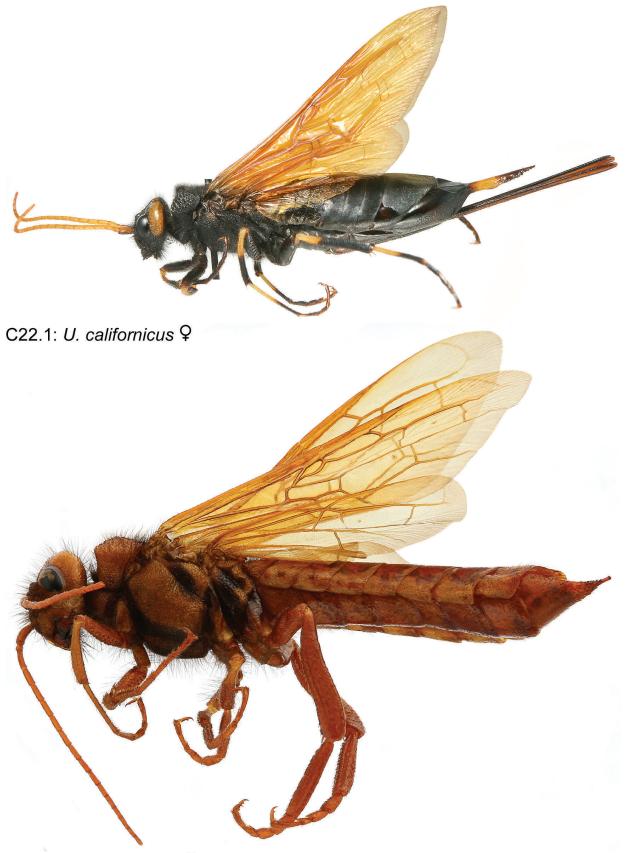
CANADA: BC. **MEXICO:** Hidalgo, Parque Nacional El Chico (specimen not seen; data from correspondence

with R. L. Westcott). **USA:** CA (Middlekauff 1960), CO, ID, MT, NV, OR, UT, WA. *Urocerus californicus*, a western North American species, is recorded from southern British Columbia to northwestern Mexico (Fig. C22.6). Cameron (1883) and Middlekauff (1960) also mention Mexico without a specific locality, in addition to the record above. A few specimens were recorded from lumber in eastern North America (Burks 1967). One intercepted specimen was reported from England (Benson 1945), and one female from Port Angeles, WA, was intercepted in Osaka, Japan (Okutani 1965).

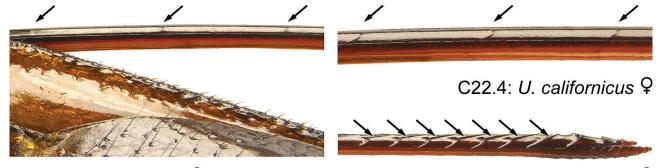
Specimens studied and included for the distribution map: 341 females and 75 males from BYUC, CNC, NCSU, NFRC, OSAC, UAMC, UASM, UCRC, USFS– GA, and USNM.

Specimens for molecular studies: 14 specimens. See Fig. E2.4b.

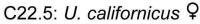
CANADA. British Columbia: 2006, *CBHR 420*, 658. **USA. California**: 2005, *CBHR 97*, 658; 1999, *CBHR 99*, 658; 1999, *CBHR 100*, 658. **Idaho**: 2008, *CBHR 1354*, 493. **Montana**: 2006, *CBHR 371*, 658. **Oregon**: 2003, *CBHR 2*, 658; 2003, *CBHR 10*, 658; 2007, *CNCS 1071*, 649. **Washington**: 2005, *CBHR 212*, 658; 2005, *CBHR 237*, 658; 2005, *CBHR 253*, 573; 2005, *CBHR 257*, 658; 2007, *CNCS 1070*, 596.

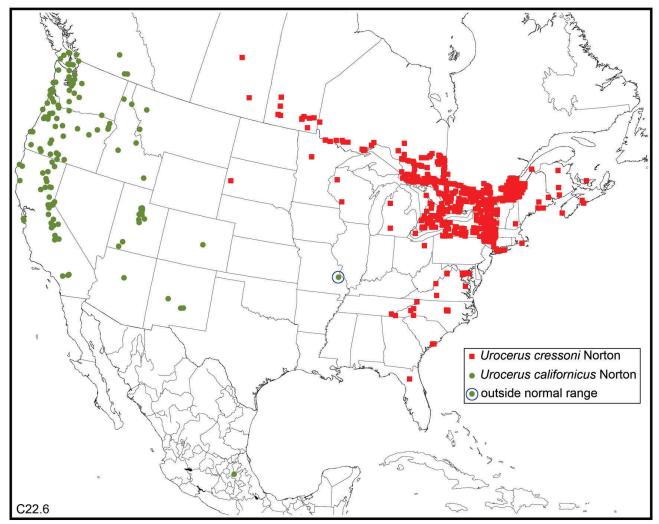


C22.2: U. californicus o



C22.3: U. californicus Q





23. Urocerus cressoni Norton

Fig. C23.1, Schiff *et al.* 2006: 68, 69 (female habitus) Fig. C23.2, Schiff *et al.* 2006: 67 (male habitus) Fig. C22.6 (map)

- *Urocerus Cressoni* Norton, 1864: 16. Holotype female (ANSP), examined by DRS. Cresson 1928: 10, Ries 1951: 84, Marshall 2000 (male photograph). Type locality: "Pennsylvania".
- *Urocerus tricolor* Provancher, 1868: 17. Holotype female (ULQC), examined by DRS (Smith 1975a). Synonymy by Ries 1951: 84; accepted by Smith 1975a: 302, Smith 1979: 128. Type locality: Trois Rivières, QC (Norton, 1869: 362).
- *Sirex dimidiatus* Westwood, 1874: 115, pl. XXI, fig. 5. Holotype female (OXUM), images prepared by James E. Hogan and sent to HG for study. Synonym by Cresson 1880: 67; accepted by Smith 1979: 128. Type locality: "America Septentrionalis".

Sirex tricolor; Kirby, 1882: 382 (change in combination).

- *Sirex Fiskei* Ashmead, 1904: 63. Holotype female (USNM), examined by DRS. Synonymy by Konow, 1905b: 321; accepted by Ries 1951: 84, Smith 1979: 128. Type locality: Tryon, North Carolina.
- *Sirex cressoni* var. *tricolor*; Bradley 1913: 21 (change in rank).
- *Urocerus cressoni* var. *unicolor* Bradley, 1913: 22, fig. 31. Holotype female (ANSP), examined by DRS (Smith, 1975). This name is treated here as infrasubspecific as mentioned clearly by Bradley. Based on the International Code of Zoological nomenclature (1985), article 45(c) stipulates that an infrasubspecific name is excluded from the species group and the provisions of the code do not apply to it. Synonym by Ries 1951: 84; accepted by Smith 1979: 128. Type locality: Joliette, Quebec

Diagnostic combination

Among **both sexes** with the basal 0.3–0.7 of the flagellum black and sharply separated from the white apical section [*taxodii*], **females** are recognized by the reddish brown terga 6–10, and **males** by the black thorax and legs.

FEMALE. Description

Color. Head black except for white spot behind eye (Fig. B1.64). Maxillary palp and mandible black. Scape and pedicel black, flagellum (Fig. B4.16) black in basal 0.3–0.6 (usually flagellomeres 2–10), and white in apical 0.4–0.7 (apex of last flagellomere almost always darkened, rarely completely white or dark brown). Thorax black. Coxae and femora (except apex of profemur in a few

specimens) black. Tibiae and tarsi highly variable in extent of white pattern. **Extreme dark pattern**: pro- and mesotibia, pro- and mesotarsus, apical 0.8 of metatibia and apical 0.9 of metatarsomere 1 black; **extreme pale pattern**: apical half of protibia and mesotarsomeres 3, 4 and apical half of 5, apical 0.2 of mesotibia and apical half of mesotarsomeres 3–5, none of metatibia and none of metatarsus black; **common pattern**: metatibia and metatarsomere 1 black in apical 0.6–0.9, remaining tarsomeres black (Fig. B4.27), mesotibia and mesotarsomere 1 with black more extended than on hind leg, protibia and protarsomere 1 mostly black except at base. Fore and hind wings very darkly tinted with purple reflections. Abdomen reddish brown, or terga 1 up to 1–6 black (tergum 2 usually whitish yellow) (Fig. B4.3).

Head. Vertex densely pitted between the white genal spots (Fig. B4.47).

Thorax. Metatarsomere 2 about 2.0 times as long as high (Fig. B4.27), and its tarsal pad about 0.5 as long as ventral length of tarsomere (Fig. C23.3).

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 2.0 times as wide as median length, with maximum width 2.2-2.5 times as wide as median length, and with median length 0.25-0.30 times as long cornus length (Fig. B1.75). Cornus in dorsal view constricted near base, and minimum width of constriction 0.7–0.8 times maximum width of cornus subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) with clearly impressed meshes, and sculpticells raised and scale-like (thus, surface matt) (Fig. A3.14); tergum 9 with dorsal surface lateral to median basin smooth and without meshes (Fig. B4.25), and ventral surface with meshes, and sculpticells scale-like and slightly elevated posteriorly. Sheath. Length 0.85-0.95 times length of fore wing, apical section 1.18–1.54 times as long as basal section. Ovipositor. Lancet with 26-32 annuli (annuli in basal 0.5 of lancet outlined but difficult to see); junction of basal and apical sections of sheath aligned between 5th and 6th, 6th and 7th, or 7th and 8th ovipositor annuli; apical part of lancet with 17-22 pits. Pits 0.25-0.3 times as long as annulus, becoming gradually small, and disappearing at the base of apical sheath section or on subapex of basal section; edge of last 8-10 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head capsule (except white genal spot, and in many specimens reddish brown surface of capsule below eye often including clypeus) black. Scape and pedicel black; flagellum black in basal 0.3–0.6 and white in apical 0.4–0.7 except for darkened last flagellomere (Fig.

B4.37). Gena from middle of eye almost to postocellar furrow white. Fore and hind wings very darkly tinted. Thorax and legs (apical articles maybe reddish brown in some specimens) black (Figs. B4.45 & B4.47). Abdomen mostly light reddish brown (Fig. B4.41), the following black or brown: tergum 1, tergum 1 and 2, side of terga 3–7, posterior margin of terga 3–6, median area of tergum 8, sterna 1 to 1–6.

Head. Vertex densely pitted between the white genal spots (Fig. B4.47).

Thorax. Metatibia 5.0–6.5 times as long as maximum width. Metatarsomere 1 in lateral view 4.0–5.0 as long as maximum height (Fig. B4.45).

Taxonomic notes

Many of the above synonyms are due to great color variation in females. However, when numerous females are available from the same region and even the same locality the leg and abdominal color variation is great. No geographical pattern is associated with this color variation.

Hosts and phenology

The host range of *U. cressoni* is rather wide (Craighead 1950, Smith, 1979: 128). All published host records are Pinaceae, and only 2 reared and confirmed specimens were examined: *Abies balsamea*, *A. fraseri*, *Larix occidentalis* (2), *Picea sitchensis, Pinus contorta*, *P. rigida*, *P. taeda*, *P. virginiana*, and *Pseudotsuga*

menziesii.

Based on 846 field-collected specimens, the earliest and latest capture dates are June 26 and September 27. The main flight period is from the second half of July to the first half of September, with a peak in August.

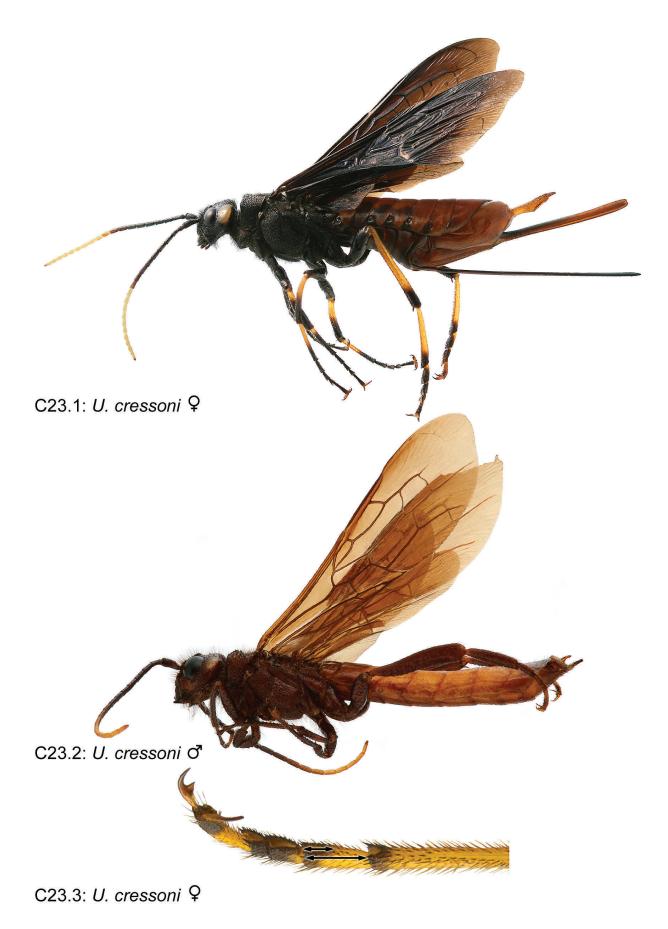
Range

CANADA: MB, NS, NB, ON, PI, QU, SK. **USA:** CO, CT, DC, FL, GA, IA, IN, MA, MD, MN, NC, NE, NJ, NY, OH, PA, SC, TN, VA, WV, WI. *Urocerus cressoni*, an eastern species, is known from southern Saskatchewan to Nova Scotia, and south to Florida (Lintner 1898, Rohwer 1928, Craighead 1950, Burks 1958, Burks 1967, Smith 1979) (Fig. C22.6).

Specimens studied and included for the distribution map: 1493 females and 44 males from BYUC, CNC, CUCC, CUIC, DEBU, EDUM, FRLC, GLFC. LECQ, LEMQ, MNRQ, NCSU, NFRC, UCRC, USFS–GA, and USNM.

Specimens for molecular studies: 12 specimens. See Fig. E2.4b.

CANADA. Nova Scotia: 2006, *CBHR 299*, 658. **Ontario**: 2007, *SIRCA 034*, 639; 2007, *SIRCA 038*, 639. **USA. Colorado**: 2005, *CBHR 192*, 658; 2005, *CBHR 559*, 658. **Georgia**: 200, *CBHR 517*, 658. **Illinois**: 2006, *CBHR 169*, 658. **Indiana**: 2005, *CBHR 176*, 658. **New York**: 2005, *CBHR 196*, 658; 2005, *CBHR 200*, 658; 2005, *CBHR 204*, 658. **South Carolina**: 2006, *CBHR 893*, 658.



24. Urocerus flavicornis (Fabricius), n. stat.

Fig. C24.1, Schiff *et al.* 2006: 72, 73 (female habitus) Fig. C24.2, Schiff *et al.* 2006: 71 (male habitus) Fig. C24.3 (map)

- *Sirex flauicornis* [recte: *flavicornis*] Fabricius, 1781: 418. Type female (HMUG), not examined. The spelling *flavicornis*, introduced by Gmelin (1790), is in prevailing use. Type locality: "Labrador Americae". *Sirex bizonatus* Stephens, 1829: 342 (nomen nudum).
- *Sirex bizonatus* Stephens 1835: 114, pl. 36, fig. 2. Holotype female (BMNH), not examined. Synonymy by Cresson 1865b: 247; accepted by Smith 1979: 128, Harrington 1882a. Type locality: "near London".
- *Urocerus riparius* MacGillivray, 1893: 244. Lectotype male (INHS, Webb 1980), designated by Frison (1927), not examined. Synonymy by Bradley 1913: 18; accepted by Smith 1979: 128. Type locality: Skokomish River, Washington. Described from "2 males."
- *Urocerus flavicornis*; Bradley 1913: 18 (change in combination); Fitch 1858a: 45, under *U. abdominalis*; Burks 1958: 16.
- Sirex latifasciatus Konow, 1898: 77 (not Westwood, 1874: 114, pl. XXI, fig. 2).
- Urocerus gigas flavicornis, Benson, 1943: 39 (change in rank); accepted by Middlekauff 1960, Smith 1979: 128.

Diagnostic combination

Among **females** with light reddish brown protarsomeres 2–5 [*gigas* and *sah*], those of *U. flavicornis* are recognized by the black pronotum and tergum 9. **Males** are recognized by a black head and pronotum, black abdominal segments 7–9, and, in North American specimens, by the narrow metatarsomere 1 (5.5–8.0 times as long as high).

FEMALE. Description

Color. Head black except for white spot behind eye, spot extending from ventral edge of eye almost to postocellar furrow (Fig. B4.12). Maxillary palp and mandible black. Scape, pedicel, and flagellum light reddish brown, and apex of last flagellomere not darkened. Thorax black (Fig. B4.8). Coxae, basal 0.5–0.7 of pro- (Fig. B4.4) and mesofemur, and metafemur (except extreme apex) (Fig. B4.10) black; tibiae and tarsi light reddish brown (in most specimens, metatibia with brown cloud in apical 0.3 on inner surface) (Fig. B4.10). Fore and hind wings basically clear. Abdomen black, but light reddish brown on terga 1 (some specimens), 2, 7, 8 (basal half of almost all specimens) and 10 (cornus only) (Fig. B4.1).

Head. Vertex densely pitted between the white genal spots. Surface below genal white spot widely pitted.

Thorax. Metatarsomere 2 in lateral view about 2.0 times as long as high, and its tarsal pad about 0.8 as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) about 1.6 times as wide as median length, with maximum width about 1.7 times as wide as median length, and with median length about 0.4 times as long as cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction about 0.8 times maximum width subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) with clearly impressed meshes, and sculpticells flat; tergum 9 with dorsal surface lateral to median basin smooth and without meshes, and ventral surface with meshes and flat sculpticells. Sheath. Length 0.7-0.9 times length of fore wing; apical section 1.1-1.5 times as long as basal section. Ovipositor. Lancet with 24-32 annuli (annuli in basal 0.5 of lancet outlined but difficult to see); junction of basal and apical sections of sheaths aligned between 5th and 6th, or 6th and 7th annuli; apical part of lancet with 14-20 pits. Pits 0.2-0.3 as long as an annulus, becoming gradually small, and disappearing at base of apical sheath section. Edge of last 7-9 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head capsule black, except for white spot behind eye extending from ventral edge of eye almost to postocellar furrow. Flagellum black or brown to light reddish brown in basal half. Thorax black. Legs black but pro- and mesotarsus, and pro- and mesotibia (brown dorsally in a few specimens) reddish brown; basal 0.25 of metatibia and basal 0.25 and extreme apex of metatarsomeres 1 light reddish brown (Figs. B4.64 & B4.62 hind leg). Fore and hind wings clear. Abdomen black, but light reddish brown on most of terga 3–6. **Head.** Vertex densely pitted between the white genal spots. Surface below genal white spot widely pitted. **Thorax.** Metatibia 6.8–9.0 times as long as maximum width (Fig. 4.64). Metatarsomere 1 in lateral view 5.5–8.0 times as long as maximum height (Fig. B4.62).

Taxonomic notes

The types of *S. flavicornis*, *S. bizonatus* and *U. riparius* were not examined, but the descriptions match our concept of *U. flavicornis*.

Urocerus flavicornis has long been regarded as a subspecies of *U. gigas*. We have seen specimens of *U. gigas* from Kamchatka and Alaska. They show no evidence of gene flow. Moreover, the information from

morphology and DNA barcoding shows a clear difference between the two populations. Therefore, we consider them specifically distinct.

Females are easily distinguished from other species of *Urocerus* in the Western Hemisphere but males have been commonly mixed in collections with those of *U. albicornis* despite a paper by Peck (1937) distinguishing them by the proportion of the length and height of metatarsomere 2. Males of *U. flavicornis* are quite similar to those of *U. gigas*, but are distinguished on color pattern and, for most specimens, by the proportions of metatarsomere 1 and metatibia.

Biological notes

Males of *U. flavicornis* have been observed aggregating at the highest spot of a mountain top where they wait to intercept females (Chapman 1954).

Hosts and phenology

The host range of *U. flavicornis* is wide (Felt 1906 [under *U. abdominalis*], Essig 1926, Burks 1958: 16, Middlekauff 1960, Cameron 1965, Morris 1967, Kirk 1975, Smith, 1979: 128). Based on 51 reared and confirmed specimens, all but one host are Pinaceae: *Abies concolor* (13), *A. lasiocarpa* (4), *Larix occidentalis* (2), *Picea engelmannii* (3), *P. glauca* (19), *P. sitchensis, P.* sp. (1), *Pinus banksiana* (3), *P. contorta* (1), *P. strobus* (4), and *Pseudotsuga menziesii*. One specimen has been reared from *Thuja occidentalis* (Cupressaceae).

Based on 338 field-collected specimens, the earliest and latest capture dates are June 25 and November 17. The main flight period is from early June to the first half of September with a peak in the second half of July and the first half of August. Twenty-seven males were caught at hill top in Montana from late June till early September (Chapman 1954).

Range

CANADA: AB, BC, MB, ON, PI, NB, NF, NS, NT, NU, QC, SK, YT. **MEXICO.** Uncertain record mentioned by Cameron (1883) without a specific locality. **USA:** AK, CA (Middlekauff 1960), ID, CO, ME, MT, NH, NY, OR, PA, UT, WA, WY.

Urocerus flavicornis is known from all forested regions of Canada and the United States (Harrington 1882a, Rohwer 1928, Weber 1950, Burks 1958: 16, Cameron 1965, Smith 1979) (Fig. C24.3). It was recorded as an interception in Réunion Island (Bordage 1914) and England (Cameron 1890, Benson 1943).

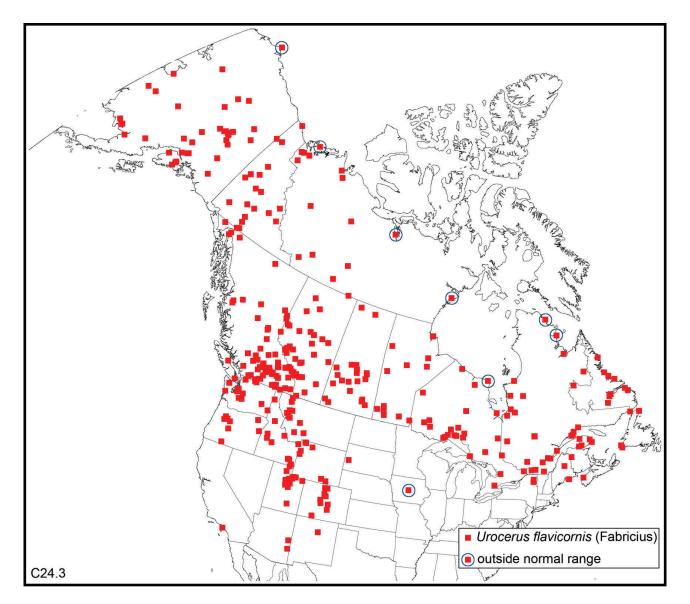
Specimens studied and included for the distribution map: 914 females 122 males from BYUC, CASS, CNC, DEBU, EDUM, GFLC, LECQ, LEMQ, MNRQ, NCSU, NFRC, OSAC, PFRC, UAM, UASM, UCRC, USBD, USFS–AK, and USNM.

Specimens for molecular studies: 32 specimens. See Fig. E2.4c.

CANADA. Ontario: 2007, *SIRCA 039*, 620; 2007, *SIRCA 040*, 619.

USA. Alaska: 2005, *CBHR 231*, 658. Colorado: 2005, *CBHR 560*, 658; 2005, *CBHR 561*, 658; 2005, *CBHR 562*, 658; 2005, *CBHR 563*, 658; 2005, *CBHR 565*, 658; 2005, *CBHR 566*, 658; 2005, *CBHR 567*, 658; 2005, *CBHR 568*, 658; 2005, *CBHR 569*, 658. Montana: 2006, *CBHR 324*, 658; 2006, *CBHR 325*, 658; 2006, *CBHR 326*, 658; 2006, *CBHR 332*, 658; 2006, *CBHR 333*, 658; 2006, *CBHR 335*, 658; 2006, *CBHR 336*, 658; 2006, *CBHR 337*, 658; 2006, *CBHR 338*, 658. Oregon: 1999, *CBHR 12*, 658; 1999, *CBHR 107*, 658. Utah: 2008, *CBHR 1950*, 658: 1999, *CBHR 107*, 658. Utah: 2008, *CBHR 1950*, 658; 2005, *CBHR 234*, 658; 2005, *CBHR 234*, 658; 2005, *CBHR 234*, 658; 2005, *CBHR 234*, 658; 2005, *CBHR 250*, 658.





25. Urocerus gigas (Linnaeus)

Fig. C25.1 (female habitus) Fig. C25.2 (male habitus)

- *Ichneumon gigas* Linnaeus, 1758: 418. Holotype female (LSUK) images of type seen by HG. Thomson 1871: 328, Malaise and Benson, 1934: 12. Type locality: "Suecia".
- Sirex marisca Linnaeus, 1758: 560. Taeger et al. 2010.
- Sirex hungaricus Christ, 1791: 414–415. Taeger et al. 2010.
- Sirex psyllius Fabricius, 1793: 124–125. Taeger et al. 2010.
- Urocerus Lefebvre Guérin, 1833: 68. Taeger et al. 2010.
- Sirex Faustus Costa, 1894: 258. Taeger et al. 2010.
- Urocerus gigas taiganus Benson, 1943: 39-41. Taeger et al. 2010.
- Urocerus gigas var. luteigaster Berland, 1947: 77. Taeger

et al. 2010.

Sirex gigas var. montana Ermolenko, 1957: 85.
Sirex gigas var. montanus Ermolenko, 1957: 6, not available. Nomen nudum. Taeger et al. 2010.

Diagnostic combination

Among **females** with light reddish brown protarsomeres 2-5 [*flavicornis* and *sah*], those of *U. gigas* are recognized by the black pronotum and light reddish brown tergum 9. **Males** of *U. gigas* are recognized by the black head, the reddish brown terga 2-8 or 3-8 (rarely 3-7) and usually the less narrow metatarsomere 1 (4.5–6.3 times as long as high).

FEMALE. Description

Color. Head black except for white spot behind eye extending from ventral edge of eye almost to postocellar furrow. Maxillary palp and mandible black. Scape, pedicel, and flagellum light reddish brown, and apex of last flagellomere not darkened. Thorax black. Coxae, basal 0.5–0.7 of pro- and mesofemur, and metafemur (except extreme apex) black; tibiae and tarsi light reddish brown. Fore and hind wings lightly yellow tinted. Abdomen black, but terga 1 (at least apical half), 2, 7, 8–10 (except side in most specimens) light reddish brown (Fig. B4.14).

Head. Vertex densely pitted between the white genal spots. Surface below white genal spot narrowly pitted.

Thorax. Metatarsomere 2 in lateral view about 2.0 times as long as high, and its tarsal pad about 0.8 as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) about 1.7 times as wide as median length, with maximum width about 1.8 times as wide as median length, and with median length about 0.4 times as long as cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction about 0.8 times maximum width subapically. Microsculpture of sublateral surface of tergum 8 (between spiracle and pitted sculpticells on central area) with meshes outlined and sculpticells flat; tergum 9 with dorsal surface lateral to median basin smooth and without meshes, and ventral surface with meshes and flat sculpticells. Sheath. Length 0.85-0.95 times length of fore wing; apical section 1.31–1.48 times as long as basal section. Ovipositor. Lancet with 24-32 annuli (annuli in basal 0.5 of lancet outlined but difficult to see); junction of basal and apical sections of sheath aligned between 6th and 7th annuli; apical part of lancet with 14-22 pits. Pits 0.2–0.3 times as long as an annulus, becoming gradually small, and disappearing at base of apical sheath section. Edge of last 8–11 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head capsule black (below antennal sockets with one or more light reddish brown spots in a few specimens), except white genal spot behind eye extending from ventral edge of eye almost to postocellar furrow. Flagellum mostly white or light reddish brown, rarely darkened in apical 0.25. Thorax black. Legs black, but light reddish brown on pro- and mesotibia, white in basal 0.3 of metatibia, and reddish brown in basal 0.15 and on apex of metatarsomeres 1 (Fig. B4.69 hind leg). Wings clear. Abdomen black except light reddish brown on most of terga 2–8, or rarely on terga 3–8 or 3–7 (Fig. B4.67). **Head.** Vertex densely pitted between the white genal

spots. Surface ventral to genal white spot narrowly pitted. **Thorax.** Metatibia 5.7–8.5 times as long as maximum width. Metatarsomere 1 in lateral view 4.5–6.3 times as long as maximum height (Fig. B4.69).

Taxonomic notes

Females of *U. gigas* are distinguished from *U. flavicornis* females by abdominal color pattern. Males are very similar but are distinguished on abdominal color pattern and, in most specimens, on proportions of metatarsomere 1 and metatibia.

Biological notes

The life cycle extends over three or more years. The biology was treated by Hanson (1939).

Hosts and phenology

The host range of *U. gigas* is wide (Allard, 2008). All but one hosts are Pinaceae: *Abies sp., A. alba, Cedrus* sp., *Larix* sp., *Picea* sp., *P. abies, P. sitchensis, Pinus* sp., *P. radiata, P. sylvestris*, and *Pseudotsuga menziesii*. One specimen was recorded from *Chamaecyparis* (Cupressaceae).

Based on 7 field-collected specimens from the southern Hemisphere, the earliest and latest capture dates are October 31 to May 18, with peak flight in November and December.

Range

ARGENTINA: first discovered in the provinces of Chubut, Rio Negro and Neuquén in 1993 (Klasmer, 2002, Allard, 2008). **BRAZIL**: Matto Grosso, Itumana River (an earlier record in 1880 (Ries, 1946: 218)). **CHILE**: Arauco (Contulmo, Pino), Temuco (Tronco), Bio-Bio, Italia, Malleco (Angel, Conguillio Nat. Park), Mulchen (Caledonia), and Nuble. First found after 1970 in North American conifer plantations (Allard, 2008). *Urocerus gigas* is an adventive species in temperate regions of South America. The species was commonly intercepted at United States ports and even in central Alberta. It was also often intercepted in New Zealand (FRNZ, NZAC and PANZ).

Specimens studied and included for the distribution map: 18 females and 11 males from AEI, AMNH, ANSP, CNC, NFRC, and USNM.

Specimens for molecular studies: 18 specimens. See Fig. E2.4c.

ARGENTINA: 2004, *CBHR 51*, 658. **FINLAND**: 2005, *CBHR 840*, 658; 2005, *CBHR 841*, 658; 2005, *CBHR 842*, 658; 2005, *CBHR 843*, 658; 2005, *CBHR 844*, *CB*

844, 658; 2005, CBHR 845, 658; 2005, CBHR 846, 658; 2005, CBHR 847, 658; 2005, CBHR 847, 658; 2005, CBHR 848, 658; 2005, CBHR 849, 658; 2006, CBHR 851, 658; 2006, CBHR 853, 658; 2006, CBHR 856, 658; 2006, CBHR 857, 658; 2006, CBHR 860, 658; 2006, CBHR 861, 658; 2006,

CBHR 865, 658; 2006, *CBHR 866*, 658; 2006, *CBHR 870*, 658; 2006, *CBHR 871*, 658; 2006, *CBHR 872*, 658. **FRANCE**: 1973, *CBHR 158*, 658. **GREECE**: *CBHR 581*, year unknown, 658.



26. Urocerus sah (Mocsáry)

Fig. C26.1, Schiff *et al.* 2006: 75, 76 (female habitus) Fig. C26.2 (male habitus) Fig. C26.3 (map)

Sirex Sah Mocsáry, 1881: 36. Holotype female (HNHM), not examined. Type locality: "Persia".

Sirex Shach; Mocsáry, 1881 (misspelling).

Urocerus augur sah; Benson, 1943: 41 (change in combination and rank).

Urocerus sah; Smith 1978: 81 (change in combination).

Diagnostic combination

Both sexes of *U. sah* are recognized by very few pits on the vertex (without pits except narrowly behind edge of eye, and along postocellar and median furrows). **Females** also have light reddish brown protarsomeres 2–5, a reddish brown pronotum, and a light reddish brown apical 0.5 of tergum 9. **Males** also have a large genal spot extending from the ventral margin of eye to the postocellar furrow.

FEMALE. Description

Color. Head capsule almost completely reddish brown except for white spot behind eye extending from ventral edge of eye almost to median furrow of postocellar surface (Fig. B4.13). Maxillary palp and mandible brown or black. Scape and pedicel more or less brown; flagellum light reddish brown and apex of last flagellomere not darkened. Thorax black or brown, but reddish brown on most of dorsal surface of pronotum (Fig. B4.9) and dorsal half of mesepisternum. Coxae black; profemur reddish brown on posterior surface, mesofemur brown at base and gradually shifting to light reddish brown toward apex; and metafemur almost completely black except at extreme apex (Fig. B4.11, hind leg); pro- and mesotibia and tarsi light reddish brown; metatibia in apical 0.7 black and light yellow in basal 0.3 (Fig. B4.11, hind leg); metatarsomere 1 light reddish brown in basal 0.5 and brown in apical 0.5, otherwise tarsomeres 1-5 reddish brown. Fore and hind wings clearly yellow tinted. Abdomen black, but light reddish brown on terga 1, 2 (at least basal 0.5), 8 (basal 0.5), 9 (apical 0.5 dorsally), and 10 (including cornus) (Fig. B4.7).

Head. Vertex not pitted except narrowly behind eye and along postocellar and median furrows, but densely pitted (diameter of pits about 0.2 times that of ocelli) on frons to posterior ocelli (Fig. B4.13).

Thorax. Metatarsomere 2 in lateral view about 2.0 times as long as high, and its tarsal pad about 0.8 as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 with base (outlined

an basin of tergum 9 with t

by two lateral black longitudinal furrows) about 1.7 times as wide as median length, with maximum width about 1.9 times as wide as median length, and with median length about 0.4 times cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction about 0.75 times maximum width subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) with meshes and sculpticells flat; tergum 9 with dorsal surface lateral to median basin smooth and without meshes, and ventral surface with meshes and flat sculpticells. Sheath. Length as long as fore wing length, apical section about 1.5 times as long as basal section. Ovipositor. Lancet with about 34 annuli (annuli in basal 0.5 of lancet outlined but difficult to see); junction of basal and apical section of sheath aligned between 6th and 7th annuli; lancet with about 30 pits. Pits 0.2-0.3 times as long as an annulus, becoming gradually small, and disappearing at base of basal sheath section (lacking on annuli 2-4). Edge of about last 11 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head capsule black, except white genal spot extending from about ventral edge of eye to postocellar furrow (Figs. B4.54 & B4.56). Flagellum black to light reddish brown (usually paler in basal half). Thorax black except for small pale spot at anterodorsal angle. Coxae black; profemur reddish brown on posterior surface, mesofemur brown at base and gradually shifting to light reddish brown toward apex; and metafemur mainly black except in apical 0.25 (Fig. B4.58, hind leg); pro- and mesotibia and tarsi light reddish brown; metatibia and metatarsomere 1 brown or black and narrowly reddish brown (Fig. B4.58, hind leg). Abdomen light reddish brown (Fig. B4.58, hind leg). Abdomen light reddish brown except black on terga 1 (partly or completely), 6–8 or 7 and 8, sterna 2, 6–9 or 7–9 (Fig. B4.60).

Head. Vertex not pitted except narrowly behind edge of eye, and along postocellar and median furrows (Fig. B4.54). Surface ventral to genal white spot scarcely pitted (Fig. B4.56).

Thorax. Metatibia about 6.0 times as long as maximum width. Metatarsomere 1 in lateral view about 5.0 times as long as maximum height (Fig. B4.58).

Taxonomic notes

Smith (1987) was the first to recognize this adventive species, known from North Africa, Asia Minor, and as far east as Afghanistan. The species as been treated as *U. augur sah*. More recently, this subspecies has been regarded as specifically distinct from *U. augur*. Smith

(1978) accepted this, especially because *U. sah* and *U. augur* are sympatric, at least in Asia Minor. Two subspecies cannot be sympatric, therefore, *U. augur* and *U. sah* are specifically distinct.

Biological notes

Over the years males of U. sah were observed aggregating at the highest spot of Mount Rigaud, Quebec (about 220 m above the plain). On June 15, 2011, 200 to 300 specimens were observed. Although no female were captured, we assume that both sexes mate there.

Hosts and phenology

Urocerus sah was reared from Pinaceae (Abies sp.,

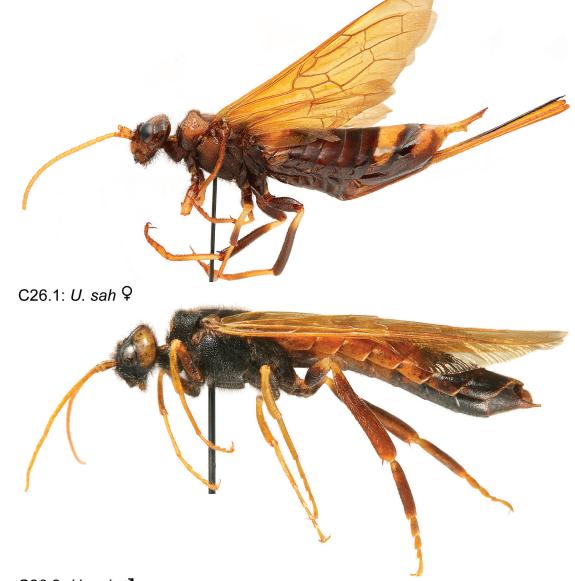
Picea sp., and *Pinus* sp.). No specimens have been reared in North America.

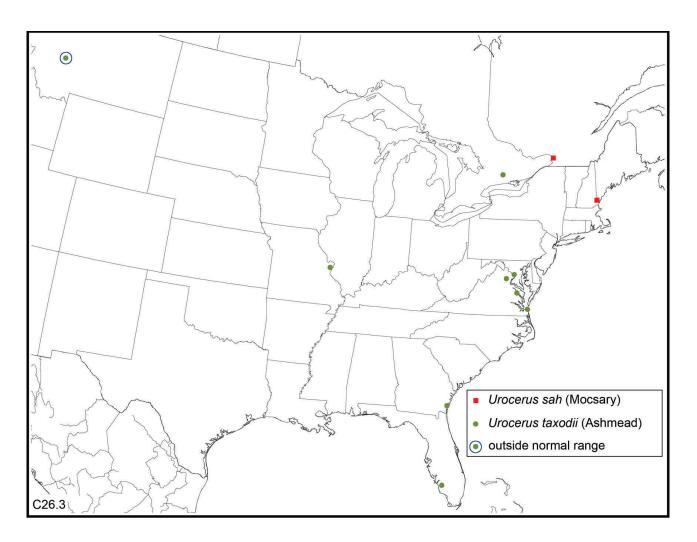
Based on 15 field-collected specimens, the capture dates are June 15, June 22, July 11, August 22 and September 7.

Range

CANADA: QC (Rigaud). **USA:** NH (Smith 1987: Rocking Co, Newmarket 1 female; Durham). *Urocerus sah*, an adventive species, is known from very few localities in eastern North America (Fig. C26.3).

Specimens studied and included for the distribution map: 3 females and 15 males from CNC, DENH, and USNM.





27. Urocerus taxodii (Ashmead)

Fig. C27.1, Schiff *et al.* 2006: 78, 79 (female habitus) Fig. C27.2, Schiff *et al.* 2006: 77 (male habitus) Fig. C26.3 (map)

- *Sirex taxodii* Ashmead, 1904: 63. Lectotype female (USNM), here designated and examined by DRS, and labeled "1611b Hopk. U.S.", "Fiske Colr., Brunswick, GA.", "Taxodium distichum", "female Type No. 7681, U.S.N.M.", "Sirex taxodii Ashm [handwritten]".
- Paralectotypes: 1 female and 1 male. All three types are from "Brunswick, Ga.", not Tryon, N.C. as mistakenly stated by Ashmead. The rest of the label data was correctly given by Ashmead: "No. 1611; bred by Mr. W. F. Fiske from the Cypress (Taxodium distichum, L).". We have no specimens of *U. taxodii* from Tryon, though other species mentioned in Ashmead's paper are from Tryon, N.C. Type locality: Brunswick, Ga.
- *Urocerus taxodii*; Bradley, 1913: 17, 20 (change in combination); accepted by Burks 1958: 17; Smith 1979: 129.

Diagnostic combination

Among adults of *U. taxodii* with the basal 0.3–0.7 of the flagellum black and sharply separated from the white apical section [*cressoni*], **females** are recognized by the black abdominal segments 1–9 and a light reddish brown cornus, and **males** by the metatibia with white in basal 0.25, and reddish brown pro- and mesotibia and pro- and mesotarsus.

FEMALE. Description

Color. Head black except for white spot behind eye. Maxillary palp and mandible black. Scape, pedicel, and flagellum (basal 0.3–0.6) black; flagellum white in apical 0.4–0.7, and apex of last flagellomere clearly darkened. Thorax black. Legs black but white basal 0.25 of metatibia and metatarsomere 1. Fore and hind wings very darkly tinted. Abdomen black, but light reddish brown in apical 0.7 of cornus (Fig. B4.24).

Head. Vertex densely pitted median to the white genal spots.

Thorax. Metatarsomere 2 in lateral view about 3.0 times

as long as high (Fig. B4.28), and with tarsal pad about 0.7 as long as ventral length of tarsomere (Fig. C27.3).

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 2.0 times as wide as median length, with maximum width about 2.2 times as wide as median length, and with median length about 0.25 times cornus length. Cornus in dorsal view constricted near base, and minimum width of constriction 0.6-0.9 times maximum width subapically. Tergum 8 with microsculpture of sublateral surface (between spiracle and pitted sculpticells on central area) with meshes, and sculpticells raised and scale-like (thus, surface matt); tergum 9 with dorsal surface lateral to median basin with meshes and scale-like sculpticells, smooth and without meshes near anterior portion of median basin (Fig. B4.26), and ventral surface with meshes and scale-like and slightly elevated sculpticells. Sheath. Length 0.87-1.0 time length of fore wing, apical section 1.25-2.0 times as long as basal section. Ovipositor. Lancet with 24-29 annuli (annuli in basal 0.5 of lancet outlined but difficult to see); junction of basal and apical section of sheath aligned between 4th and 5th annuli; apical part of lancet with 9-10 pits. Pits 0.05-0.1 times as long as an annulus, becoming gradually small, and disappearing in basal 0.4 of apical sheath section. Edge of last 6-8 annuli before teeth annuli extending as ridge to ventral margin of lancet.

MALE. Description

Color. Head black except for white genal spot extending from level of lower eye margin to top of eye, and light reddish brown in ventral third (Fig. B4.48). Scape, pedicel, and flagellum (basal 0.3–0.6) black; flagellum white in apical 0.4–0.7, and apex of last flagellomere clearly darkened. Thorax mainly black but reddish brown over most of dorsal surface of pronotum (Fig. B4.48), mesoscutellum and metanotum. Legs black but reddish brown on pro- and mesotibia, pro and mesotarsus, and

metatarsomeres 3–5; light reddish brown basal 0.25 of metatibia and metatarsomere 1 (Fig. B4.46 hind leg). Fore and hind wings darkly tinted. Abdomen light reddish brown.

Head. Vertex densely pitted medial to the white genal spots.

Thorax. Metatibia 4.7 times as long as maximum width. Metatarsomere 1 in lateral view 5.6 as long as maximum width (Fig. B4.46).

Host and phenology

Based on published records and 2 reared and confirmed specimens studied, *Urocerus taxodii* has been reared from *Taxodium distichum*, (Cupressaceae) (Bradley 1913, Cameron 1965, Smith, 1979: 129). The Ontario and Virginia specimens suggest that *Juniperus virginiana*, the only unusual Cupressaceae in the area, might also be a host.

Based on 7 field-collected specimens, the earliest and latest capture dates are from late May to late September.

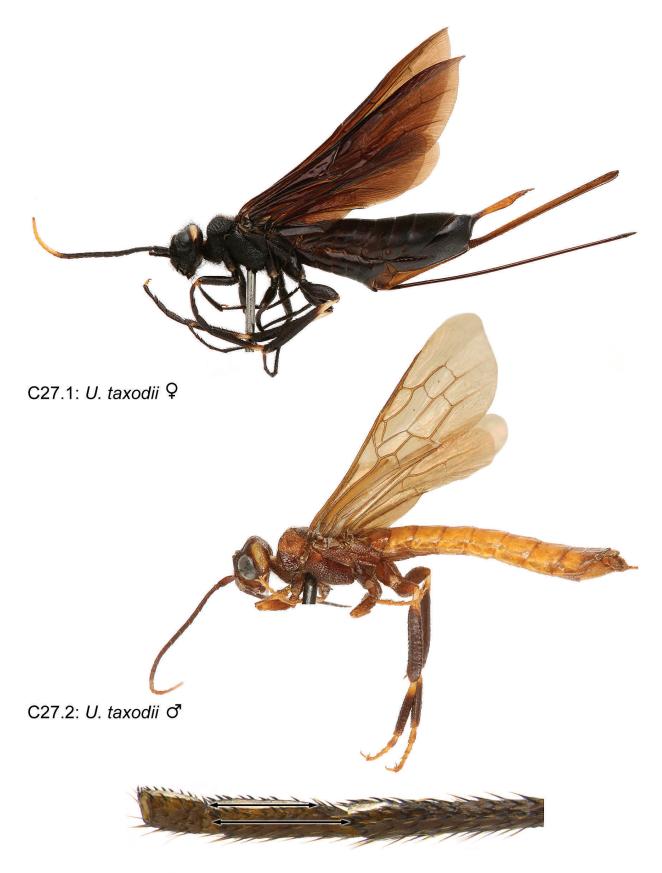
Range

CANADA: ON. **USA:** DC, FL, GA, MO, MT (mislabeled or associated with lumber from southeastern United States), NY (Rohwer 1928), VA. *Urocerus taxodii* is basically in southeastern United States, but the Ontario and Virginia records suggest an eastern North American range (Fig. C26.3).

Specimens studied and included for the distribution map: 12 females and 1 male from CNC, FSCA, and USNM.

Specimens for molecular studies: 5 specimens. See Fig. E2.4a.

USA. Mississippi: 2006, *CBHR 31*, 658; 2003, *CBHR 141*, 658; 2002, *CBHR 142*, 658; 2002, *CBHR 143*, 658; 2002, *CBHR 144*, 658.



C27.3: U. taxodii Q



C28.1: X. matsumurae Q

28. Genus Xoanon Semenov

Fig. C28.1 (female dorsal habitus) Fig. C28.2 (female lateral habitus) Fig. C28.3 (male dorsal habitus)

Xoanon Semenov, 1921: 87. Type species: *Xoanon mysta* Semenov, by original designation. Smith 1978: 89.

Description

Color. Dark body sections dark brown and without metallic reflections, and head mainly light reddish brown. **Head.** Minimum distance between inner edges of eyes 1.3 times as long as maximum eye height (Fig. C28.4, black arrows), distance between inner edges of antennal sockets about 2.0 times the distance between inner edge of eye and outer edge of socket (Fig. C28.4, white arrows). Distance between inner edges of lateral ocelli 0.7 times as long as distance between outer edge of lateral ocellus

and nearest edge of eye (Fig. C28.5). Head with setae sharp at apex. Gena rounded behind eye, without ridge, and densely pitted (Fig. C28.6). Antenna with 13–15 flagellomeres, the flagellomeres round or almost round in cross section, and middle flagellomeres about 3.0 times as long as high.

Thorax. Metatibia with two apical spurs. Fore wing angularly rounded at apex, with vein 2r–m joined to cell 3M, with cell 1Rs2 long (2r–m and 3r–m slightly or very clearly shorter than veins Rs2 and M above and below), with cell 3R1 3.5 times as wide as long, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even after junction with vein 2r-rs (Fig. B1.70), with vein 1cu–a joining vein Cu about mid way between veins 1m–cu and M, without vein Cu1, with vein 2A extending near posterior edge of fore wing for 0.3 times cell length (Fig. C28.7), and with vein 3A stump-like (Fig. C28.7). Hind wing with hamuli present mainly apically and basally (length of basal hamuli section 0.4–

1.0 times as long as apical section) from junction of veins R1 and C (as in Fig. B1.11 and Fig. C28.8), and with cell 1A closed.

Abdomen. Female. Tergum 9 with median basin about as long as wide and convex, without setae and pits, and sharply outlined anteriorly with short and slightly divergent ridges. Cornus about 1.7 times as long as median basin length, very narrow, and clearly constricted at middle (Fig. B1.74); cercus present and disc-like. *Sheath.* Basal section about 0.45 times as long as apical section, and length about 0.9 times as long as fore wing length.; teeth on dorsal surface of apical section present in apical 0.25, and each tooth with a small sharp apical spine (Fig. C28.10).

Male. Terga 1–8 and sterna 2–9 densely pubescent (Fig. C28.9).

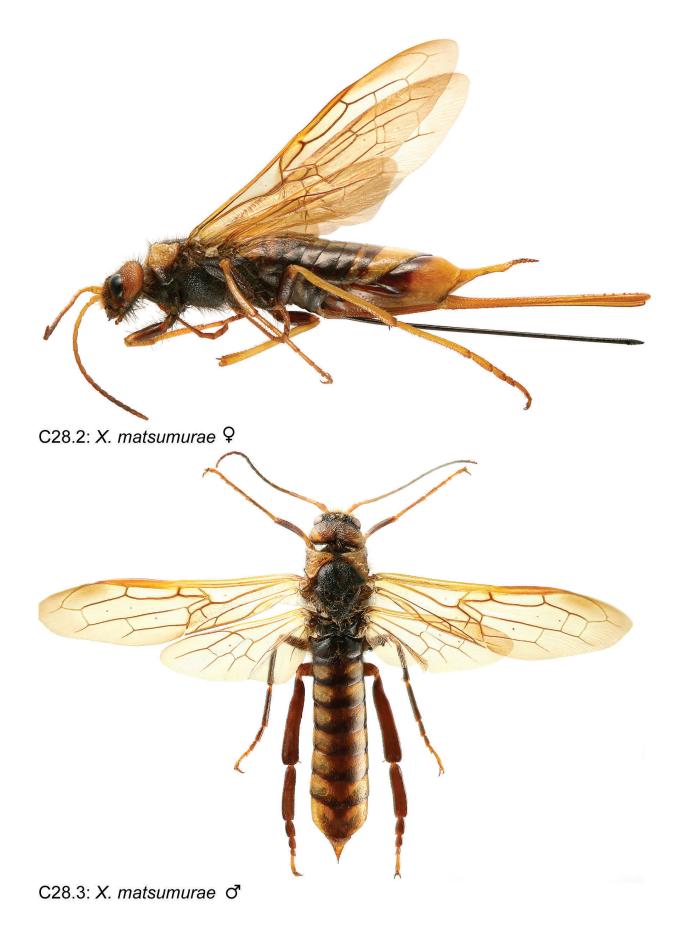
Notes

Smith (1978), Taeger and Blank (2011) and Taeger *et al.* (2010) listed two species from eastern Asia, *X*.

matsumurae (Rohwer, 1910) from eastern Russia, China, Japan, and Korea, and *X. praelongus* Maa, 1949, from China.

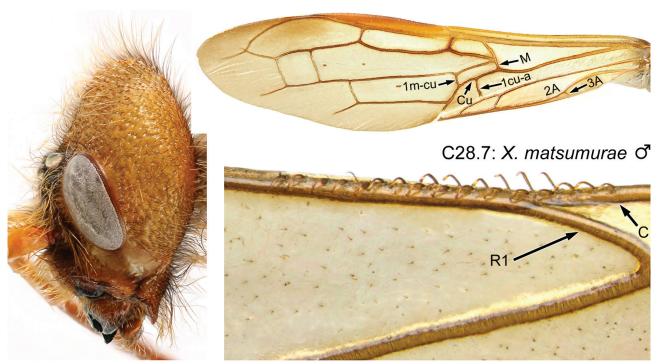
Semenov-Tian-Shanskij (1921) included only his new species, *X. mysta*, in his new genus *Xoanon*, but questionably considered *X. mysta* as a possible synonym of *Sirex matsumurae* Rohwer, 1910, because he was unable to see Rohwer's type. *Xoanon mysta* was described from 1 male and 1 female from "insula Sachalin" and "Vladivostok". We have seen many specimens of *Xoanon* from Vladivostok and they match Rohwer's type perfectly. *Xoanon mysta* is almost certainly Rohwer's species. We agree with Takeuchi (1938: 191) that *Xoanon mysta* Semenov, 1921 is a synonym of *X. matsumurae* (Rohwer, 1920).

We studied 20 specimens of both sexes of *X. matsumurae*, including the holotype, and two specimens for molecular studies (Fig. E2.1). All specimens studied are in CNC, NSMT, and USNM.





C28.4: X. matsumurae Q



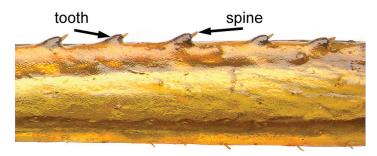
C28.8: X. matsumurae o

C28.5: X. matsumurae Q

C28.6: X. matsumurae Q



C28.9: X. matsumurae o



C28.10: X. matsumurae Q

29. Subfamily Tremicinae

Diagnostic combination

Both sexes of Tremicinae are recognized by the metatibia with one spur, the hind wing without anal cell (single male of *Teredon latitarsus* with cell – this may be an aberration), and the fore wing with junction of veins 1 cu–a and Cu clearly closer to junction of veins M and M+Cu (except in *Teredon*).

Diversity and Hosts

There are six genera and 58 extant species in the world, and three genera and 3 native species in the Western Hemisphere. Taeger *et al.* (2010) recognized 4 genera, but we consider that there are six genera because we transferred *Siricosoma* and *Xeris* from the Siricinae to the Tremicinae in this work. Reared specimens (only three genera with known hosts) in this subfamily were from flowering or coniferous trees.



C30.1: A. hyalinatus Q

30. Genus Afrotremex Pasteels

Fig. C30. 1 (female habitus)

Afrotremex Pasteels, 1951: 195. Type species: *Tremex hyalinatus* Mocsáry, 1891: 158, by original designation. Smith 1978: 90.

Description

We studied two females, we assumed that following character states, unless specified otherwise, apply to both sexes.

Head. Minimum distance between inner edges of eyes 1.2 times as long as maximum eye height (Fig. C30.2, in red), distance between inner edges of antennal sockets 6.0 times distance between outer edge of antennal socket and nearest inner edge of eye (Fig. C30.2, in white),

distance between inner edges of lateral ocelli 1.5–2.0 times as long as distance between outer edge of lateral ocellus and nearest edge of eye (Fig. C30.2, in black). Head with setae, except those on occiput, clubbed at apex (Fig. B1.37). Antenna with 12–14 flagellomeres, the flagellomeres flattened dorsoventrally, and flagellomere 1 0.5 times as long as flagellomere 2 (Fig. B1.33).

Thorax. Pronotum in dorsal view finely pitted with numerous prominent shiny teeth (Fig. C30.3). Mesoscutum sublaterally with smooth longitudinal band, anterolateral corner with large pits, (submedially on inner side of smooth longitudinal band) with coarse and irregular pits, with numerous prominent shiny teeth, and medially with fine pits (Fig. C30.3). Fore wing without vein 2r-m, with vein 1cu-a aligned or almost aligned with vein M, with cell 2R1 0.6 times as long as cell 3R1, with vein 2r-rs joining stigma in apical third, with stigma before junction with vein 2r-rs parallel and beyond junction abruptly attenuated (Fig. C30.4), with vein 2A at or near posterior margin of wing only near vein a (Fig. C30.4), and with vein 3A extending along wing margin. Hind wing without anal cell 1A, with hamuli present only apical to junction of veins R1 and C (as in Fig. B1.12), with vein 1r-m clearly shorter than vein M, and with vein M moderately curved.

Abdomen. Female. Tergum 9 with median basin clearly

longer than wide and flat, without setae or pits but with many small tubercules (Fig. C30.5). Cornus about 0.5 times as long as median basin length, triangular with large tooth-like projection laterally at base, and without cercus on lateroventral surface (Figs. C30.6 & C30.7). Sculpticells on surface of most abdominal terga extremely deeply pitted especially in pits of tergum 9 (Fig. A3.13). *Sheath*. Length of basal section 1.6–1.7 times as long as apical section, and total length 0.75 times as long as fore wing length, with few teeth subdorsally in apical 0.25 of apical section (Fig. C30.8). *Ovipositor*. Lancet annuli starting at base, and each annulus edge with one pit and without deep trough (Fig. 30.9).

Notes

Two sub–Saharan African species are known, *A. hyalinatus* (Mocsáry) from Gabon, Uganda, and Zaire [Democratic Republic of Congo] and *A. violaceus* Pasteels, 1951, from the Congo [Democratic Republic of Congo] (Smith 1978, Taeger and Blank 2011, Taeger *et al.* 2010). There are no keys, but the species are characterized by Pasteels (1951). We examined two females from Uganda, and Congo (USNM) representing two species near *A. hyalinatus*.



C31.1: E. formosanus Q

31. Genus Eriotremex Benson

Fig. C31.1 (live female)

Eriotremex Benson, 1943: 42. Type species: *Tremex smithi* Cameron, by original designation.

Diagnostic combination

Among specimens with no fore wing vein 2r–m [species of *Tremex* and *Afrotremex*], **both sexes** of *Eriotremex* are recognized by the fore wing cell 2R1 about 0.5 times as long as cell 3R1, the dense and long pubescence covering the body, and the antenna with at least 12 flagellomeres. **Female** also have deep pits on the basin of tergum 9 and a thumb-like cercus.

Description

Color. Variable generally body mostly or entirely black and wings black tinted, but wasps-like color patterns with less darkly tinted wings known in a few species.

Head. Antennal sockets with distance between their

inner edges 4.0-5.0 times distance between inner edge of eye and outer edge of socket. Distance between inner edges of lateral ocelli 1.7-2.2 times as long as distance between outer edge of lateral ocellus and nearest edge of eye. Maximum distance between outer edges of eyes clearly less than maximum width of head (thus, in frontal view, genal edges completely visible and not intersected by outer edges of eyes). Minimum distance between inner edges of eyes about as long as maximum eye height. Gena without ridge behind eye and without white spot, with large pits, each elevated along posterior edge as low tooth. Head with setae sharp at apex. Flagellum with 16-19 flagellomeres, and middle flagellomeres in dorsal view 0.8-0.9 times as long as wide (Fig. B1.23); middle flagellomeres with sensory pits over ventral and most of dorsal surface (part of outer lateral surface without sensilla) and ventral surface separated from dorsal surface by a sharp fold especially on inner side.

Thorax. Pronotum smooth or pitted over less than 0.5 of anterior vertical surface. Mesoscutum entirely densely pitted. Metatibia with one apical spur, and in **male**, metatibia in lateral view about 5.0 times as long as

maximum width, and in cross section rather compressed. In **both sexes** metatarsomere 1 in lateral view 0.8–0.9 times as long as maximum length of metatibia, in female, 0.7 times and in male 1.0 times as wide as maximum width of metatibia. In female, metatarsomere 2 in lateral view 2.0-3.0 times as long as maximum height. Metatarsomere 5 shorter than metatarsomeres 2 + 3. Fore wing with apex acutely and angularly rounded, without vein 2 r-m, with cell 3R1 3.0-3.8 times as wide as long, with cell 2R1 about 0.5 times as wide as cell 3R1, with vein 2r-rs joining stigma near middle, and with stigma gradually attenuated even distal to junction with vein 2r-rs (Fig. B1.25), without vein Cu1, with vein 1cu-a joining vein Cu close to or at vein M, with vein SC scarcely outlined in basal 0.15, with vein 2A extending along posterior edge of wing for 0.5 times length of cell 1A, and with vein 3A present and clearly extending along posterior margin of wing (Fig. B1.25). Hind wing without anal cell (as in Figs. B1.15 & B1.16); hamuli present apical to junction of veins R1 and C (as in Fig. B1.12).

Abdomen. Female. Cornus in dorsal view very short and lateral edges not angular, markedly convergent, but not constricted (Fig. B1.29). Tergum 1 laterally and medially and terga 2–6 laterally deeply pitted, each pit with long setae (Figs. C31.1 & C31.2). Tergum 9 with median basin deeply pitted, the pits scattered to dense, with surface markedly convex, about as long as wide, and lateral edges round and clearly outlined for 0.75 of median length of basin (Fig. B1.29). Sterna 2–7 pitted at side, more finely so toward middle. Cercus present, quite small, and thumblike. *Sheath.* Basal and apical sections clearly separated by a membrane; basal section more than 2.0 times as long as apical section (Fig. C1.40); apical section with teeth

dorsomedially; median margin of basal section on ventral surface of sheath at very base without transverse ridges, but with setigerous pits in basal 0.3 each clearly raised as a forward directed tooth. *Ovipositor*. Lancet with 13 annuli, but annuli not outlined at base for a distance equal or greater than length of basal section of sheath; posterior portion of apical annuli with single pit and edge without tooth; last two annuli before teeth annuli without pit, preceding two annuli with a pit, each pit sharply outlined on most of ventral edge, anterior annuli following above two pits with similar sized pits, and each pit midway between dorsal and ventral edges of the lancet; edge of last 3–4 annuli before teeth annuli not sinuate, extending toward ventral margin but not reaching it, and edge of annulus not developed as tooth (Fig. C31.3).

Diversity and distribution

This genus with 12 species (we studied eight species) is moderately diverse in southeastern Asia (from Japan, southern China including Taiwan to eastern India and Papua New Guinea) (Taeger and Blank 2011, Taeger *et al.* 2010), but in North America the genus consists of a single introduced species, *Eriotremex formosanus*. The species is reported from southeastern United States. It is common and still spreading (Smith 1996). Benson (1943) gave a key to 7 species, Maa (1956) to 8 species based on females, and Smith (2010) to 12 species based on females. Males are known only for three species, *E. formosanus* (Matsumura), *E. malayanus* Benson and *E. viridiceps* Cameron.



C31.2: *E.* formosanus Q



C31.3: E. formosanus Q

32. Eriotremex formosanus (Matsumura)

- Fig. C1.40, Schiff *et al.* 2006: 10, 11 (female habitus) Fig. C32.1, Schiff *et al.* 2006: 9 (male habitus) Fig. C32.2 (live female) Fig. C32.3 (map)
- *Tremex formosanus* Matsumura, 1912: 21. Holotype female (EIHU), examined by DRS. Type locality: "Formosa".

Eriotremex formosanus; Benson, 1943: 44 (change in combination). Smith 1978: 91.

Diagnostic combination

In North America, **both sexes** of *E. formosanus* are recognized by the black head with dark metallic reflections. **Females** also have a light reddish brown pronotum, transverse yellow transverse bands on terga 2, 3, 7, and 8 segments, and long and dense golden pubescence. **Males** also have reddish brown transverse bands on abdominal segments 2–6 and a very long flagellum (middle flagellomeres about 2.5–3.0 times as long as wide).

FEMALE. Description

Body. Setae over surface clearly long and golden (Fig.

C31.2); meshes of microsculpture over terga 1–8 present between pits and mostly consisting of pit-like sculpticells (surface rather matt), and meshes absent between pits on head, thorax, sterna, and terga 9 and 10.

Color. Head black with dark red purple metallic reflections. Antenna, maxillary palp and most of mandible black. Thorax black, but light reddish brown on pronotum. Fore wing lightly to darkly tinted yellowish brown (Fig. B1.25). Coxae, trochanter, femora and tarsomeres 2–5 black; tibiae and tarsomeres 1 light reddish brown in basal 0.3–0.7. Abdomen generally black, but with yellow transverse band on terga 2 and 3 along most of base and extending posteriorly to spiracle, with small yellow spot on terga 4 and 6 posterolateral to spiracle, with wide yellow transverse band on terga 7 and 8 in basal 0.5 and extending laterally posterior to spiracle (Fig. C1.40), and sterna 2–6 yellow medially. Sheath mainly dark brown to black (Fig. C1.40).

Head. Pits mostly touching but less dense on gena behind eye as a narrow transverse band, coarse over much of surface (diameter about 0.3 posterior ocellus diameter) but finer on frons and between posterior ocelli, near eye and posterior margin of vertex. Postocellar region in frontal view scarcely elevated. Antenna length clearly shorter than length of coastal cell of fore wing; flagellum widened centrally with middle flagellomeres about 1.25 times as wide as long; flagellum with 17–

19 flagellomeres (Fig. B1.23), with dorsal surface of flagellomeres 1 and 2 with isodiametric meshes and flat sculpticells (thus, surface bright), with bright outer surface becoming gradually narrow from flagellomeres 3 to about 7, with pegged pits on inner and dorsal surfaces from flagellomeres 3 to apex, on ventral surface from flagellomeres 1 to apex, and with setae restricted to apical margin of flagellomeres except for few setae on smooth outer surface.

Thorax. Pronotum with fine to coarse teeth over dorsal surface. Mesepisternum densely pitted (pits 0.5–1.0 pit diameter apart) and surface between pits shiny. Metatarsomere 2 with dorsal margin in lateral view straight, and about 2.0 times as long as high; tarsal pad about 0.8 times as long as ventral length of tarsomere.

Abdomen. Median basin of tergum 9 at base (length between two lateral impressions) about 0.8 times as wide as median length (Fig. B1.29). Terga 7–9 including basin densely and deeply pitted (Fig. B1.29). Tergum 10 in dorsal view about 0.7 times as long as median length of basin, with teeth over most of surface and along lateral edges (Fig. B1.29). *Sheath.* Apical section of sheath about 0.3 times as long as fore wing length. *Ovipositor.* Lancet with about 13 annuli, with visible annuli outlined only under apical section of sheath; annulus 1 weakly outlined and without pit, annuli 2–8 with pits, each pit about 0.5–0.7 times height of lancet, and about 0.3 as long as length of annulus, edge of last two annuli before teeth annuli with a wide and very shallow concavity outlined with short and sharp fold ventrally.

MALE. Description

Color. Pronotum black. Legs black, but reddish brown on profemur and protibia, and on mesotibia and mesotarsus. Tergum 1 black, terga 2–6 or 2–7 black at base and apex but broadly reddish brown in between, terga 7 and 8 or 8 black; sterna 2–7 mainly black but yellow medially, terga 8 and 9 black.

Head. Antenna thread-like and much longer than costal cell of fore wing (Fig. C32.1); middle flagellomeres 2.5–3.0 times as long as wide.

Thorax. Metatibia in lateral view about 5.0 times as long as maximum width (Fig. C32.1), and in cross section about 1.5 times as high as maximum ventral width. Metatarsomere 1 in lateral view about 4.0 times as long

as high (Fig. C32.1).

Abdomen. Sterna 2–9 completely and quite densely pitted. Apical edge of sternum 8 widely and deeply indented.

Hosts and phenology

The main hosts of *Eriotremex formosanus* are *Quercus alba*, *Q. laurifolia* and *Q. nigra* (Fagaceae) and various species of *Carya* (Juglandaceae). Other hosts include: *Liquidambar styraciflua* (Hamamelidaceae), *Pinus palustris*, *P. taeda*, and *P. elliottii* (Pinaceae) (Smith 1996).

Based on many field-collected specimens, adults of *E. formosanus* are recorded basically throughout the year (except March and January) with two main flight periods, one from April to June and again from September to November (Smith 1996).

Range

USA: AL, AR (Warrimer, 2008), FL, GA, LA, MS, NC, SC, TX (Hays Co., Buda), UT, VA. *Eriotremex formosanus* is known from China, Taiwan, Japan (Amami–Oshima), Vietnam, and Laos (Smith, 1981) and was accidentally introduced into southeastern United States where it is still expanding its range (Smith 1975b, Chapin and Oliver 1986, and Smith 1996). There is one record from Utah (Utah Co., Provo 40.29343°N, 111.64922°W, summer 2002, C. R. Nelson; 1 F; BYUC). It is not clear if this record is associated with lumber or represents an established population (Fig. C32.3).

Specimens studied and included for the distribution map: 26 females and 2 males from BYUC, CNC, CUCC, DEBU, FSCA, UCRC, USFS–GA, and USNM.

Specimens for molecular studies: 14 specimens. See Fig. E2.2.

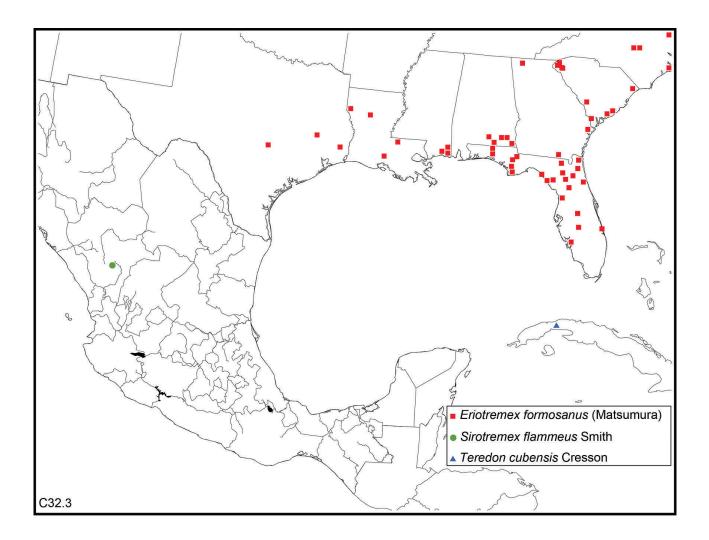
USA. Arkansas: 2009, *CBHR 1490*, 494. **Louisiana**: 2005, *CBHR 85*, 658; 2006, *CNCS 1053*, 658; 2006, *CNCS 1054*, 658; 2006, *CNCS 1056*, 658. **Mississippi**: 1997, *CBHR 4*, 658; 1997, *CBHR 135*, 658; 2007, *CBHR 1120*, 658; 2007, *CBHR 1121*, 658; 2007, *CBHR 1122*, 658; 2007, *CBHR 1123*, 658. **South Carolina**: 2007, *CBHR 1441*, 521. **Unknown State**: year unknown, *CBHR 145*, 658; 2005, *CBHR 895*, 6 58.



C32.1: E. formosanus o



C32.2: E. formosanus♀





C33.1: S. tremecoides Q

33. Genus Siricosoma Forsius

Fig. C33.1 (female habitus)

Siricosoma Forsius 1933: 173. Type species: *Siricosoma tremecoides* Forsius 1933: 174, by original designation. Smith 1978: 64.

Description

We studied only one female and we assumed that the following character states apply to both sexes except for those sex-specific characters like the ovipositor and its sheath.

Head. Minimum distance between eyes as long as maximum height of eye (Fig. B1.13), distance between inner edges of antennal sockets about 3.7 times as long as distance between outer edge of antennal socket and nearest edge of eye (Fig. B1.13), distance between inner edges of lateral ocelli subequal to distance from outer edge of posterior ocellus to the nearest edge of eye (Fig. B1.13); maximum eye height 1.6 time as high as its maximum length. Head with setae sharp at apex. Antenna flattened dorsoventrally, with 23 flagellomeres; and flagellomere 1 in lateral view 1.2 times as long as flagellomere 2 (Fig. C33.2).

Thorax. Mesoscutum entirely finely pitted (Fig. C33.1). Fore wing with vein 2r–m joined to cell 2M (as in Fig. B1.71), with the vein 2r–m present, with vein 1cu–a closed to vein M (joining vein Cu in the basal 0.2 between veins 1m–cu and M), with vein M markedly curved (Fig. B1.9), with cell 2R1 0.4 times as long as cell 3R1, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated to apex even after junction with vein 2r-rs (as in Fig. B1.25), with vein 2A along the wing posterior edge for 0.6 times cell length (Fig. B1.7), with vein Sc as well as Sc1 and Sc2 in basal 0.4, and without vein 3A. Hind wing without anal cell, with hamuli present equally basal and apical to junction with veins R1 and C, with vein 1r–m slightly longer than vein M, and with vein M curved.

Abdomen. Female. Tergum 9 with median basin with numerous setae, each seta on raised base. Cornus 2.3 times as long as median basin length, parallel sided, not constricted near base (Fig. B1.21), and cercus about as long as 0.5 width of ovipositor sheath (Fig. B1.19). *Sheath*. Length of basal section 1.25 times as long as apical section; length of sheath 0.8 times as long as fore wing length, its apical section without teeth dorsoapically, but with teeth on lateral surface in apical 0.25 (Fig. B1.19). *Ovipositor*. Lancet with annuli only in

apical 0.25, and each annulus with wide and prominent ventral tooth along edge, with small pit anteriorly and sharp ridge posteriorly, with small and narrow dorsal tooth attenuating posteriorly, and with a deep trough in between (Fig. B1.19).

Notes

Only one species is known, *S. tremecoides* Forsius from the Malay Peninsula. We have examined one female (AEI) from Pasoh Forest Reserve, Nigri S. [probably the state of Nigri Semiblan], Malaysia, collected on June 26, 1979 in a forest by P. and M. Becker.





C34.1: *T. cubensis* **G** 34. Genus *Teredon* Norton Fig. C34.1 (female habitus)

Teredon Norton, 1869: 366. Type species: *Tremex cubensis* Cresson, designated by Rohwer (1911).

Teredonia Kirby, 1882: 386. Unnecessary replacement name for *Teredon* Norton. According to Kirby, *Teredon* is preoccupied, "*nom. praeocc.*". We did not find the name *Teredon* to be preoccupied. However, Linnaeus (1758: 651) described the genus *Teredo*, a bivalve, which is not a homonym because of one letter difference (Konow 1905a).

Diagnostic combination

Both sexes of Teredon are recognized by the

strongly compressed metatarsomere 1 and fewer than 9 flagellomeres.

Description

Head. Antennal sockets with distance between their inner edges of sockets 7–8 times distance between inner edge of eye and outer edge of socket (Fig. B1.14). Distance between edges of posterior ocelli in **female** 1.4 and in **male** 1.9 times as long as distance between outer edge of lateral ocellus and nearest edge of eye (Figs. B1.14 & C34.2). Maximum distance between outer edges of eyes in **female**, clearly, and in **male** slightly, less than maximum width of head (thus, in frontal view, genal edges completely visible and not intersected by outer edges of eyes) (Figs. B1.14, C34.2). Minimum distance between inner edges of eyes about 0.95 times as long as

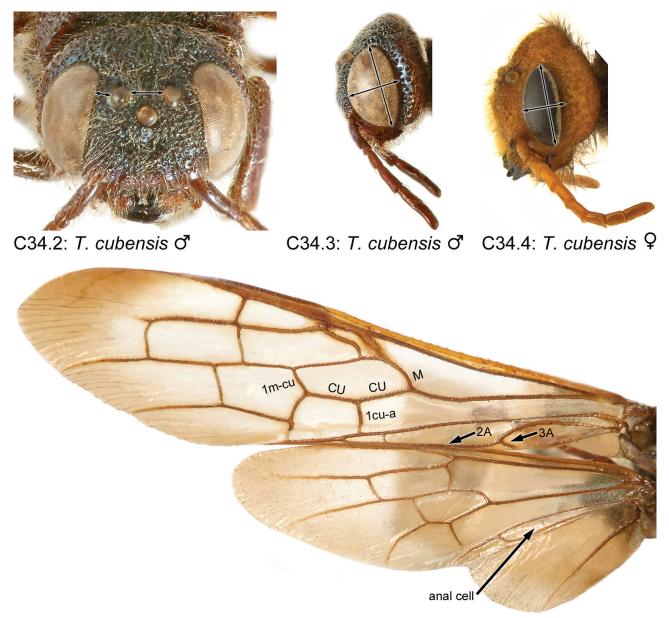
maximum eye height (Fig. B1.14). Gena without ridge behind eye and without white spot (Fig. C34.3), with large pits near antennal groove, each with posterior edge raised posteriorly as a low tooth. Head with setae sharp at apex. Eye in **female** 2.2 and in **male** 1.6 times as high as long (Figs. C34.4 & C34.3). Antenna in female with 7 or 8 and in male with 4 antennomeres (Figs. C34.4 & C34.3), and middle antennomeres in dorsal view in female 1.1-1.2 and in male 3.0 times as long as wide; pitted sensors restricted to ventral surface and sharply separated from dorsal surface by sharp fold on both sides. Thorax. Pronotum pitted only in dorsal third of anterior vertical surface. Mesoscutum entirely densely pitted. Metatibia in female quite typical in lateral view (Fig. B1.18), but in male markedly compressed laterally and enlarged in apical 0.3 (Fig. C1.8). Metatarsomere 1 (including lobe) in **both sexes** 1.1–1.2 times as long as maximum length of metatibia; enlarged in female 1.5 times (Fig. B1.18) and in male 1.3 times as wide as maximum width of metatibia (Fig. C1.8). Metatarsomere 2 in lateral view about as long as high. Metatarsomere 5 as long as metatarsomeres 2-4 (Figs. B1.18 & C1.8). Fore wing with apex acutely and angularly rounded, with vein 2r-m joined-cell 2M (as in Fig. B1.71), with vein 2 r-m present, with cell 1Rs2 clearly wider than long, with cell 2R1 about 0.7 times as long as cell 3R1, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even distal to junction with vein 2r-rs (as in Fig. B1.25), without vein Cu1, with vein 1cu-a joining vein Cu about midway between veins 1m-cu and M, with vein SC present in basal 0.3 (difficult to see), with vein 2A extending along posterior edge of wing for 0.4 times cell 1A length, and with vein 3A very clearly extending along posterior wing margin (Fig. C34.5). Hind wing in female without anal cell and in male with anal cell; hamuli present equally basal and apical to junction of

veins R1 and C.

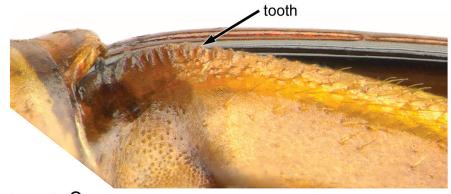
Abdomen. Female. Cornus in dorsal view with median length 0.5 times as long as median basin length, lateral edges of cornus markedly convergent and not constricted (Fig. B1.22). Terga 7–9 (except side, but including median basin) not deeply and densely pitted (Fig. B1.22). Tergum 9 with median basin not pitted, with surface concave, about as long as wide, and with lateral edges round and clearly outlined for 0.75 of length of cornus (Fig. B1.22). Cercus present but very small. Sheath. Basal and apical sections fused but a small constriction between them still present; basal section more than 2.7 times as long as apical section, and apical section of sheath without teeth dorsomedially (Fig. B1.20); with basal section of median margin at very base without transverse ridges, and each setigerous pit clearly raised as a ventrally directed tooth (Fig. C34.6). Ovipositor. Lancet with 18 annuli, all clearly outlined to its base; posterior edge of annuli 6-14 with of a prominent dorsal and ventral tooth fusing into one tooth on annulus 5; edge of annuli 7-14 markedly sinuate; pit developed in sinuation and surface of annulus deeply impressed anterior to pit, forming a longitudinal furrow between annuli 7-14 (Fig. C34.7); edge ventral to sinuation developed ventrally as a sharp and long tooth and dorsally as a low round tooth (Fig. C34.7).

Diversity and distribution

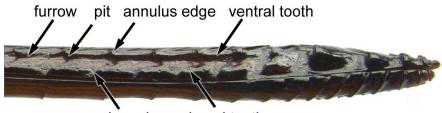
Smith (1978), Taeger and Blank (2011) and Taeger *et al.* (2010) listed two species of *Teredon*. Unfortunately, the two holotypes represent the two sexes. As expected, the male is strikingly different from the female. Therefore, we uphold Konow's (1898) synonymy and treat the two sexes as belonging to one species. Adults are the most modified Siricidae studied.



C34.5: T. cubensis o



C34.6: T. cubensis Q



annulus edge dorsal tooth

C34.7: T. cubensis Q

35. Teredon cubensis (Cresson)

Fig. C34.1 (female lateral habitus) Fig. C35.1 (female dorsal habitus)

Fig. C35.2 (male dorsal habitus)

- Fig. C32.3 (map)
- Fig. C32.3 (map)
- *Tremex cubensis* Cresson, 1865a: 2. Holotype female (ANSP), examined by DRS. Cresson 1916: 10. Type locality: Cuba.
- *Tremex latitarsus* Cresson, 1865a: 3. Holotype male (ANSP), examined by DRS and HG. Cresson 1916: 10. Synonymy by Konow 1898: 83, 90. Type locality: Cuba.
- *Teredon cubensis*; Norton, 1869: 366. Dalla Torre, 1894: 380 (change in combination); Bradley 1913 : 27, Pl. 4, Fig. 13, Hedicke 1938: 31, Smith 1969: 543, Smith 1978: 92.
- *Teredon latitarsus*; Norton, 1869: 367. Dalla Torre, 1894: 380 (change in combination); Bradley 1913: 27, Pl. 4, Figs. 10, 12, Hedicke 1938: 31, Smith 1969: 543, Smith 1978: 92.
- *Teredonia cubensis*; Kirby, 1882: 386 (unnecessary combination, see *Teredonia, above*). Konow, 1905a: 9, Konow, 1905b: 124 (misspelling as *Treodonia*).
- *Teredonia latitarsus*; Kirby, 1882: 386 (unnecessary combination, see *Teredonia, above*).

Diagnostic combination

The single species of *Teredon*, *T. cubensis*, is diagnosed under the genus. **Both sexes** have metatarsomere 1 extremely compressed laterally and fewer than 9 antennomeres.

FEMALE. Description

Body. Pubescence short on abdomen, moderately short on frons, vertex and nota, and long on occiput and lateral surface of head and thorax.

Color. Head, palps and antenna reddish brown. Median half and posterolateral areas of mesoscutum, mesoscutellum (Fig. C35.1), and pro- and mesofemur reddish brown. Propleuron, pronotum ventrolaterally (Fig. C34.1), most of mesonotum except medially and posterolaterally (Fig. C35.1), mesopleuron except upper 0.7 (Fig. C34.1), metanotum except central part of scutum and scutellum (Fig. 35.1), metepisternum and ventral section of metepimeron, coxae, and most of metafemur (Fig. C34.1) black or brown. Tergum 1 at extreme apex, terga 2 and 3 in apical 0.4 and most of side, tergum 4 in apical 0.2 and widely at side, terga 5–7 in apical 0.7, tergum 8 in apical 0.5–0.6, tergum 9 basolaterally, extreme base of sheath, and sterna 2–7 in posterolateral area (Figs. C34.1 & C35.1) black or brown.

Head. Flagellomeres clearly constricted at base, and each of middle flagellomeres about 2.7 times as long as minimum width (Fig. C35.3). Capsule with most pits adjacent, most pits large (diameter of pit about 0.3 times lateral ocellus diameter) on vertex, and very large behind eye on gena (diameter of pits about 0.5 times lateral ocellus diameter), and surface between pits smooth. Microsculpture generally lacking, or meshes shallow and sculpticells slightly convex.

Thorax. Pronotum with medium teeth over dorsal surface and quite finely pitted laterally (diameter of pits about 0.15 times lateral ocellus diameter) and smooth between pits (Fig. C35.4). Mesoscutum with net-like pits over median area, and quite finely pitted in lateral 0.3 (Fig. C35.4). Meso- and metepisternum with moderately fine (upper half) to fine pits, and pits 0.5–1.5 pit diameter apart.

Abdomen. Median basin at base (length between two lateral impressions) about 0.7 times as wide as median length (Fig. B1.22). Tergum 10 in dorsal view about 0.6 times as long as median length of median basin (Fig. B1.22). Terga with shallow and fine pits, pits on terga 1–8 restricted laterally and present on most of tergum 9 except dorsomedially. Tergum 10 with teeth over most of surface (teeth largest laterally in dorsal view). Sterna 2–7 with shallow and fine pits in lateral half. Microsculpture of terga 2–8 with pitted sculpticells in posterior 0.5 of each tergum, and extending laterally to level of dorsal margin of spiracle; terga 1, 2–8 laterally, 9 (including median basin) and 10 with isodiametric meshes and sculpticells slightly convex or scale-like. *Sheath.* Apical section about 0.13 times as long as that of fore wing.

Ovipositor. Lancet with 17 annuli outlined to base; annuli 6-14 with bisinuate edge, with a tooth above and below on annulus edge, and with a deep furrow between (Fig. C34.7). annuli 1-14 with pits; annuli 4-5 with narrow and broad pit (about 0.5 width of lancet), annuli 6-14 with small pit associated with ventral tooth, annuli 6 and 7 with very small pit associated with dorsal tooth, and both pits fused on annuli 2-5; pits from annulus 5 becoming small toward annulus 2; ventral edge of annuli 13-14 with ridge extended to ventral edge of lancet, on annuli 6-12 ridge present but not extending to ventral edge of lancet (Fig. C35.5); annuli 2-5 without ridge ventral to pit.

MALE Description

Color. Head black or brownish black with dark blue metallic reflections (surface behind head and posterior half of gena brown) (Fig. C35.2). Mesothorax, coxae, femora, metatibia, metatarsus 1 and tergum 2 medially as narrow longitudinal band and posteriorly as narrow transverse band black or dark brown with dark blue metallic reflections, pronotum dorsally except medially, middle of scutellum, central area on both sides of mesoscutum brown (Fig. C35.2); antenna, pro- and mesotibiae and tarsi brown (Fig. C1.8). Wings clear but darkened near stigma and in apical 0.25 (Fig. C34.5). Abdomen reddish brown except for black spot on tergum 2 (Fig. C35.2).

Head. Antenna with only 3 or 4 flagellomeres (Fig. C34.3). Flagellomere 1 about 0.5 times as long as length of 2 (Fig. C34.3). Maximum height of eye 1.3 times as long as minimum distance between eyes (Fig. C34.2); distance between inner edges of lateral ocelli 2.3 times as long as minimum distance from outer edge of lateral ocellus to nearest edge of eye (Fig. C34.2); eye high but very wide, thus 1.6 times as high as long (thus gena about 0.4 times as long as eye length) (Fig. C34.3). Vertex with pits about 0.3 times as large as diameter of lateral ocellus and dense (Fig. C35.6), and gena with pits about 0.5 times as large as diameter of lateral ocellus and dense (Fig. C34.3). Distance between inner edges of antennal sockets about 10 times distance from outer edge of antennal socket to nearest edge of eye (Fig. C34.2).

Thorax. Mesoscutum coarsely pitted (pits about 0.3

times of lateral ocellus diameter) in median half, but fine in lateral half (pits 0.1–0.2 times of lateral ocellus diameter). Metatibia and metatarsomere 1 laterally compressed and lobed at apex; metatibia 3.0 times as long as wide; metatarsomere 1 in lateral view (with lobe) 2.8 times as long as high; metatarsomere 1 1.3 times as high as maximum width of metatibia, and maximum length (excluding lobe) 0.9 times as long as metatibial length (Fig. C1.8). Fore wing with vein Rs between veins 1r and M clearly sinuate (Fig. C34.5).

Taxonomic notes

The male is unusual in two features. The eye is very large, as high as in the female but remarkably longer. Eye length affects gena width, so the gena is narrow. The hind wing anal cell is complete in the only male studied. In the female, hind wing vein 2A is much longer than in other genera [Sirex, Sirotremex, Urocerus, and Xoanon] with an open anal cell. Because of the unusual variability of wing veins in Siricidae, we do not know how significant this closed cell is in the male. The male and female are very different in color pattern, as in most species of Siricidae. The hind leg of the male is remarkable, but is similar to the hind leg differences one would expect to see between the sexes of other Siricidae. In other features (except for flagellomere number and the hind wing anal cell development), the male matches the female. Therefore, we agree with Konow (1898) and consider T. latitarsus as a synonym of *T. cubensis*.

Host and phenology

The host is unknown. The single adult with a capture date was on March 31.

Range

CUBA. La Habana Province. *Teredon cubensis* is known only from Cuba (Fig. C32.3) and has very rarely been collected.

Specimens studied and included for the distribution map: 2 females and 1 male from ANSP and IES.



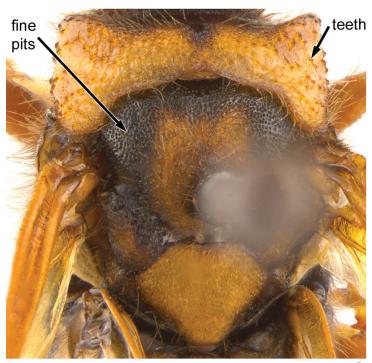
C35.1: *T. cubensis* Q



C35.2: T. cubensis o



C35.3: T. cubensis Q



C35.4: T. cubensis Q



annulus ridge (#9) not extended to edge

annulus ridge (#14) extended to edge



C35.6: T. cubensis o

C35.5: T. cubensis Q



C36.1: T. columba Q

36. Genus Tremex Jurine

Fig. C36.1 (live female)

- *Tremex* Jurine, 1807: 80. Type species: *Sirex fuscicornis* Fabricius, designated by Latreille, 1810: 436.
- Sirex (Xyloterus) Hartig, 1837: 385. Type species: Sirex fuscicornis Fabricius, designated by Rohwer, 1911: 92. Name preoccupied by Xyloterus Erichson, 1836.
- *Xyloecematium* Heyden, 1868: 227. Replacement name for *Xyloterus* Hartig.

Diagnostic combination

Both sexes of *Tremex* are easily distinguished from other genera with antennal sockets far apart [all Tremecinae genera except *Xeris*] by cell 2R1 about as long as or longer than cell 3R1, and fewer than 15 flagellomeres. **Females** also have a mainly smooth median basin and no cercus.

Description

Head. Antennal sockets with distance between their inner edges 4.0–5.0 times distance between inner edge of eye and outer edge of socket (Fig. B1.3). Distance between inner edges of lateral ocelli 1.6–2.2 times as long as distance between outer edge of lateral ocellus and nearest

edge of eye (Fig. B1.1). Maximum distance between outer edges of eyes clearly less than maximum width of head (thus, in frontal view, genal edges completely visible and not intersected by outer edge of eyes) (Fig. B1.1). Minimum distance between inner edges of eyes about as long as maximum height of eye (Fig. B1.1). Gena without ridge behind eye and without white spot (Fig. B3.1), with large pits, each with posterior edge raised as low tooth (Fig. C36.2). Head with setae sharp at apex. Antenna with 11-14 antennomeres, and middle flagellomeres in dorsal view 0.8–0.9 times as long as wide (Fig. B1.24); middle flagellomeres with sensory pits over ventral and most of dorsal surface (part of outer lateral surface without sensilla) and ventral surface not sharply separated from dorsal surface by a fold, especially on inner side.

Thorax. Pronotum smooth or pitted over less than 0.5 of anterior vertical surface. Mesoscutum densely pitted over median 0.5–0.7 only. Metatibia in **male** in lateral view metatibia about 5.0 times as long as maximum width, and in cross section about 1.5 times as high as maximum ventral width. Metatarsomere 1 0.8–0.9 times as long as maximum length of metatibia, and about as wide as maximum width of metatibia. In **female**, metatarsomere 2 in lateral view 2.0–3.0 times as long as maximum height. Metatarsomere 5 as long as metatarsomere 2 or, in **male of some species**, as long as metatarsomeres 2 +

3. Fore wing with apex acutely and angularly rounded, without vein 2 r-m, with cell 3R1 0.7–1.1 times as long as length of cell 2R1, with vein 2r-rs joining stigma in apical 0.2–0.3, with stigma parallel before junction but abruptly attenuated after junction with vein 2r-rs (Fig. B1.26), without vein Cu1, with 1cu–a joining vein Cu close to or at vein M, with vein SC scarcely outlined in basal 0.15, with vein 2A extending along posterior edge of wing for 0.5 times length of cell 1A, and with vein 3A present, long and clearly extending along posterior margin of wing (Fig. B1.26). Hind wing without anal cell (Fig. C1.26); hamuli present apical to junction of veins R1 and C (Fig. B1.12).

Abdomen. Female. Cornus in dorsal view short and lateral edges markedly convergent, but not constricted (Fig. B1.30). Terga 7, 8 and 9 (except laterally and ventrally, but including median basin) not pitted. Tergum 9 with median basin clearly wider than long, round, and sharply outlined for about 0.75 of median basin length (Fig. B1.30). Cercus absent. Sheath. Basal and apical sections clearly separated by membrane; basal section 1.1-1.2 times as long as apical section; apical section slightly convex for most of its length, and with teeth dorsomedially in apical 0.2; median margin of basal section of sheath at very base without transverse ridges, but with setigerous pits in basal 0.3, each clearly raised as a forward directed tooth. Ovipositor. Lancet with 10-40 visible annuli: annuli outlined or not outlined at base (then present only under apical section of sheath); last annulus and first tooth annulus without pits or pits large and not sharply outlined on most of ventral edge, the preceding annuli with pits (Fig. C36.3); edge of last 3 annuli before teeth annuli and first tooth annulus extending as ridge toward ventral margin but not reaching it; edge of annuli

before teeth annuli not sinuate (Fig. C36.3); each annular pit midway between dorsal and ventral edges of lancet not otherwise impressed; its edge sharp but not developed as tooth.

Taxonomic Notes

The genera *Tremex* and *Afrotremex* are very similar. The similar width of fore wing cell 2R1 equal to as much as 1.5 times as long as cell 3R1, the lack of a large tooth-like projection at the base of the cornus in females, the uniform pitted surface of the mesoscutum, the dense pits on the frons, the sharp setae of the frons and vertex, and the moderately deep pit sculpticells on the abdominal terga differentiate *Tremex* from *Afrotremex*. The size of cell 2R1 relative to cell 3R1 is the only character state supporting *Tremex* as a natural lineage distinct from *Afrotremex*.

Diversity and distribution

This genus is found over the Holarctic region and is especially diverse in eastern Asia. There are 33 known species (Taeger and Blank 2011, Taeger *et al.* 2010). Thirty two of these species are restricted to the Old World (Taeger and Blank 2011, Taeger *et al.* 2010). The New World diversity is very small. Only one indigenous species, *T. columba* (Linnaeus), and one introduced species, *T. fuscicornis* (Fabricius) are recorded. Because we studied only six additional species of this diverse Asiatic genus, our generic concept may be incomplete and one should expect that some Asiatic species may not fit one or more character states in the above description.





C36.2: T. columba Q

37. Tremex columba (Linnaeus)

Fig. C37.1, Schiff *et al.* 2006: 14, 15 (female with black wings and mainly black banded abdomen, habitus)

Fig. C37.2 (female with yellowish brown wings and mainly black banded abdomen, habitus)

Fig. C37.3 (female with black wings and almost completely reddish brown abdomen, habitus)

Fig. C37.4 (female with yellow wings and mainly yellow banded abdomen, habitus)

Fig. C37.5, Schiff *et al.* 2006: 13 (male habitus)

Fig. C36.1 (live female with yellowish brown wings and mainly black banded abdomen)

Fig. C37.6 (live male) Figs. C37.8, C37.9 & C37.10 (maps)

Sirex columba Linnaeus, 1763: 29. Syntype female (LSUK), images of type studied. Malaise and Benson 1934: 12, T. W. Harris 1827: 211. Type locality: "America".

Sirex pensylvanicus DeGeer, 1773: 593, pl. 30, fig. 13. Syntype female (depository unknown), not examined. Synonymy by Fabricius 1781: 418, Fabricius 1793: 124; accepted by Say 1825: [page not numbered], plate 32, Bradley, 1913: 26, Ries 1951: 84, Smith 1978: 96, Smith 1979: 130. Type locality: "Pensylvanie".

Sirex Cinctus Drury, 1773: 72, [2] of "Index to the second volume", pl. XXXVIII, fig. 2. Syntype female (depository unknown, indicated as "in the possession of Dr. Fothergill"), not examined. Synonymy by Norton

C36.3: *T. columba* ♀

annulus ridge

no pit

1869: 364; accepted by Bradley 1913: 26, Ries 1951: 84, Smith 1978: 96, Smith 1979: 130. Type locality: "New York".

- Sirex americana Christ, 1791: 412. Indication on "Drury Tom. 2. Tab 38. f. 2,", which is the illustration of Sirex cinctus Drury, 1773. Objective synonym of S. cinctus due to identical type specimen; Konow 1898: 91, Bradley 1913: 26, Ries 1951: 85, Smith 1978: 96, Smith 1979: 130. Type locality: "Neuyork".
- *Tremex columba*; Say, 1825: [pages not numbered on 73rd page], plate 32 (change in combination); accepted by T. W. Harris 1827: 211, Hedicke 1938, Benson 1943, Ross 1937, Ries 1951: 84, Middlekauff 1960: 70–71, Smith 1979: 129, Harris 1827: 211, Walker 1873, Riley 1888 (illustration of larva, pupa and adult male and female), Bradley 1913: 26, Yuasa 1922 (larva), Smith 1943: 387, White and Salisbury 2000, (photograph), Marshall, 2006 (photographs of female, male and larva).
- *Tremex obsoletus* Say, 1823: 73. Holotype male (type probably lost), not examined. Synonymy by Norton 1869: 364; accepted by Cresson 1880: 67, Bradley 1913: 26, Ries 1951: 85, Smith 1978: 96, Smith 1979: 130. Type locality: Missouri.
- Tremex sericeus Say, 1823: 73. Holotype female (type probably lost), not examined. Synonymy by Cresson 1880: 67; accepted by Bradley 1913: 26, Ries 1951: 85, Smith 1978: 96, Smith 1979: 130. Type locality: Missouri.

- *Tremex Servillei* Brullé, 1846: 645, pl. 45, fig. 2. Syntype female (probably MNHN), not examined. Synonymy by Norton 1869: 366; accepted by Cresson 1880: 67, Konow 1905b: 123, Bradley 1913: 26, Ries 1951: 85, Smith 1978: 96, Smith 1979: 130. Type locality : "I'Amérique septentrionale".
- *Tremex maurus* Westwood, 1874: 116, pl. XXI, fig. 3. Syntype male (OXUM), images of male prepared by James E. Hogan and sent to HG for study. Synonymy by Cresson 1880: 67; accepted by Bradley 1913: 26, Ries 1951: 85, Smith 1978: 96, Smith 1979: 130. Type locality: "America Septentrionalis".
- *Tremex columba* race *sericeus*; Bradley 1913: 26 (change in rank).
- Tremex hospes Cockerell, 1889: 37. Nomen nudum.
- *Tremex columba* race *aureus* Bradley, 1913: 26. Syntype females [the types of this taxon should be in the CUIC collection, but the last catalogue of Hymenoptera types (Hoebeke 1980) does not list this taxon, thus the type depository remains unknown], and number of specimens not given. The word "race" is interpreted as a subspecific name based on Bradley's comments. Synonymy by Ries 1951: 85; accepted by Smith 1978: 96, Smith 1979: 130. Type localities: Colorado, Clear Creek, Sept. 5, 1898; Berkeley, Sept. 11, 1898; Denver, Sept. 13, 1898; Oct. 15, 1899; Ft. Collins, Sept. 6, 1899; New Mexico (Albuquerque); Arizona.
- *Tremex obsoletris* Bradley, 1913: 26, Smith 1979: 130 (misspelling of *T. obsoletus* Say).
- Common name: This species is known as the "pigeon tremex" from the species name "columba" meaning "pigeon".

Diagnostic combination

Both sexes of *Tremex columba* have short setae covering the body, e.g., setae of frons about 0.5 times as long as distance between inner edges of the lateral ocelli. **Females** have the cornus angular in lateral view along its ventral edge near the base. **Males** have metatarsomere 5 as long as metatarsomere 2.

FEMALE. Description

Color. Head mainly reddish brown. Surface around ocelli, often behind dorsal margin of eye, and medially behind ocelli black; antenna light reddish brown, but sometimes blackened in middle (Fig. B1.24); maxillary palp black to reddish brown; mandible mainly black. Pronotum reddish brown and ventrolaterally black; propleuron black; mesonotum mainly reddish brown, black in lateral half of mesoscutum; mesepisternum black and reddish brown over 0.5 to entire lateral surface;

metathorax black. Coxae and trochanters black; pro- and mesofemur mostly reddish brown, and metafemur mostly black; tibiae and tarsi pale yellow. Wings almost black, lightly to darkly yellowish brown, or yellow tinted. Tergum 1 or 1 and 2 mostly, terga 2–8 or 3–8 at side, narrowly or broadly across base, tergum 9 from a small lateral spot to most of surface, and tergum 10 completely to mainly reddish brown (Fig. A3.3), remaining surfaces black, or completely reddish brown. Sterna 2–7 black in basal 0.5 and reddish brown in apical 0.5, or completely light reddish brown. Sheath mainly reddish brown.

Head. Frons in lateral view with setae about 0.5 times as long as distance between lateral ocelli (Fig. B3.1), and with mostly contiguous and large pits (diameter about 0.4–0.5 times lateral ocellus diameter), but as a narrow band less dense on gena behind eye (Fig. B3.1). Postocellar region in frontal view scarcely elevated. Antenna clearly shorter than coastal cell length of fore wing; flagellum widened at middle, and with 11–14 flagellomeres (Fig. B1.24).

Thorax. Pronotum in dorsal view with numerous coarse teeth over surface. Mesonotum densely (pits 0.5–1.0 pit diameter apart) and coarsely pitted. Metatarsomere 2 in lateral view with dorsal margin clearly convex, about 3.0 times as long as high (Fig. B3.7), and tarsal pad 0.3 times as long as its ventral length. Fore wing with length of cell 2R1 subequal to cell 3R1 length.

Abdomen. Setae short and present on median region of terga 1, 5 and 6, more widespread on posterior half of terga 7 and 8 and laterally on terga 1-9, dense only medially on tergum 1, scattered elsewhere (distance about as far apart as length of setae). Tergum 9 laterally with surface anterior to each seta slightly raised and smooth (pits not clearly outlined), and distant from other raised surfaces (Fig. B3.5). Median basin of tergum 9 flat, 1.5–1.7 as wide as long, with base (delimited by small longitudinal furrows) 0.8-0.9 times as long as median length, with small teeth present posterolaterally, each tooth with small seta (Fig. B1.30). Tergum 10 in dorsal view about 1.2 times as long as median length of median basin, with teeth over dorsal surface and along lateral edges in apical half, and with round angular projection in basal 0.3 laterally (also visible in lateral view) (Figs. B1.30 & B3.3). *Sheath.* Basal section 1.15–1.25 times as long as apical section. Apical section about 0.4 times as long as fore wing length. Ovipositor. Lancet with 18-22 annuli, and with annuli outlined only under apical section of sheath (Fig. C37.7). Pitted section about as long as length of apical section of sheath (Fig. C37.7); annulus 1 outlined and without or with a very small pit, last annulus before teeth annuli with small pit (Fig. C36.3), preceding annuli each with a well defined pit, and each pit about 0.4 times as long as annulus length; first tooth annulus with sensilla grouped together in a slight impression.

MALE. Description

Color. Tibiae and tarsi color pattern variable. In **dark specimens**, tibiae light reddish brown in basal 0.5 (protibia) to 0.25 (metatibia), and tarsi black dorsally on tarsomeres 1 and 2 of protarsus, completely black on tarsomeres 1–3 of mesotarsus, and on tarsomeres 1–4 of metatarsus; in **pale specimens**, tibiae and tarsi reddish brown or paler. Abdomen color pattern mainly black to completely reddish brown. In **dark specimens**, tergum 1 and most of 2 black, terga 3 and 4 black with reddish-brown transverse band, terga 5–7 black, but pale at side, tergum 8 light reddish brown and reddish brown medially, and sterna 2–8 mainly black; in **pale specimens**, terga 1–8 and sterna 1–9 completely reddish brown.

Head. Antenna almost thread-like and clearly shorter than costal cell length of fore wing, and middle flagellomeres in lateral view about 1.5 times as long as wide.

Thorax. Metatibia in lateral view about 5.0 times as long as its maximum width and in cross section about 1.5 times as high as its maximum ventral width. Metatarsomere 1 in lateral view about 4.0 times as long as high. Metatarsomere 5 as long as metatarsomere 2 (Fig. B3.9).

Abdomen. Sterna completely and quite densely pitted. Sternum 8 with apical widely (about 0.5 times width of apical edge) and deeply indented.

Taxonomic notes

Except for *T. maurus*, we did not examine the type specimens of the other nominal species of *T. columba*. To determine the synonymy, we referred to the species descriptions, the type localities, and the available illustrations. All descriptions match our concept of *T. columba* and each name can be assigned to one of the color forms discussed below.

Geographical variation

Bradley (1913) recognized three color forms based mainly on abdominal color patterns. We agree with his concept. The palest form (body reddish brown and wings dark brown) is found mainly in the southeastern states north to southern New York and Illinois (Fig. C37.3). The names *T. sericeus* and *T. servillei* match this form (Bradley 1913). The darkest form (abdomen mainly black with yellow markings and wings dark brown to yellowish brown) is widespread in eastern North America and is recorded from Saskatchewan to the Atlantic coast and south to Georgia. Dark-winged specimens are found south of southern New York (Fig. C37.1) but become uncommon northward where they are replaced by specimens with yellowish brown wings (Fig. C37.2). The names *S. columba, S. pensylvanicus, S. cinctus, S.*

americana, T. obsoletus and T. maurus are associated with this form (Bradley, 1913). The moderately dark form (abdomen mainly pale reddish brown with black transverse bands and wings yellow tinted) is found in the prairie region north to the extreme southern portion of the Canadian prairies and as far east as Illinois and southernmost Ontario near Lake Erie, and in the Rocky Mountain region south into northern Mexico (Fig. C37.4). The name T. columba aureus applies to this form (Bradley 1913). Specimens with intermediate color pattern are known only from the bordering prairie regions in Saskatchewan and Manitoba. The latter specimens are similar to the eastern form with dark abdomen, but the wings are yellow and the apex of the abdomen in females is often more widely pale. The two forms found in the southern half of eastern United States are sympatric and are part of two discrete color forms. We found one female with the abdomen showing the pattern of the two forms, one on each side of the abdomen. Despite some evidence of gene flow in the northernmost part of its range (in the Canadian prairies), females of the western form remain sharply distinct in central Illinois where all three forms occur. Females probably mimic a common vespid species with a matching body and wing color pattern in each of the regions that are present during the main T. columba flight period. The most likely models commonly flying at the time that females of *T. columba* are ovipositing probably belong to the genus Polistes (Vespidae). Tremex columba females of the reddish abdomen form are similar to P. perplexus Cresson, P. bellicosus Cresson or P. carolinus (Linnaeus), females of the dark form with black wings are similar to P. annularis (Linnaeus), P. metricus Say, or dark winged (southern) specimens of P. fuscatus fuscatus (Fabricius), females of the dark abdomen form with reddish-brown wings are similar to the pale winged P. fuscatus laurentianus Bequaert, and females of the moderately dark form with yellow wings are similar to *P. aurifer* Saussure and probably other similarly colored western species. Information from morphology and DNA barcoding shows no difference between the three color forms. Therefore, we treat them as discrete color forms of one species.

Biological notes

Early summaries of the biology of *T. columba* were given by T. W. Harris (1827, 1857), Thomas (1876), Harrington (1882a,1882b), Saunders 1883, Harrington (1893), Riley (1888), Packard (1890), Ashmead (1900), Felt (1905 – damage and life history), and Herrick (1935). Smith and Schiff (2002) provided a recent synthesis, much of it derived from Stillwell (1964, 1967). They also published the emergence times for both *T. columba* and one of its parasitoid *Ibalia anceps*. Females attack dead

or weaken limbs of deciduous trees. Oviposition starts in mid August and lasts till late September. Females lay 2–7 eggs in each oviposition hole. The oviposition holes are at about a right angle with the bark and go to a depth of 2–15 mm in the sapwood. Eggs either hatch within 15–30 days or over winter and hatch the following spring.

Newly hatched larvae make their tunnels roughly parallel to the bark at a depth less than 4 cm. Larvae go through at most 11 instar stages. Larval development lasts two or more years in cold temperate regions. Larvae cannot develop without the presence of the wood fungus Cerrena (Daedalea) unicolor Bull. Murr. This fungus is associated with females in all stages of development. Females adults carry the fungal spores in mycangia located in the abdomen anterior to the ovipositor. Eggs pick up the fungus as they pass down the ovipositor and the fungus is also injected into the wood at oviposition and starts developing immediately, so by the time a larva hatches there is plenty of fungus to eat. Female larvae have special hypopleural organs to carry the fungal oidia (Stillwell 1965). This organ is found between the first and second abdominal segments below the level of the spiracle (it is also seen in some specimens between the metathorax and the first abdominal segment). At molting, the fungus in the hypopleural organ is not transferred to the later instar larva, but must be picked up again.

In the prepupa, a wax-like substance covers the oidia held in the hypopleural organ. After molting, the spores are introduced into the mycangia of the newly emerged female. Galleries are filled with sawdust and frass and may extend for 1–3 m. Pupae are found in the sapwood to as deep as 30 cm in the heartwood. It takes 3–5 weeks for the pupa to complete its development.

In Canada, emergence of new adults starts in mid August, reaches a peak in early September, and ends in early October. Males start their emergence about one week before females. Females may have to tunnel up to 1 m to emerge. Under such condition a female may lay several hundreds eggs on the way out. These unfertilized eggs will become males. Mated females produce offspring of both sexes. An amazing density of 162 specimens in a small 20" by 10" (50 cm by 25 cm) portion trunk was reported by Laurent (1931). Damage by larvae was described by Thomas (1881).

The main parasitoids are Ichneumonidae (*Megarhyssa atrata* (Fabricius), *M. greenei* Viereck and *M. macrura* (Linnaeus)) and Ibaliidae (*Ibalia anceps* Say). Species of *Megarhyssa* are keyed in Townes and Townes (1960), and those of *Ibalia* in Smith and Schiff (2002).

Hosts and phenology

Tremex columba has been reared from a wide variety of angiosperm trees (T. W. Harris 1827, T. W. Harris

1841, Fitch 1858a, 1857, 1859, Clementi 1868, Walsh and Riley 1868, Riley 1870, Thomas 1876, Thomas 1881, Harrington 1882a, Harrington 1882b, Saunders 1883, Dimmock 1885, 1887, Packard 1881, Packard 1890, Lintner 1897, Fyles 1917, Blackman and Stage 1924, Essig 1926, Davis 1932, Herrick 1935, Smith 1943, Beal and Massey 1945, Middlekauff 1960, Smith 1979: 129, Smith and Schiff 2002). The main hosts are hickories, maples and, elms (83% of records). Based on 218 reared and confirmed specimens, hosts are: Acer sp. (16), Acer negundo (1), A. rubrum (31), A. saccharum (3), Betula sp. (Herrick 1935), Carpinus sp., Carya sp. (86), C. illinoensis (1), Castanea dentata (1), Celtis sp. (3), C. laevigata (4), C. occidentalis (1), Fagus grandifolia (4), Fraxinus sp. (1), Juglans cineria (1), Malus sp., Nyssa sylvatica (2), Platanus sp. (1), Populus sp. (8), Pyrus sp., Quercus sp. (8), Robinia sp. (3), Salix sp. (1), Ulmus sp. (35), U. americanus (6), U. glabra (1). Three host records gymnosperms are unlikely: Picea abies (1), Pinus resinosa (1) (Pinaceae), and Helianthus (2) (Asteraceae).

Based on 126 field-collected specimens, the earliest and latest capture dates are June 3 and October 10. The main flight period is from the second half of July to the first half of October with a peak in the first half of August Stillwell (1964, 1967). Adults of *T. columba* were not captured at hill tops, but we observed several hundreds specimens swarming around an old dying sugar maple tree. Most specimens were out of reach, above 4–5 m.

Range

CANADA: AB, NB, NS, ON, QC, SK. **USA:** AL, AR, CA (probably adventive), CO, CT, DC, FL, GA, IA, ID, IL, IN, KS, KY, LA, MA, MD, ME, MI MN, MO, MS, MT, NC, ND, NE, NH, NJ, NV, NY, OH, PA, RI, TN, TX, UT, VA, VT, WI, WV, WY. *Tremex columba* is recorded in southern Canada from Alberta to Nova Scotia south to Arizona and Florida (Bradley 1913, Rohwer 1928, Ries 1951, Middlekauff 1960, Stange 1996, Smith 1979) (Figs. C37.8, C37.9 & C37.10). Specimens originating from Mexico were intercepted at entry ports along the United States and Mexico border.

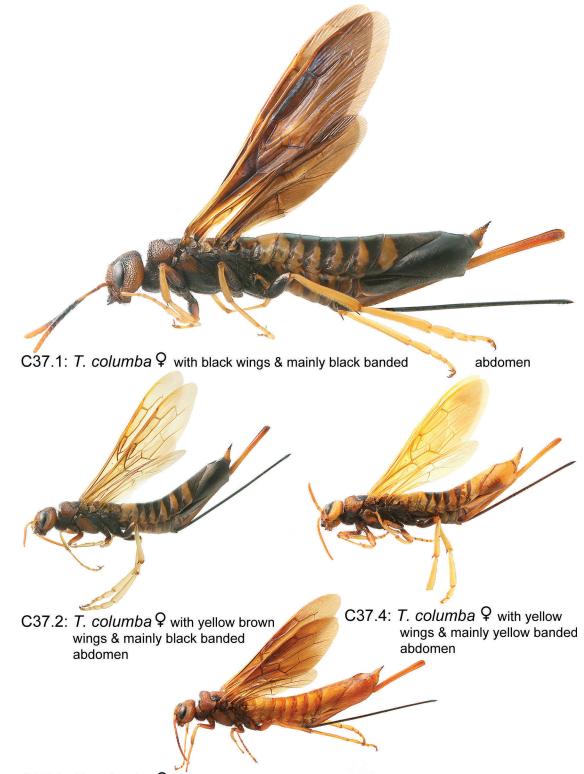
Specimens studied and included for the distribution maps: 955 females and 323 males from BYUC, CASS, CNC, CUCC, CUIC, DEBU, EDUM, FRLC, FSCA, GLFC, LEMQ, MNRQ, NCSU, NFRC, OSAC, UASM, UCRC, USGFS–GA, and USNM.

Specimens for molecular studies: 21 specimens. See Fig. E2.2.

CANADA. Ontario: 2007, *SIRCA 023*, 604; 2007, *SIRCA 025*, 618; 2007, *SIRCA 026*, 619; 2007, *SIRCA 027*, 624; 2007, *SIRCA 028*, 624. **USA. Arkansas**: 1999, *CBHR 110*, 658. **Georgia**: 2006, *CBHR 573*, 658. **Illinois**: 2006, *CBHR 373*, 658. **Michigan**: 2007, *CNCS*

1047, 616; 2007, *CNCS 1048*, 557; 2007, *CNCS 1050*, 596; 2007, *CNCS 1051*, 628; 2007, *CNCS 1052*, 609. **Minnesota**: 2008, *CBHR 1464*, 597. **Mississippi**: 1997, *CBHR 5*, 658; 2002, *CBHR 131*, 658; 2002, *CBHR 132*,

658. Montana: 2006, *CBHR 37*0, 658. New York: 2005, *CBHR 201*, 658. Oregon: 2008, *CBHR 400*, 658. South Carolina: 2006, *CBHR 892*, 508.



C37.3: *T. columba* **Q** with black wings & reddish brown abdomen



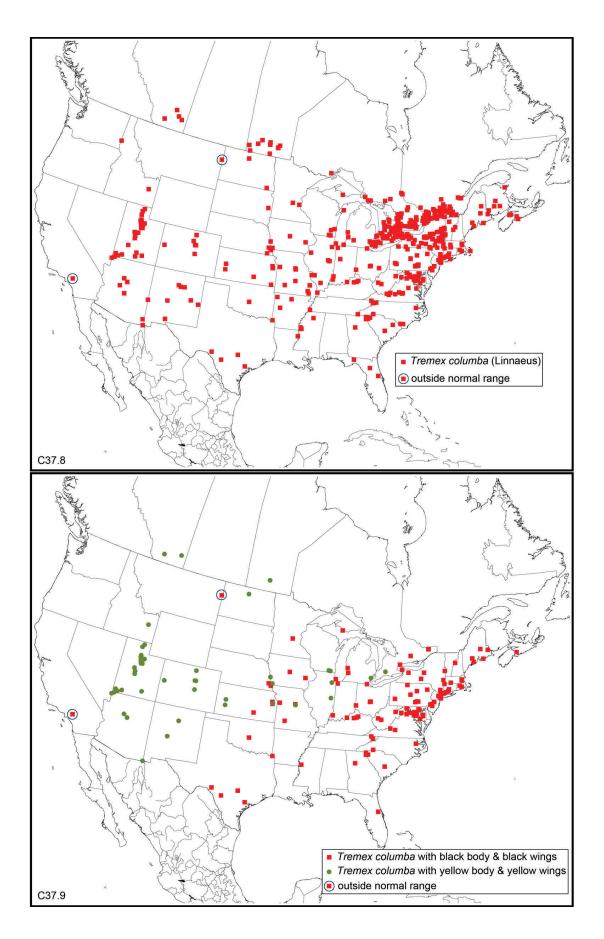
C37.5: T. columba 🗗

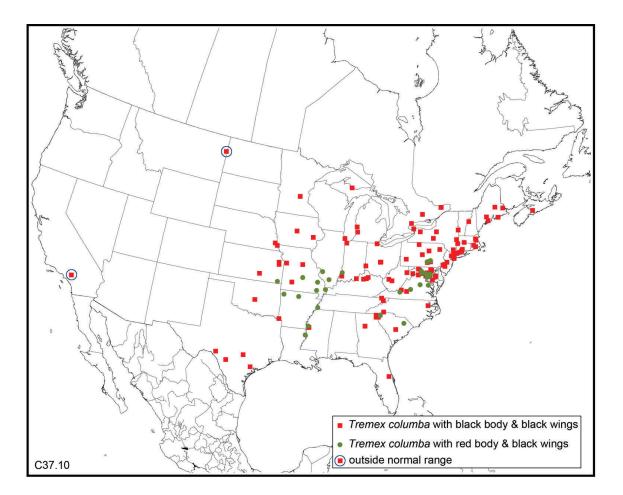


C37.6: *T. columba O*



C37.7: *T. columba* 9





38. Tremex fuscicornis (Fabricius)

- Fig. C38.1 (female dorsal habitus) Fig. C38.2 (female lateral habitus) Fig. C38.3 (male dorsal habitus) Fig. C38.4 (male lateral habitus)
- Fig. C38.5 (map)
- *Sirex fuscicornis* Fabricius, 1787: 257. Type female (ZMUC), not examined. Thomson, 1871: 326. Type locality: "Halae Saxonum".
- Sirex Struthiocamelus Villers, 1789: 132–133. Taeger et al. 2010.
- Sirex Camelogigas Christ, 1791: 411. Taeger et al. 2010.

Diagnostic combination

Both sexes of *Tremex fuscicornis* have long setae covering the body, e.g., setae of frons in lateral view are about as long as or longer than the distance between the inner edges of the lateral ocelli. **Females** have the cornus in lateral view not protruded and angular along the ventral edge near its base. **Males** have metatarsomere 5 as long as length of metatarsomere 2 + 3.

FEMALE. Description

Color. Head brown or black. Antenna light reddish brown or black on middle antennomeres; maxillary palp black to reddish brown; mandible mainly black. Pronotum mainly reddish brown and black at side; propleuron black (Fig. C38.2); mesonotum black to partly black and reddish brown; mesepisternum black; metathorax black. Coxae and trochanters black; pro- and mesofemur mostly reddish brown, and metafemur mostly black; tibiae and tarsi pale yellow. Wings lightly tinted yellowish brown. Tergum 1 black, tergum 2 or 2 and 3 mostly, terga 3–8 or 4–8 at side, narrowly or broadly across base, tergum 9 across middle, and tergum 10 completely to mainly yellow, remaining surfaces black. Sterna 2–7 in black in basal 0.5 and reddish brown in apical 0.5, or completely light reddish brown. Sheath mainly reddish brown.

Head. Frons in lateral view with setae on frons as long as or longer than distance between lateral ocelli (Fig. B3.2), and with mostly contiguous and small pits (diameter about 0.3 times lateral ocellus diameter), but as a narrow band less dense on gena behind eye (Fig. B3.2). Postocellar region in frontal view scarcely elevated. Antenna clearly shorter than coastal cell length of fore wing ; flagellum slightly widened centrally, and with 10–13 flagellomeres.

Thorax. Pronotum in dorsal view with numerous coarse teeth over surface. Mesonotum densely (pits 0.3–0.5 pit diameter apart) and moderately pitted on central portion. Metatarsomere 2 in lateral view with dorsal margin almost straight, about 3.0 times as long as high (Fig. B3.8), and tarsal pad 0.8 as long as its ventral length. Fore wing with length of cell 2R1 1.2–1.5 times as long as length of cell 3R1.

Abdomen. Setae long and few on median region of terga 1, 5 and 6, more widespread on posterior half of tergum 7 and posterior 0.7 of tergum 8 and laterally on terga 1–9, dense only medially on tergum 1, scattered elsewhere (distance about as far apart as length of setae). Tergum 9 laterally with surface anterior to each seta markedly elevated as a tooth (pit coarsely outlined), and very close or fused to tooth (Fig. B3.6). Median basin of tergum 9 flat, 1.4-1.6 as wide as long, base (delimited by small longitudinal furrows) about 0.9 times as long as median length, with small teeth present posterolaterally, each tooth with small seta. Tergum 10 in dorsal view 1.1-1.2 times as long as median length of median basin, with few teeth over dorsal surface and along lateral edges in apical half, and without round angular projection in basal 0.3 laterally (best seen in lateral view) (Fig. B3.4). Sheath. Basal section 1.3–1.4 times as long as apical section. Apical section about 0.5 times as long as fore wing length. **Ovipositor.** Lancet with about 12 annuli, and with annuli outline only under apical section of sheath. Pitted section 0.5–0.6 times as long as length of apical section of sheath; annulus 1 outlined and without pit, last annulus before teeth annuli without pit, preceding 6 annuli each with a clearly defined pit, and each pit about 0.25 times as long as annulus length; first tooth annulus with a long narrow impression with a double row of sensilla.

MALE. Description

Color. Coxae and metafemur (except extreme base) black, tibiae, and tarsi of fore and middle legs reddish brown. Abdomen mainly black

Head. Antenna almost thread-like and clearly shorter than costal cell of fore wing, and middle flagellomeres about 2.0 times as long as wide.

Thorax. Metatibia in lateral view about 4.5 times as long as its maximum width and in cross section about 1.5 times as high as its maximum ventral width. Metatarsomere 1 in lateral view about 3.5 times as long as high. Metatarsomere 5 as long as length of metatarsomeres 2 + 3 (Fig. B3.10).

Abdomen. Sterna completely and quite densely pitted. Sternum 8 with apical edge widely (about half of the width of apical edge) deeply indented.

Taxonomic notes

Illustrations of the holotype were examined and match closely our specimens from Europe. We have seen two specimens from Chile and they seem to match closely the European specimens we examined. Although a large number of *Tremex* species exist in China, it is possible that the European species may be different in China (Stephan Blank, personal communication). For the purposes of this paper we accept the identity of Chilean specimens as the Palaearctic *T. fuscicornis*.

Biological notes

Information on the biology of *Tremex fuscicornis* and its associated fungus were published by Palma *et al.* (2005), Parra (2007), and Pažoutová and Šrutka (2007).

Hosts

In Chile, *Tremex fuscicornis* is most destructive to poplar (*Populus nigra*), but it is also recorded from *Robinia pseudoacacia* and *Acer negundo* (Baldini 2002; Palma *et al.* 2005; Parra 2007).

Range

CHILE: Near Santiago: Provincia de Aconcagua, V Región (Palma *et al.* 2007); Región Metropolitana (Baldini 2002); Región Valparaiso (Parra 2007), Región: R. M., Communa: NOS, Col., César Hernández, Fecha: 17/03.01 (1 F, 1 M; OSAC). *Tremex fuscicornis* is a Palaearctic species known from Europe to Japan. It was accidentally introduced into central Chile (Fig. C38.5) and was first reported by Baldini (2002). It apparently entered the country in wooden crates infested with larvae from China (Baldini 2002; Pažoutová and Šrutka 2007).

Specimens studied (two specimens from Chile and a few specimens from Europe and Asia) are included for the distribution maps: 11 females and 4 males from CNC, OSAC and USNM.

Specimens for molecular studies: 7 specimens. See Fig. E2.2.

CHINA: 2006, *CBHR 387*, 658; 2006, *CBHR 391*, 658; 2006, *CBHR 392*, 658; 2006, [associated pre-adult], *CBHR 394*, 658, 2006, [associated pre-adult], *CBHR 395*, 658; 2007, *CBHR 1201*, 658; 2007, *CBHR 1202*, 658.



C38.1: *T. fuscicornis* ♀



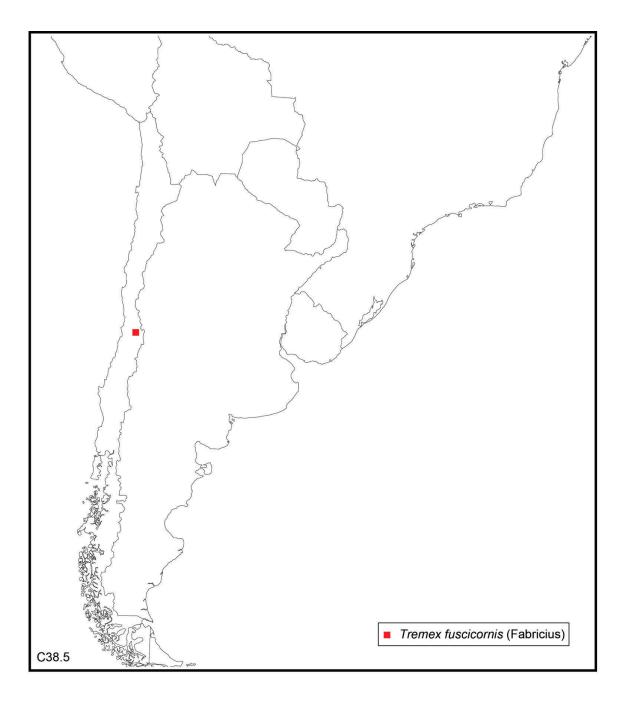
C38.2: T. fuscicornis Q



C38.3: T. fuscicornis o



C38.4: T. fuscicornis o





C39.1: X. indecisus Q

39. Genus Xeris A. Costa

Fig. C39.1 (live female)

- *Xeris* A. Costa, 1894: 259. Type species: *Ichneumon spectrum* Linnaeus; monotypic.
- *Neoxeris* M.S. Saini and D. Singh, 1987: 177. Type species: *Neoxeris melanocephala* M.S. Saini and D. Singh; monotypic. NEW SYNONYM.

Diagnostic combination

Both sexes of *Xeris* are easily recognized by the small vertical ridge on the gena posterior to the eye, and the hind wing without an anal cell.

Description

Color. Black portions of body without metallic reflections. Head. Antennal sockets with distance between their inner edges 1.5-2.0 times distance between outer edge of socket and nearest edge of eye (Fig. B5.4). Distance between inner edges of lateral ocelli 0.5-1.2 times as long as distance between outer edge of lateral ocellus and nearest inner edge of eye (Figs. B5.3 & B5.4). Maximum distance between outer edges of eyes either less than maximum width of head (thus, in frontal view, genal edges completely visible and not intersected by outer edges of eyes) (Fig. B5.4) or as long as maximum width of head (thus, in frontal view, genal edges intersected by outer edges of eyes) (Fig. B5.3). Minimum distance between inner edges of eyes about 1.6 times as long as maximum eye height (Fig. B5.4). Gena with ridge behind eye, with white spot almost always in dorsal half (Fig. B1.41), and in lower 0.5 with posterior edge of pits not elevated. Head with setae sharp at apex. Antenna with 14 or more flagellomeres (smallest specimens have the lowest number), and middle flagellomeres in dorsal view 3.0-4.0 times as long as high; in female apical

5–10 flagellomeres with sensory oval impressions on dorsal and ventral surfaces, in **male** only with ventral sensory oval impressions; in **female** middle and apical flagellomeres with sensory pits over most surfaces except outer surface, in **male** sensory pits present over inner surface and a small section of outer surface.

Thorax. Pronotum smooth on anterior vertical surface. Mesoscutum densely pitted only over median 0.5-0.7. Mesotarsomere 1 in lateral view not enlarged, its dorsal and ventral edges almost parallel, and base of tarsomere 0.7 or less its maximum width. Metatibia in male in lateral view 5.5-9.0 times as long as maximum width. In female metatarsomere 2 in lateral view with dorsal edge 4.0-6.0 times as long as maximum height. Metatarsomere 5 0.5–0.7 as long as metatarsomere 2 (Fig. B5.51). Fore wing with apex acutely and angularly rounded, with vein 2r-m present and joined to cell 2M (as in Fig. B1.71), with cell 1Rs2 clearly wider than long, with cell 3R1 3.5-4.5 times as wide as long, with vein 2r-rs joining stigma near middle, with stigma gradually attenuated even distal to junction with vein 2r-rs (as in Fig. B1.25), without vein Cu1, with vein 1cu-a joining vein Cu close to M, and with vein 3A well developed, stump-like or absent. Hind wing with hamuli clearly present basal and apical to junction of veins R1 and C (as in Fig. B1.11), and without anal cell.

Abdomen. Female. Cornus in dorsal view long, narrow, and lateral edges either not constricted or constricted near middle (Fig. C39.2). Tergum 9 with median basin with lateral edges markedly divergent, straight then rounded near lateral angle, and sharply outlined for about 0.5 times median length of basin, and with base (outlined by black furrows laterally) 0.5–0.9 times as wide as median length of basin (Fig. C39.2). Cercus present but very small. *Sheath.* Length of basal section 0.2–0.5 as long as apical section (Figs. B5.11, B5.13 & B5.13); apical section with lateral surface sharply folded except at very base and apex (Fig. B5.13, insert), or not folded (in one

species, X. tarsalis), and without teeth in apical third of dorsal margin (Fig. B 5.11, insert). Ovipositor. Lancet with any of annuli 3-10 aligned with junction of basal and apical sections of sheath; first tooth annulus with ridge on ventral edge with shallow, long and open ended pit (Fig. B5.15); for most species annuli 4-6 anterior to teeth annuli with medium pit and pits decreasing in size anteriorly in following 3-5 annuli, and following annuli without pit or with very small pit present from anterior annulus to as many annuli as starting at annulus 2, or in one species, X. tarsalis, with many large pits starting at annulus 2 up to teeth annuli (Fig. B5.14); edge of last 5 to 7 annuli before teeth annuli ventral to pit sharply and acutely produced, and edge of last 7 to 14 annuli before teeth annuli extended as a sharp ridge to ventral edge of lancet.

Taxonomic notes

Neoxeris melanocephala M.S. Saini and D. Singh, based on three females, is a typical species of *Xeris*. The eye proportions (1.25 as high as long) are the same as for all Xeris specimens we examined (range 1.18-1.63, based on 62 specimens and 5 species). The lack of a white spot on the gena in females is not a good criterion for a genus level classification. For example, 30 females examined of X. himalayensis (Bradley) from India and Pakistan showed a complete range from a large white spot to no spot on the gena, and we have seen a few specimens of *Xeris melancholicus* and *X. spectrum* with a completely black head. The ovipositor of N. melanocephala near the apex is typical of almost all *Xeris*, except *X. tarsalis*. Other described character states are typical of females of most Xeris species. We suspect that N. melanocephala is simply a dark color form of X. himalayensis. The only significant difference in the description is the reddish brown apical section of the flagellum. This color pattern is seen occasionally in specimens with a black flagellum. The Indian species is therefore transferred to Xeris as X. melanocephalus (M.S. Saini and D. Singh), new combination.

The gender of *Xeris* is questionable. The name of its type species, *Ichneumon spectrum*, is a noun. In the latest catalog (Taeger *et al.* 2010) it is treated as masculine in *X. morrisoni indecisus*, and as feminine in *X. indiana*, the latter being an inadvertent misspelling of Saini *et al.* (2006). (Stephen Blank, pers. comm.). *Xeris* as a classical name means a kind of plant (Bradley 1913). This name does not make sense. Costa (1894) does not give the origin of the generic epithet, but very likely it is an palindrome of the name *Sirex*. We follow Maa (1949) and consider *Xeris* as masculine.

Biological notes

Not much has been published on the biology of *Xeris* species. The European *X. spectrum* (and the Japanese population of this species) is clearly distinct from the North American *X. caudatus*. Because we have no information about on *X. caudatus*, we present biological information under the genus heading.

The most interesting feature of X. spectrum and also *X. caudatus* is that females do not carry symbiotic fungus in their mycangia (Francke-Grosmann 1939, Fukuda and Hijii 1997, confirmed by NMS). The question is therefore what do larvae eat during their development? Females of most species of Siricidae carry arthrospores of Amylostereum, a genus of basidiomycete fungi. During oviposition the fungus is deposited on each egg placed in the sap wood. The fungus produces an enzyme to decompose the wood cellulose or lignin, changing it into a form that can be assimilated by the larvae and making larval development possible. Fukuda and Hijii (1997) clearly showed that larvae of X. spectrum in Japan develop only if A. chailletii or A. areolatum are present at the oviposition site. Both species of fungi are equally accepted by Xeris larvae. Fukuda and Hijii's observations confirm earlier observations in Europe that X. spectrum females often deposit their eggs in trees already infested with Sirex and Urocerus spp. (Francke-Grosmann 1954). Moreover, the emergence holes of X. spectrum in Japan are in close proximity to those of other horntails. This suggests that females of Xeris are attracted by odors emitted by Amylostereum fungi inoculated by other fungus carrying horntails.

Xeris spectrum in Japan shows two periods of emergences, one in spring and one in summer (Fukuda and Hijii 1997). We have no evidence of a similar pattern in the Nearctic *X. caudatus*. The spring oviposition cycle offers *X. spectrum* larvae a very viable fungus but more competition with other horntail larvae, whereas a summer oviposition cycle offers the *Xeris* larvae a less viable fungus with less competition from other horntail larvae.

Diversity and distribution

Xeris is a moderate sized genus with 10 species and subspecies. Three species are recorded from Eurasia (Taeger and Blank 2011, Taeger *et al.* 2010). All are in the northern hemisphere. In the New World, seven endemic species are known. They are recorded from southern Mexico to boreal regions of Canada and Alaska. The greatest diversity is in western North America.



C39.2: X. melancholicus Q

40. Xeris caudatus (Cresson), sp. rev.

Fig. C40.1 (female habitus) Fig. C40.2 (male habitus) Fig. C40.6 (map)

Urocerus caudatus Cresson, 1865b: 247. Holotype female (ANSP), examined by DRS. Cresson 1916: 10. Type locality: "Colorado Territory".

Sirex caudata; Kirby, 1882: 382 (combination).

Xeris caudata; Ashmead, 1898: 180 (combination).

- *Xeris spectrum* race *caudata*; Bradley 1913: 23 (change in combination and rank).
- *Xeris spectrum*; Maa, 1949: 86 (not Linnaeus, 1758: 560). Burks 1958: 17, Smith and Schiff 2002: 185.
- *Xeris spectrum spectrum*; Maa, 1949: 86 (status); accepted by Burks 1958: 17, Middlekauff 1960: 70 (in part), Burks 1958: 17, Smith 1979: 129.

Diagnostic combination

Among specimens with a marginal longitudinal band on the pronotum and with short setae on the head [*melancholicus*], **both sexes** of *X. caudatus* are recognized by the very small pits (pit diameter 0.05–0.15 times lateral ocellus diameter) on the gena between the upper and lower limits of the genal ridge, and the small white spot that usually does not extend to the genal ridge. **Females** also have completely light reddish brown coxae (except the black anterior and posterior dorsal edges) and generally longer apical section of the sheath (basal section/apical section ratio less than 0.25 for most specimens). **Males** of *caudatus* cannot be separated from males of *melancholicus*.

FEMALE. Description

Color. Head black except for small white spot on gena

dorsal to middle of eye; white spot usually not extending down to genal ridge (as in Fig. B5.41); antenna black. Thorax black except for white longitudinal band extending from posterolateral to anterolateral angles including vertical portion of anterior angle (as in Fig. C43.3). Legs including coxae light reddish brown (coxae black on anterior and posterior dorsal edges) (Fig. C40.1). Fore wing clear except for lightly tinted band before stigma, in apical 0.25, and in cell 2CU; costal cell brown and most of area ventral to anal cells yellowish brown; veins black (including veins C, R and stigma on both sides of junction with vein 1r-rs) (as in Fig. B5.17). Abdomen black. Sheath with apical section black and basal section reddish brown.

Head. Eye in lateral view (20 specimens measured) with maximum height 1.37-1.64 times as long as maximum length (as in Fig. B5.43), and maximum height of eye 0.42-0.51 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head) (as in Fig. B5.7). Gena in dorsal view with maximum distance between outer edges clearly wider than maximum distance between outer edges of eyes (in frontal view outer edges of eyes clearly not intersecting genae) (as in Fig. B5.4), and in lateral view distance between outer edge of eye and genal ridge 0.48-0.61 times as long as maximum length of eye (as in Fig. B5.27). Transverse ridge above mandible narrow, sharp and mainly smooth (as in Fig. B5.21). Head in dorsal view with pits restricted to vertex (scarcely pitted from dorsoposterior edge of eye to occiput) and postocellar area (scattered or absent on most of median furrow, but a little more widespread near lateral ocelli) (as in Fig. B5.2), in lateral view almost absent on gena ventral to genal ridge, and few and small (diameter of pit 0.1-0.2 times lateral ocellus diameter) between outer edge of eye and genal ridge (mainly near eye) (as in Fig. B5.43).

Thorax. Fore wing vein 3A absent (58%), reduced to a

stump (37%), rarely extending slightly as a nebulous vein (5%), but not extending along posterior margin of wing. Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.8 times as wide as median length, with maximum width of basin 1.6 times as wide as median length and basin about 0.5 times as long medially as median length of cornus (as in Fig. C39.2). Cornus constricted in dorsal view, its minimum width (at constriction) 0.8 times as wide as maximum width subapically (as in Fig. C39.2). Sheath. Length 1.2-1.4 times as long as fore wing length; basal section 0.20-0.27 times as long as apical section (Fig. C40.3); lateral surface of apical section with well defined ridge (as in Fig. B5.13, insert). Ovipositor. Lancet with 22-32 annuli (first 15 annuli hard to see, but still outlined; N = 9) (as in Fig. B5.15); junction of basal and apical sections of sheath aligned between 2nd and 3rd, or occasionally at 3rd annuli; medium pits present on last 4–5 apical annuli before teeth annuli, and very small pit on 7-15 preceding annuli (as in Fig. B5.15).

MALE. Description

Color. Coxae, tibiae (except very base) and tarsomeres 1–5 black (apical articles sometimes brown or reddish brown in old or teneral specimens); femora completely or mainly, and extreme base of tibiae (not sharply outlined but gradual shift) reddish brown (as in Fig. B5.51).

Thorax. Metatibia with shallow notch on dorsal edge in basal 0.25.

Taxonomic notes

In the Old World, five species and subspecies of Xeris are recorded (Taeger and Blank 2011, Taeger et al. 2010): X. spectrum cobosi Viedma and Suarez (1961), X. himalayensis Bradley 1934, X. indianus Vasu and Saini (1999), X. spectrum (Linnaeus 1758) and X. spectrum malaisei Maa (1949). We also include X. melanocephalus (Saini and Singh 1987, Taeger et al. 2010). In previous works, X. caudatus was known as Xeris spectrum spectrum (Maa 1949, Smith 1978 & 1979, Smith & Schiff 2002, Schiff et al. 2006). We have seen the types of all the above taxa except X. indianus and X. melanocephalus. The North American specimens of X. caudatus are rather similar in many character states to many specimens of the European Xeris spectrum and to the types of the Asiatic X. spectrum malaisei. Xeris spectrum malaisei differs in many character states from American specimens and from X. spectrum spectrum. We recognize X. caudatus as specifically distinct from both subspecies of X. spectrum. All studied specimens of the X. spectrum complex consists of the subspecies of X. spectrum, X. caudatus, and X. melancholicus; the complex is recognized by

the well developed longitudinal band on each side of the pronotum in dorsal view and the low density of pits on each side of the postocellar area. However, there are differences between the Eurasian species of the complex and the North American specimens. A revision of *Xeris* is ongoing, so we discuss here only the currently described taxa of the complex.

Based on color pattern, females of the transpalaearctic *X. spectrum* with dark coxae and males with reddish brown apical 0.15-0.2 of metatarsomere 1 are easily distinguished from females and males of *X. caudatus*. We studied 135 specimens of *X. spectrum* and the females match the Linnean type of *X. spectrum* (Linnaeus).

X. caudatus:

Gena between eye and ridge with very few small to very small pits (0.05–0.2 times lateral ocellus diameter) (as in Fig. B5.43). In **both sexes**, genal spot near upper eye margin small (rarely absent) and usually not extending to genal ridge (as in Fig. B5.43); fore wing veins C and R brown to black (paler only in old specimens), vein R at junction with vein 1r–rs brown to black, and membrane between veins C and R tinted yellowish brown (paler only in old specimens) (as in Fig. B5.17). In **female**, coxae light reddish brown (as in Fig. B5.37). In **male**, tibiae completely to almost completely black, with reddish brown spot at base, when present, narrow and diffusedly outlined, and tarsi black (teneral specimens may be paler) (as in Fig. 5.51).

Xeris spectrum spectrum:

Gena between eye and ridge with few medium size pits (0.2–0.25 times that of the lateral ocellus). In female, genal spot near upper eye margin brownish yellow and ill-defined but sometimes extending over both sides of genal ridge. In male, spot usually large and not sharply outlined, quite white, and extending over both sides of the genal ridge (Fig. C40.4); fore wing vein C and R mainly reddish brown to brown but whitish at extreme base, vein R at junction with vein 1r-rs whitish, and membrane between veins C and R clear to light whitish yellow tinted (paler only in old specimens). In female, coxae at least black or mostly black on outer surface, ventral and inner surfaces black, brown or reddish brown (metacoxa sometimes the palest) (Fig. C40.5). In male, protibia reddish brown, usually with narrow black longitudinal band along outer margin, and protarsus light reddish brown; mesotibia light reddish brown but black in apical half, mesotarsus light reddish brown, metatibia with sharply outlined white spot in basal 0.1-0.2, metatarsomere 1 black but white at extreme base and reddish brown in apical 0.15-0.2, metatarsomeres 2-5 light reddish brown.

The holotype female of *Xeris spectrum malaisei* Maa is distinguished from females of *X. caudatus* by a narrow head, black coxae and femora, and reddish brown flagellum in apical 0.2–0.3.

X. caudatus:

In **female**, coxae light reddish brown and flagellum black. Gena between eye and ridge with very few small to very small pits (0.05–0.2 times lateral ocellus) (as in Fig. B5.43). Maximum distance between outer edges of genae, in frontal view, clearly greater than maximum distance between outer edges of eyes. Fore wing veins 1A and 2A of cell 1A not parallel in apical half of cell. Vein 2A not close to posterior wing edge and more curved, and vein 1A quite clearly curved (as in Fig. A3.30).

Xeris spectrum malaisei:

In **female**, coxae black and flagellum black becoming reddish brown in apical third. Gena between eye and ridge with few medium size pits (0.2–0.25 times that of the lateral ocellus diameter). Maximum distance between outer edges of genae in frontal view slightly greater than maximum distance between outer edges of eyes. Fore wing veins 1A and 2A of cell 1A subparallel in apical half of cell. Vein 2A close to posterior wing edge and vein 1A almost straight.

Xeris himalayensis and *X. cobosi*, the third and fourth Euroasiatic species studied by us (38 specimens seen), are not particularly close to *X. caudatus*. In these two species, the pronotum has no white longitudinal band, pits are more abundant (denser) and larger on the vertex and the space between the genal ridge and the eye (quite similar to those of *X. indecisus* or *X. morrisoni*), in **females** the genal spot is small to absent, and in **males** (only known for *X. himalayensis*) the spot is very large and tarsomeres 3–5 are reddish brown.

In summary, the North American *X. caudatus* is distinct from all named Old World *Xeris* on structure and color pattern in both sexes. We have not seen specimens of *X. caudatus* from temperate and boreal Asia. The nearest Asiatic populations studied are from Japan and China and the Russian Far East. They are also very distinctive in color pattern from *X. caudatus* (including specimens from Alaska). Thus, there is no evidence that *X. caudatus* has a Holarctic range. Our morphological data supports our decision to classify *X. caudatus* as specifically distinct from any of the Eurasian *X. spectrum* species complex. Our DNA barcoding results support this conclusion.

Despite the above clarifications, there is still a problem associated with *X. caudatus*. The barcodes of specimens from eastern North America differ by 3.5% from the barcodes of specimens from western Washington (three specimens only). More specimens studied for these two forms confirmed the above difference. A study based on females from the western states and provinces (western Alberta and central and southern British Columbia) and samples from eastern Alberta to Nova Scotia show a different trend in the ratio of the length of the basal and apical sections of the sheath. In the western population, the apical section of the sheath is generally longer relative to the basal section. For 73 females from the western states and provinces, the relation between the basal section and the apical section shows a lower mean = 0.237 (one standard deviation = 0.015) and for 42 females in the East (e.g., Saskatchewan to Nova Scotia), the relation between the basal section and the apical section shows a higher mean = 0.296 (one standard deviation = 0.030). The differences between the means of the two samples are 1.25 standard deviations apart. Basically, 75% of specimens could be distinguished if the ratio is smaller than 0.25 for the western unit (specimens from Alaska, British Columbia, Alberta and southward including western South Dakota) or greater than 0.27 for the transcontinental unit (specimens from Alberta and eastward). Specimens with values between 0.25 and 0.27 are of uncertain status. Moreover, in Alberta both populations exist sympatrically. Therefore, we consider the two units as specifically distinct.

Two names apply to the North American units, *Sirex melancholicus* Westwood and *Urocerus caudatus* Cresson. The female holotype of *U. caudatus* is from Colorado and matches the western species. It is the oldest name.

Hosts and phenology

Xeris caudatus has a wide host range within Pinaceae (Middlekauff 1960, Cameron 1965, Morris 1967, Kirk 1975). The main hosts are firs. Based on 340 reared and confirmed specimens, the hosts are: *Abies concolor* (298, Kirk, 1975), *Picea engelmannii*, and *Pinus ponderosa*. Other hosts are *Abies balsamea* (15), *A. concolor, A. lasiocarpa* (3, Morris 1967), *Picea engelmannii, P. glauca* (4), *P. pungens* (11), *P. contorta* (7), *P. ponderosa*, and *Pseudostuga menziesii* (2) (Morris 1967).

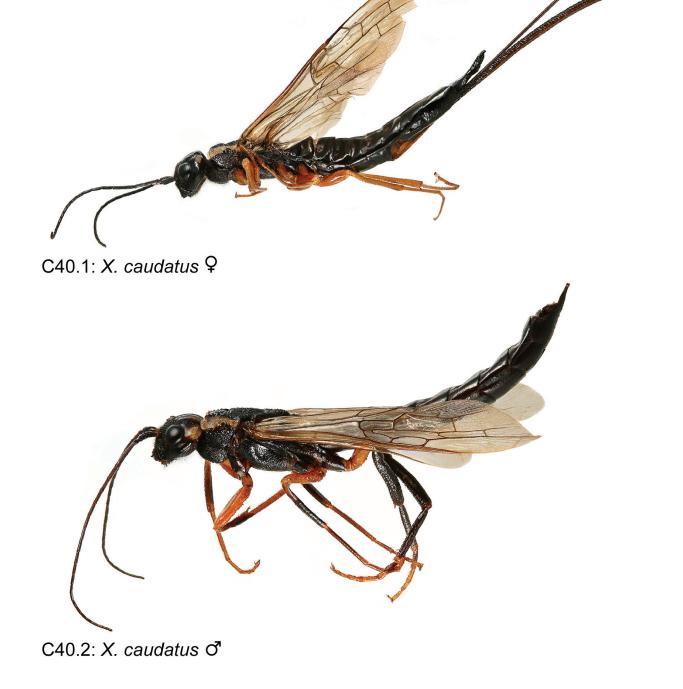
Based on 213 field-collected specimens, the earliest and latest capture dates are June 12 and August 18. The main flight period is from the second half of June to the first half of August with a peak in the second half of July.

Range

CANADA: AB, BC (Cascades eastern slope and eastward), SK. **USA:** AK, CA, CO, ID, MT, OR, SD, UT, WA, WY. *Xeris caudatus*, a western species, is known from Alaska, British Columbia, and Alberta south to California and New Mexico (Cameron 1965) (Fig. C40.6).

Specimens studied and included for the distribution map: 237 females and 13 males from, BYUC, CNC, MTEC, OSAC, UAIC, UAM, UCRC, USFS–GA, USFS–MS, and USNM. Specimens for molecular studies: 14 specimens. See Fig. E2.3.

CANADA. Alberta: *CNCS 1090*, 2008, 587. **USA. Colorado:** *CBHR 2008*, 2010, 658. **Montana:** 2007, *CNCS 1084*, 654. **Utah:** 2008, *CBHR 1943*, 658; 2008, *CBHR 1944*, 658; 2008, *CBHR 1945*, 658. **Washington:** 2005, CBHR 214, 658; 2005, CBHR 229, 658; 2005, CBHR 236, 658; 2005, CBHR 236e, 658; 2005, CBHR 238b, 658; 2005, CBHR 238b, 658; 2005, CBHR 238c, 658; 2005, CBHR 238d, 658.





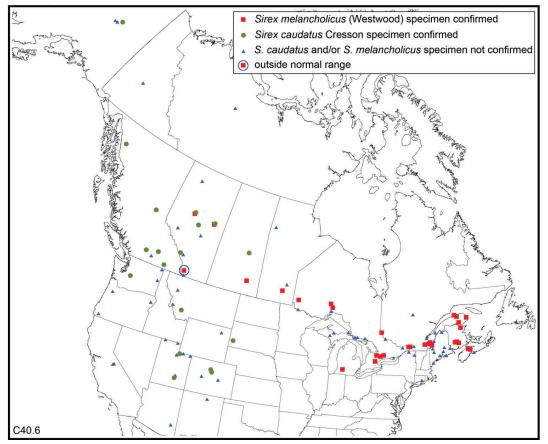
C40.3: X. melancholicus Q



C40.4: X. spectrum o



C40.5: X. spectrum Q



41. Xeris chiricahua Smith, n. sp.

Fig. C41.1 (female habitus) Fig. C41.2 (male habitus) Fig. C41.3 (map)

Diagnostic combination

Among specimens with mainly clear wings and a white longitudinal band on the lateral margin of the pronotum [*caudatus* and *melancholicus*], **both sexes** of *X. chiricahua* are recognized by the long setae on the frons and vertex of the head, the dense pits on the head between the eyes and the postocellar furrows, and the pits on the gena ventral to the genal ridge which are continuous with pits on the occiput.

FEMALE. Description

Color. Head black except for large white spot on gena dorsal to middle of eye extending down to genal ridge; antenna black (apical 0.25 dark brown). Thorax black except for white longitudinal band extending from posterolateral to anterolateral angles, narrowing toward posterior angle, and extending on vertical portion ventral to anterior angle. Legs light reddish brown but black on pro- and mesocoxae, black on metacoxae or mostly light reddish brown on metacoxae. Fore wing clear except for a lightly tinted band before stigma and in apical 0.25, very lightly tinted in cell 2CU; costal cell brown and most of area ventral to anal cells yellowish brown; veins black (including veins C, R, and base of stigma on both sides of junction with vein 1r-rs). Abdomen completely black. Sheath with apical section black and basal section reddish brown.

Head. Eye in lateral view (N = 5) with maximum height 1.3–1.6 times as long as maximum length, and maximum height of eye 0.34-0.48 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head). Gena in dorsal view with maximum distance between outer edges clearly wider than maximum distance between outer edges of eyes (in frontal view outer edges of eyes clearly not intersecting genae), and in lateral view distance between outer edge of eye and genal ridge 0.50–0.66 times as long as maximum length of eye. Transverse ridge near mandible narrow, sharp and mainly smooth. Head in dorsal view with pits very dense (many pits polygonal in outline on most of vertex) and numerous on gena below ventral margin of eye and genal ridge, pitted area of gena broadly connected to pitted area of occiput, and with many moderate size pits (diameter of pits 0.2-0.25 times lateral ocellus diameter) between outer edge of eye and genal ridge.

Thorax. Fore wing vein 3A absent, or reduced to a stump, but not extending toward posterior wing edge.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.8 times as wide as median length, with maximum width of basin 1.3-1.6 times as wide as median length and basin 0.6-0.8 times as long as medially median length of cornus. Cornus constricted in dorsal view, its minimum width (at constriction) 0.8 times as wide as maximum width of cornus subapically. Sheath. Length 1.4-1.5 times as long as fore wing length; basal section 0.22-0.27 times as long as apical section (N = 4); lateral surface of apical section with well defined ridge (as in Fig. B5.13, insert). Ovipositor. Lancet with 26-30 annuli (first 15 annuli very hard to see, but still outlined) (N = 2); junction of basal and apical sections of sheath aligned between 3rd and 4th annuli; major pits present on 4–5 apical annuli before teeth annuli, and at most one preceding annulus with a very small pit.

MALE. Description

Color. Femora (except for light reddish brown at extreme apex), tibiae (except for light reddish brown at very base) and tarsi (except for light reddish brown tarsomeres 3–5 or 4 and 5) black.

Thorax. Metatibia with deep notch on dorsal edge in basal 0.25 (Fig. B5.39).

Type Material

Holotype female (USNM) in prefect condition; labeled [White] "RustlerPark ChiricahuaMts 13Jun56 ARIZ OLCartwright"; [Red] "HOLOTYPE Xeris chiricahua D. R. Smith, 2011". Type locality: U.S.A., Arizona, Chiricahua Mountains, Rustler Park.

Paratypes. 3 females and 1 male. **USA. Arizona**: *Cochise Co.*, same data as holotype (1F, 1M, CNC, USNM); *Coconino Co.*, Kaibab National forest, 35.381°N 111.901°W, 6.VI–29.VIII.2008, R. Hofstetler (1F, CNC). Colorado: Florissant vi,24,14, resting on pine tree (1F, USNM).

Taxonomic notes

At first sight, specimens of *X. chiricahua* are similar to those of *X. caudatus* because they share the white longitudinal band on the lateral margin of the pronotum. But they differ in the length of frontal clypeal setae, the much denser pits on the vertex and dense and widespread field of pits on the gena below ridge merging with pits of the occiput.

Origin of specific epithet

The name chiricahua refers to the mountains where

the species was discovered, stressing the insularity of the mountains in this region. The name is a noun in apposition.

Hosts and phenology

The host of *X. chiricahua* is unknown, but females of *Xeris* with a long ovipositor and few pits on the ovipositor are known to attack Pinaceae. The Chiricahua Mountains

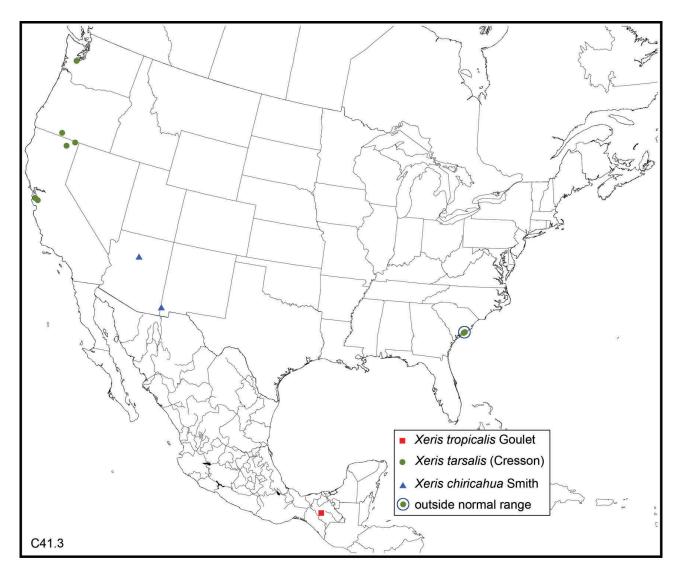
are rich in pines at high elevations. The three specimens were captured on June 13.

Range

United States: AZ. CO. We suspect the species may also occur in Mexico (Fig. C41.3).



C41.2: X. chiricahua 🗸



42. Xeris indecisus (MacGillivray) species re-instated

Fig. C42.1, Schiff *et al.* 2006: 84, 85 (female with reddish brown abdomen, habitus)

Fig. C42.2, Schiff *et al.* 2006: 95, 96 (female with black abdomen, habitus)

Fig. C42.3, Schiff *et al.* 2006: 83 (male with reddish brown abdomen, habitus)

Fig. C42.4, Schiff *et al.* 2006: 91 (male with black abdomen, habitus)

Fig. C39.1 (live female with dark abdomen)

- Fig. C42.5 (live male with dark abdomen)
- Fig. C42.6 (map)
- *Urocerus indecisus* MacGillivray, 1893: 243. Holotype male (INHS, Webb 1980), not examined. Type locality, near Olympia, Washington.
- *Xeris morrisoni* Bradley, 1913: 24 (not Cresson, 1880: 35); accepted by Ries 1951: 84, Middlekauff 1960: 69.

- *Xeris morrisoni indecisus*; Maa, 1949: 85 (change in combination and rank); accepted by Burks 1958: 17, Smith 1979: 129.
- *Xeris spectrum townesi* Maa, 1949: 88. Holotype female (USNM), examined by DRS and HG. Burks 1958: 17, Burks 1967: 27, Smith 1979: 129. **NEW SYNONYM**. Type locality: "Hoquiam [Washington]".
- *Xeris spectrum* Middlekauff 1960: 70 (in part) (not Linnaeus, 1758: 560).

Diagnostic combination

Among adults without a longitudinal band on the lateral margin of the pronotum [morrisoni, tarsalis and tropicalis], **both sexes** of X. indecisus are recognized by the wide gena (in frontal view maximum width between the outer edges of eyes clearly less than maximum width between genae), and the narrow, sharp and mainly smooth transverse ridge above the mandible. **Female** also have

completely light reddish brown femora. **Males** also have the width of the gena between the genal ridge and the outer edge of eye generally more than half as wide as the maximum eye length.

FEMALE. Description

Color. Head black except for large white spot on gena dorsal to middle of eye extending down to genal ridge (Fig. B5.19); flagellum black but reddish brown on 8-12 apical flagellomeres (black abdomen form) (Fig. B5.49), or completely light reddish brown (reddish brown abdomen form, but unusually also for the black abdomen form) (Fig. B5.50). Thorax completely black or with small to large white spot present on vertical surface near anterolateral angle of pronotum (spot very narrow if visible in dorsal view) (Fig. B5.38). Legs light reddish brown except for coxae; coxae almost all light reddish brown except on surface at dorsal angle (especially in specimen with reddish brown abdomen) to brown or black with reddish brown apex (Fig. B5.38). Fore and hind wings tinted very light brown but clearly darker in cells 1R1, 1M and 2CU (almost completely clear except for a dark band before stigma and somewhat darkened in apical 0.25 in old preserved specimens) or, in southwestern United States completely darkly tinted (Fig. B5.16); costal cell brown and most of surface behind anal cells yellowish brown; veins dark brown or black (including veins C and R, and vein 1r-rs near junction with stigma). Abdomen segments 1 or 1 and 2 black, and segments 2-10 or 3-10 reddish brown (pale form) (Fig. B5.46), or abdomen completely black (dark form, not found in southwestern United States) (Fig. B5.47). Sheath with apical section black and basal section reddish brown.

Head. Eye in lateral view (20 specimens measured) with maximum height 1.36–1.66 times as long as maximum length, and maximum height of eye 0.42-0.50 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head) (as in Fig. B5.7). Gena in dorsal view with maximum distance between outer edges clearly wider than maximum distance between outer edges of eyes (in frontal view outer edges of eyes clearly not intersecting genae) and in lateral view distance between outer edge of eye and genal ridge 0.50–0.64 as long as maximum length of eye (Fig. B5.27). Transverse ridge above mandible narrow, sharp and mainly smooth (Fig. B5.21). Head in dorsal view with pits restricted to vertex (quite densely pitted from dorsoposterior edge of eye to occiput) and postocellar area (medially and a little more widespread near lateral ocelli) (Fig. B5.33); in lateral view pits almost absent on gena ventral to genal ridge (Fig. B5.19), and pits scattered (mainly near eye) and small (diameter of pit 0.2-0.3 that of ocellus) between outer edge of eye and genal ridge (Fig. B5.19).

Thorax. Fore wing vein 3A absent (81%), reduced to a stump (18%), or rarely extending slightly as a nebulous vein (1%), but not extending along posterior margin of wing.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.7 times as wide as median length, with maximum width of basin 1.3 times as wide as median length, and basin 0.5 times as long medially as median length of cornus. Cornus constricted in dorsal view, its minimum width (at constriction) 0.8 times as wide as maximum width of cornus subapically. Sheath. Length 1.2-1.5 times as long as fore wing length; basal section 0.20-0.31 times as long as apical section (Fig. B5.25); lateral surface of apical section with well defined ridge (as in Fig. B5.13, see insert). Ovipositor. Lancet with 25-33 annuli (first 15 annuli difficult to see, but still outlined); junction of basal and apical sections of sheath aligned between 2nd and 3rd, at 3rd, or between 3rd and 4th annuli; major pits present on last 4-6 apical annuli before teeth annuli, and at most 6 preceding annuli with a very small pit.

MALE. Description

Color. Antenna, coxae, femora (at least metafemur mostly black, but pro– and mesofemur black in most specimens to mainly reddish brown), tibiae (except for brown at very base in some specimens) and tarsi (except reddish brown tarsomeres 3–5 or 4 and 5) black. Pronotum completely black, or vertical surface in front of dorsolateral angle with small to large white spot; dorsal surface of pronotum black or with white spot extending at most toward posterolateral angle. Abdomen black on segments 1 and 2 and laterally on terga 3–8, and reddish brown elsewhere (pale form), or completely black (dark form).

Thorax. Metatibia with shallow notch on dorsal edge in basal 0.25 (Fig. B5.40).

Taxonomic notes

The holotype of *U. indecisus* was not examined. The description (especially the femora and pronotal color pattern) matches our concept for this species.

Xeris spectrum townesi specimens share with *X. indecisus* the large spot size on the gena, and the denser pits on the gena and vertex; **females** share the flagellum and the pronotum color, and **males** share the pronotum and metafemur color. Males of the pale abdomen form match the description of the type of *Xeris indecisus*, and females of the black abdomen form match *Xeris spectrum townesi*. **Both sexes** of both color forms are easily associated. Both color forms have the same range

except from Utah and the Black Hills of South Dakota and south where only the pale color form occurs), and adults are often found together.

The pale abdomen and dark abdomen forms were classified until now as two species (Maa 1949, Ries 1951, Middlekauff 1960, Smith 1979). Information from morphology and DNA barcoding confirms that the two discrete color forms of both sexes belong to one species. Therefore, these color forms are treated here as one species.

Xeris indecisus has been ranked as a subspecies of *X. morrisoni* (Maa 1949, Ries 1951, Middlekauff 1960, Smith 1979). However, the information from morphology and DNA barcoding confirms that the two taxa are different. Moreover, the two species are sympatric in Colorado and females are easily distinguished on color pattern. Therefore, we consider *X. indecisus* and *X. morrisoni* as specifically distinct.

Geographical variation

Adults of *X. indecisus* have two distinct color forms: the abdomen is either mainly reddish brown or completely black. Both color forms are known from coastal and interior regions of British Columbia south to California. However, the reddish brown abdomen form is the only form recorded in southwestern United States (Arizona, Colorado, Nevada, South Dakota and Utah). Dark winged specimens are recorded from the latter states. Wings less darkly tinted where both color forms occur.

Less obvious are variations in ovipositor length. The basal section of the sheath is proportional to body size, but the apical section is not. We calculated the ratio between the basal and apical section as a general measure of relative size for the ovipositor, based on 72 specimens. In South Dakota, females (18) have generally a short ovipositor with a ratio of basal to apical sections of 0.24-0.31 (mean = 0.27). At the other extreme, specimens (10) from Lake Tahoe, California, have a ratio of 0.20-0.25 (mean = 0.23). In Oregon and British Columbia, females (44) have ratios of 0.20-0.32 (average 0.25). Therefore specimens from California have a relatively longer apical section of the sheath than most of specimens from elsewhere. DNA barcodes based on 21 specimens from regions with long and short ovipositors does not segregate specimens into two groups. We see no reasons to recognize subspecies.

Hosts and phenology

Xeris indecisus has a wide host range (Bedard 1938 – under X. morrisoni, Cameron 1965, Morris 1967). Based on 121 reared and confirmed specimens, all but one host are Pinaceae: Abies sp. (13), A. concolor (17), A. grandis (10), A. lasiocarpa (8), A. magnifica, Larix occidentalis (12), Picea sp. (1), P. sitchensis (10), Pinus contorta (2), P. ponderosa, Pseudotsuga menziesii (28), and Tsuga heterophylla (20). There is one record from Calocedrus decurrens (Cupressaceae).

Based on 24 field-collected specimens, the earliest and latest capture dates are May 18 and September 11 The main flight period is from the first half of June to the first half of September.

Range

CANADA: BC. **USA:** CA, CO, ID, MT, NV, OR, SD, UT, WA. *Xeris indecisus*, a widespread western species in forested regions, is recorded from British Columbia to California and Colorado (Burks 1967, Cameron 1965, Smith 1979) (Fig. C42.6). The specimens of *X. indecisus* recorded by Burks (1967) under *X. spectrum townesi* from Arizona needs confirmation as they could be specimens of *X. chiricahua*. One female was intercepted in Osaka, Japan, from United States (Okutani 1965) and we have seen a female intercepted in New Zealand (FRNZ and PANZ).

Specimens studied and included for distribution map: 232 females and 113 males BYUC, CFIA, CNC, DEBU, EDUM, MTEC, OSAC, PFRC, UASM, UCRC, USFS–GA, USFS–MS, and USNM.

Specimens for molecular studies: 21 specimens. See Fig. E2.3.

CANADA. British Columbia: 2006, *CBHR 418*, 658; 2006, *CBHR 419*, 658; 2004, *SIRCA 092*, 658; 2004, *SIRCA 093*, 658. **USA. California**: 1999, *CBHR 98*, 658; 2007, *CNCS 1076*, 600; 2007, *CNCS 1077*, 576; 2007, *CNCS 1078*, 654. **Colorado**: 2005, *CBHR 189*, 658. **Oregon**: 1999, *CBHR 108*, 658; 2006, *CBHR 385*, 658; 2006, *CBHR 1078*, 658; 2007, *CNCS 1080*, 615. **Washington**: 2005, *CBHR 215*, 658; 2005, *CBHR 216*, 658; 2005, *CBHR 228*, 658; 2005, *CBHR 235*, 658; 2005, *CBHR 241*, 658; 2005, *CBHR 254*, 658; 2008, *CBHR 1310*, 658.



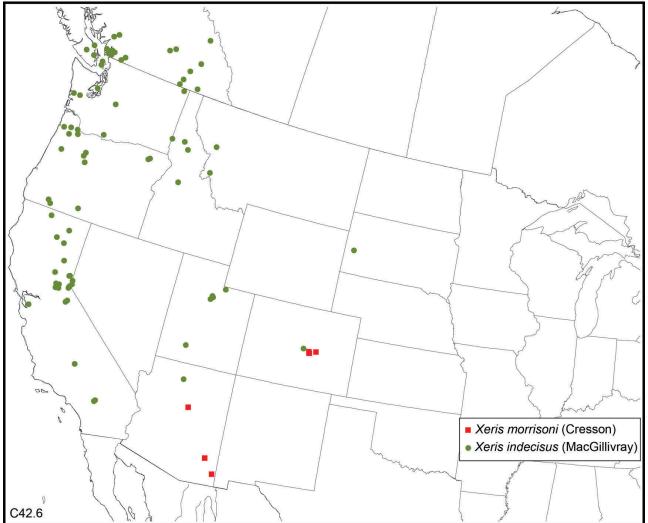
C42.1: X. indecisus Q with reddish brown abdomen







C42.5: X. indecisus of with black abdomen



43. Xeris melancholicus (Westwood), n. stat.

Fig. C43.1, Schiff *et al.* 2006: 92, 93 (female habitus) Fig. C43.2 (male habitus) Fig. C40.6 (map)

- *Sirex melancholicus* Westwood, 1874: 116, pl. XXI, fig. 8. Holotype male (OXUM), images of male prepared by James E. Hogan and sent to HG for study.
- *Urocerus caudata*; Cresson, 1880: 67 (not Cresson, 1865: 247–248).
- *Xeris spectrum*; Maa, 1949: 86 (not Linnaeus, 1758: 560). Burks 1958: 17, Smith and Schiff 2002: 185.
- *Xeris spectrum spectrum*; Maa, 1949: 86 (change in status); accepted by Burks 1958: 17, Middlekauff 1960: 70 (in part), Burks 1958: 17, Smith 1979: 129.

Diagnostic combination

Among specimens with a lateral longitudinal band on the pronotum and with short setae on the head [*caudatus*], **both sexes** of *X. melancholicus* are recognized by the very small pits (pit diameter 0.1–0.2 times lateral ocellus diameter) and very few pits on the gena between the upper and lower limits of the genal ridge, and the small white spot that usually does not extend to the genal ridge. **Females** also have completely light reddish brown coxae (except for the black anterior and posterior dorsal edges), and generally longer apical section of the sheath (basal section/apical section ratio more than 0.27 for most specimens). **Males** of *melancholicus* cannot be separated from males of *caudatus*.

FEMALE. Description

Color. Head black except for small white spot behind eye; white spot usually not extending down to genal ridge (Fig. B5.41); antenna completely black. Thorax black except for white longitudinal band extending from posterolateral to anterolateral angles including vertical portion of anterior angle (Fig. C43.3). Legs light reddish brown but narrowly black at dorsal coxal articulation (Fig. C43.1). Fore and hind wings almost completely clear except for a very lightly tinted darkened band before stigma and in apical 0.25; fore wing very lightly tinted in cell 2CU, costal cell brown and most of surface behind anal cells yellowish brown, veins black (including veins C and R, and vein 1r-rs near junction with stigma) (Fig. B5.17). Abdomen completely black. Sheath with apical section black and basal section reddish brown.

Head. Eye in lateral view (20 specimens measured) with maximum height 1.37–1.64 times as long as maximum length, and maximum height of eye 0.42–0.51 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head) (as in Fig. B5.7).

Gena in dorsal view with maximum distance between outer edges clearly wider than maximum width between outer edges of eyes (in frontal view outer edges of eyes clearly not intersecting genae) (Fig. B5.4), and in lateral view distance between outer edge of eye and genal ridge 0.48-0.61 times as long as maximum length of eye (as in Fig. B5.27). Transverse ridge above mandible narrow, sharp and mainly smooth (as in Fig. B5.21). Head in dorsal view with pits restricted to vertex (scarcely pitted from dorsoposterior edge of eye to occiput) and postocellar area (scattered or absent on most of median furrow, but a little more widespread near lateral ocelli) (Fig. B5.2), in lateral view pits almost absent on gena ventral to genal ridge, and few and very small (diameter of pit 0.1–0.2 lateral ocellus diameter) between outer edge of eye and genal ridge (mainly near eye) (Fig. B5.43).

Thorax. Fore wing vein 3A absent (73%), reduced to a stump (24%) or rarely extending toward posterior wing edge as a nebulous vein (3%), but not extending along posterior margin of wing.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.8 times as wide as median length, maximum width of basin 1.6 times as wide as median length, and basin 0.5 times as long medially as median length of cornus (Fig. C39.2). Cornus constricted in dorsal view, its minimum width (at constriction) 0.8 times as wide as maximum width subapically (Fig. C39.2). Sheath. Length 1.2-1.4 times as long fore wing length; basal section 0.24–0.35 times as long as apical section (Fig. C43.4); lateral surface of apical section with well defined ridge (Fig. B5.13, see insert). Ovipositor. Lancet with 25-29 annuli (first 15 annuli hard to see, but still outlined; N = 14) (Fig. B5.15); junction of basal and apical sections of sheath aligned between 2nd and 3rd, at 3rd, or 3rd and 4th annuli; major pits present on 4-5 apical annuli before teeth annuli (Fig. B5.15), and 7–15 preceding annuli with a very small pit (as in Fig. B5.15).

MALE. Description

Color. Coxae, tibiae (except very base) and tarsomeres 1–5 black (apical articles sometimes brown or reddish brown in old or teneral specimens); femora completely or mainly, and extreme base of tibiae (not sharply outlined but gradual shift) reddish brown (Fig. B5.51).

Thorax. Metatibia with shallow notch on dorsal edge in basal 0.25.

Taxonomic notes

Initially we thought that *X. caudatus* was a well defined and widespread species. We had several barcoded specimens from eastern North America confirming our

concept. However, it was not to remain so straight forward. NMS reported a population from the Cascade Mountains, Washington, based on a rather distinct barcode relative to eastern specimens. For more information see "taxonomic notes" under *X. caudatus*.

As more specimens from western North America became available, we noticed that the eastern population had a shorter apical section of the sheath relative to the basal section. We carefully measured all the available specimens and confirmed a marked difference in the sheath length between the eastern and western populations. We also measured the basal and apical sections of the sheath. To insure an accurate measurement of the apical section we had to consider two situations. If the apical section covered the ovipositor we recorded its length because the apical section is straight or almost so, but if the apical section was separated from the ovipositor we measured its length up to the end of the ovipositor because the ovipositor is straight whereas the apical section of the 'detached' sheath is curved and therefore gives a shorter (and inaccurate) length measurement. The ratio derived from the basal section length relative to that of the apical section for the eastern unit (42 specimens) gave a mean = 0.295 (standard deviation = 0.031) and the western unit (73 specimens) gave a mean = 0.237 (standard deviation = 0.016). There is a difference of 1.25 standard deviations between the mean of the two populations. Based on a difference of two standard deviations, the overlapping zone is 0.25–0.27. Therefore, 75% of the females of each population could be segregated correctly, and specimens with values between 0.25 and 0.27 are of uncertain status. Moreover, in Alberta both populations exist sympatrically. Therefore, we consider the eastern and western populations as specifically distinct.

Two names apply to this complex. Cresson's type of U. caudatus is a female from Colorado and is associated with the western species. Cresson's name is older, However, we do not know if the eastern species is named or not. We could not assign the male holotype of S. melancholicus to this species with certainty because we did not have a diagnostic character for distinguishing males of the western X. caudatus from those of the eastern species. The male of S. melancholicus is probably a specimen from a region east of the Rocky Mountains because most of Westwood's new species of Siricidae are from eastern North America. If so, Westwood's type would match the eastern species. However, we are not certain because Westwood did describe one western species of Siricidae. In spite of this and to avoid creating a synonym, we decided to assign Westwood's name to X. *melancholicus* rather than describing it with a new name.

Specimens of X. melancholicus, like X. caudatus,

are quite easily distinguished from other New World species of *Xeris* using the key. We discussed under *X. caudatus* the differences between *X. caudatus* and named species of the *X. spectrum* species complex from Eurasia. The discussion about the Eurasian species and *X. melancholicus* is the same as that given under *X. caudatus* and so is not repeated.

Biological notes

Males and females of *X. melancholicus* were observed aggregating at the highest point of Mount Rigaud, Quebec. Though mating was not observed then, we assume that both sexes get together for this purpose.

Hosts and phenology

Xeris melancholicus has a wide host range (Middlekauff 1960, Stillwell 1960, Cameron 1965, Morris 1967, Kirk 1975). Based on 24 reared and confirmed specimens, all are Pinaceae: *Abies balsamea* (15), *Larix occidentalis*, *P. glauca* (4), and *Pinus banksiana* (5).

Based on 155 field-collected specimens, the earliest and latest capture dates are June 12 and August 18. The main flight period is from the second half of June to the first half of August with a peak in the second half of July. We collected 11 specimens (3 females and 8 males) though more were seen at the summit of Mount Rigaud, Quebec, between June 15 and June 27 (1985 to 2011).

Range

CANADA: AB, BC, MB, NB, NS, ON, QC, SK. **USA:** CT, ME, MI. *Xeris melancholicus*, a widespread species, is recorded from the central Alaska, northernmost British Columbia and central Alberta to Newfoundland, Michigan and Connecticut (Fig. C40.6).

Specimens studied and included in the distribution map: 126 females and 54 males from BDUC, CNC, FRLC, GLFC, LEMQ, MNRQ, NFRC, UAM, USFS– AK, USFS–GA, USFS–MS, and USNM.

Specimens for molecular studies: 13 specimens. See Fig. E2.3.

CANADA. Alberta: 2008, *CNCS 1086*, 576; 2008, *CNCS 1087*, 563; 2008, *CNCS 1088*, 515; 2008, *CNCS 1089*, 579. **Nova Scotia**: 2006, *CBHR 297*, 658; 2005, *CBHR 300*, 658. **Ontario**: 2007, *SIRCA 041*, 624; 2007, *SIRCA 042*, 616. **USA. Michigan**: 2005, *CBHR 203*, 658. **Minnesota**: 2008, *CBHR 1375*, 658; 2008, *CBHR 1461*, 534; 2008, *CBHR 1462*, 578. **New York**: 2006, *CBHR 603*, 658.



C43.2: X. melancholicus o



C43.3: X. melancholicus Q



C43.4: X. melancholicus Q

44. Xeris morrisoni (Cresson)

Fig. C44.1, Schiff *et al.* 2006: 88, 89 (female habitus) Fig. C44.2, Schiff *et al.* 2006: 87 (male habitus) Fig. C42.6 (map)

- *Urocerus morrisoni* Cresson, 1880: 35. Lectotype female (ANSP), designated by Cresson (1916), examined by DRS and HG. Cresson 1916: 10. Type locality: "Colorado, Utah and Washington Territory".
- *Sirex morrisonii*; Kirby, 1882: 382 (change in combination and spelling).
- *Xeris morrisoni*; Ashmead, 1898: 180 (change in combination); accepted by Bradley, 1913: 24; Ries 1951: 84.
- *Urocerus tarsalis*; synonym proposed by Konow, 1898:88 (not Cresson, 1880:35); accepted by Bradley, 1913: 24; Ries 1951: 84.
- *Urocerus indecisus*; synonym proposed by Konow, 1898:226 (not MacGillivray, 1893: 243); accepted by Bradley, 1913: 24; Ries 1951: 84.
- *Xeris morrisoni morrisoni*; Maa, 1949: 85 (change in rank); accepted by Burks 1958: 17, Smith 1979: 129.

Diagnostic combination

Among adults without a marginal longitudinal band on the pronotum [*indecisus*, *tarsalis* and *tropicalis*], **both sexes** of *X. morrisoni* are recognized by the wide gena (in frontal view maximum width between the outer edges of eyes clearly less outer edges of genae), and the narrow, sharp and mainly smooth transverse ridge above the mandible. **Females** have black femora. **Males** have the width of the gena between the genal ridge and the outer edge of eye generally less than 0.5 times as wide as the maximum eye length.

FEMALE. Description

Color. Head and thorax black except for small white spot behind eye extending ventrally to level of middle of eye (as in Fig. B5.35); antenna black but reddish brown in apical 0.5 (Fig. B5.30). Legs black but light reddish brown at apex of femora (metafemur almost white in basal 0.15), tibiae and tarsi (Fig. B5.28). Fore and hind wings very darkly tinted, veins black (including veins C and R, and vein 1r-rs near junction with stigma). Abdomen segments 1 or 1 and 2 black, segments 2–10 or 3–10, and apical section of sheath reddish brown.

Head. Eye in lateral view (20 specimens measured) with maximum height 1.35–1.60 times as long as maximum length, and maximum height of eye 0.49 times as long as maximum head height (from transverse ridge on gena above mandible to top of head) (as in Fig. B5.7). Gena in dorsal view with maximum distance between outer edges

clearly wider than maximum width between outer edges of eyes (in frontal view, outer edges of eyes clearly not intersecting genae), and in lateral view distance between outer edge of eye and genal ridge 0.43-0.50 times as long as maximum length of eye (Fig. B5.26). Transverse ridge above mandible narrow, sharp and mainly smooth (as in Fig. B5.21). Head in dorsal view with pits restricted to vertex (from dorsoposterior edge of eye to occiput) and postocellar area (on median furrow and a little more widespread near lateral ocelli), in lateral view pits almost absent on gena ventral to genal ridge (as in Fig. B5.35), and scattered (mainly near eye) and small (diameter of pit 0.2-0.3 times ocellus diameter) between outer edge of eye and genal ridge (Fig. B5.26). Frons ventral to median ocellus impressed but not very clearly outlined, quite long, and smooth.

Thorax. Fore wing vein 3A presence or absence not recorded.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.7 times as wide as median length, with maximum width of basin 1.3 times as wide as median length, and basin 0.7 times as long medially as median length of cornus. Cornus constricted in dorsal view, its minimum width (at constriction) 0.8 times as wide as maximum width subapically. Sheath. Length 1.2-1.5 times as long fore wing length; basal section 0.22–0.30 times as long apical section (N = 6); lateral surface of apical section with well defined ridge (as in Fig. b5.13 see insert). Ovipositor. Lancet with 31-34 annuli (first 15 annuli very hard to see, but still outlined); junction of basal and apical section of sheaths aligned between 3rd and 4th annuli; major pits present on 5 apical annuli before teeth annuli, and at most with a very small pit on preceding annulus.

MALE. Description

Color. Antenna, femora, tibiae and tarsi (except for reddish brown tarsomeres 3–5 or 4 and 5) black. Abdomen black on segments 1 and 2 and at side of terga 3–8, reddish brown elsewhere. Pronotum in dorsal view with brown spot on anterolateral angle.

Thorax. Metatibia with shallow notch on dorsal edge in basal 0.25.

Taxonomic notes

Xeris morrisoni is similar to *X. indecisus* (pale abdomen form). Females of *X. morrisoni* are easily distinguished on leg and flagellum color and **both sexes** on the narrow gena. The DNA barcodes support the species level status between the two species. No specimens with intermediate structures and color pattern are known.

Xeris morrisoni has a moderately wide host range. Based on 232 reared and confirmed specimens, all are Pinaceae: *Abies concolor* (228; most specimen records from Kirk (1975)), *Picea pungens* (1), and *Pseudotsuga menziesii* (3). Based on other, better sampled species of this genus, we expect that this species has a wider host range than this.

Based on 13 field-collected specimens, the earliest and latest capture dates are from early June to late July.

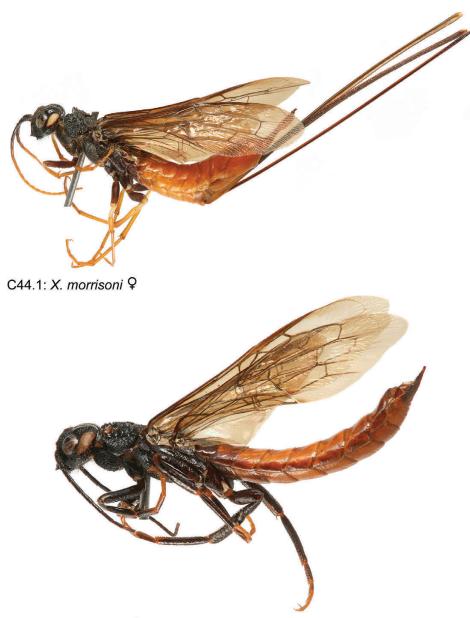
Range

United States: CO. *Xeris morrisoni* is recorded from forested regions of southwestern United States (Burks 1958, Burks 1967, Cameron 1965, Smith 1979) (Fig. C42.6).

Specimens studied and included for the distribution map: 7 females and 6 males from OSAC, UAIC, and USNM.

Specimens for molecular studies: 6 specimens. See Fig. E2.3.

USA. Colorado: 2005, *CBHR 190*, 658; 2005, *CBHR 533*, 627; 2005, *CBHR 534*, 658; 2005, *CBHR 535*, 608; 2005, *CBHR 536*, 658; 2005, *CBHR 537*, 658.



C44.2: X. morrisoni o

45. Xeris tarsalis (Cresson)

Fig. C45.1, Schiff *et al.* 2006: 98, 99 (female habitus) Fig. C45.2, Schiff *et al.* 2006: 97 (male habitus) Fig. C41.3 (map)

Urocerus tarsalis Cresson, 1880: 52. Holotype female (ANSP), examined by DRS. Cresson 1916: 10. Type locality: "Washington Territory".

Sirex tarsalis; Kirby, 1882: 382 (change in combination).

- *Xeris macgillivrayi* Bradley, 1913: 24, figs. 30, 35. Holotype female [published measurements suggest one specimen] (CUIC) [according to Maa (1949), but not listed by Hoebeke (1980)], not examined. Middlekauff 1960: 69. Synonym by Maa 1949: 82; accepted by Burks 1958: 17, Smith 1979: 129. Type locality: "near Olympia, Washington", as hand stamped in some copies, but no locality, number of specimens and depository given.
- *Xeris tarsalis*; Maa, 1949: 82 (change in combination); accepted by Burks 1958: 17, Smith 1979: 129.
- *Xeris morrisoni*; synonym by Konow 1898: 88 (not Cresson, 1880: 35) accepted by Ries, 1951: 84.

Diagnostic combination

Both sexes of *X. tarsalis* are easily recognized by the narrow gena (in frontal view, the outer edges of eyes touch or slightly intersect the genae), and the widespread and dense pits covering almost all the dorsal surface of the head and gena ventral to the genal ridge. **Females** have a quite short apical section of the sheath (basal section of sheath about 0.6 times apical section), no ridge on the apical section of the sheath, and a broad and not constricted cornus in dorsal view.

FEMALE. Description

Color. Head and thorax black except for small white spot on gena dorsal to middle of eye; white spot not extending down to genal ridge (Fig. B5.5); antenna black but shifting to reddish brown in apical 0.3. Thorax black. Legs black but reddish brown at apex of metatibia, and tarsi (Fig. C45.1). Fore and hind wings darkly tinted (including C cell), veins black (including veins C and R, and vein 1r-rs near junction with stigma). Abdomen segments 2–10 and sheath reddish brown but black on tergum 1, and lateral edge of terga 2 to 7 and sterna 2–7.

Head. Eye in lateral view (20 specimens measured) with maximum height 1.21–1.37 times as long as maximum length (Fig. B5.5), and maximum height of eye 0.52–0.60 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head) (Fig. B5.5). Gena in dorsal view with maximum distance between outer edges as wide as maximum width between

outer edges of eyes (in frontal view, outer edges of eyes touching or slightly intersecting genae) (Fig. B5.3), and in lateral view distance between outer edge of eye and genal ridge 0.42–0.64 times as long as maximum length of eye (Fig. B5.5). Transverse ridge near mandible narrow, sharp and mainly smooth (as in Fig. B5.21). Head in dorsal view with pits dense but sometimes narrowly absent submedially (Fig. B5.21); pits quite numerous between eye and genal ridge, and not extending below ventral level of eye and genal ridge (thus separated by smooth area from pitted surface of occiput) (Fig. B5.5).

Thorax. Fore wing vein 3A extending toward posterior wing margin as a nebulous vein.

Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.7 times as wide as median length, maximum width of basin 1.2 times as wide as median length, and basin 0.6 times as long as median length of cornus (Fig. C45.3). Cornus not constricted in dorsal view, its minimum width (where constriction normally seen in other species of Xeris) equal to maximum width subapically (Fig. C45.3). Sheath. Length about as long as length of fore wing; basal section of sheath 0.6 times as long as apical section (Fig. B5.11); lateral surface of apical section without longitudinal ridge (Fig. B5.11 insert). Ovipositor. Lancet with 35-37 annuli (all annuli clearly outlined); junction of basal and apical sections of sheath aligned between 8th and 9th, or 9th and 10th annuli; pits present on all annuli before teeth annuli and large, with anterior end extending to preceding annulus as shallow furrow (Fig. B5.14).

MALE. Description

Color. Antenna, tibiae and tarsi (except tarsomeres 3–5 or 4 and 5) black. Abdomen reddish brown or paler on terga 2–7 or 2–8, and black on tergum 1 or 1 and 2, and on sterna 2–9.

Thorax. Metatibia with shallow notch on dorsal edge in basal 0.25.

Taxonomic notes

Females of *X. tarsalis* are unusual, with a rather short ovipositor. However, the most unusual feature is the presence of large pits along the entire length of the ovipositor. In all other species of *Xeris*, the ovipositor is smooth except for a few small pits near the apex. This structural difference may reflect a different life style. For example, the common *X. caudatus* has mycangia, but NMS confirmed the absence of fungus in them. Their larvae probably survive on fungi brought by other Siricidae, as observed by Fukuda and Hijii (1997) with *X. malaisei* in Japan (*X. spectrum* in their publication). However, we suspect that females of *X. tarsalis* may carry a fungus in its mycangia.

Hosts and phenology

Xeris tarsalis has a wide host range (Middlekauff 1960, Westcott 1971). Based on 138 reared and confirmed specimens, all host are Cupressaceae: *Cupressus macrocarpa* (131), *Juniperus sp.* (2), *J. occidentalis* (3; from scorched trees (Westcott 1998)), *Calocedrus decurrens* (5), and *Thuja plicata.*

Based on 108 field-collected specimens, the earliest and latest capture dates are early March to early October. The main flight period is from early July to early October with a peak from early September to early October.

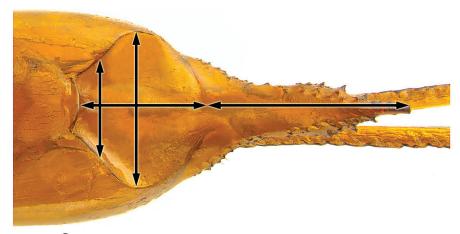
Range

USA: CA (Middlekauff), OR, SC (probably not established), WA. *Xeris tarsalis* is known from the Cascade Mountains and Sierra Nevada west to the Pacific coast (Cameron 1965, Smith 1979) (Fig. C41.3). One female was intercepted in South Carolina, and we have seen a female (FRNZ) intercepted in Auckland, New Zealand.

Specimens studied and included for the distribution map: 67 females and 77 males from CUCC, OSAC, and USNM.



C45.2: X. tarsalis o



C45.3: X. tarsalis Q

46. Xeris tropicalis Goulet, n. sp.

Fig. C46.1 (female habitus) Fig. C41.3 (map)

Xeris tarsalis; Smith, 1978: 89; Smith, 1988:243 (not Cresson, 1880: 52).

Diagnostic combination

Both sexes of *X. tropicalis* are easily recognized by the broad rounded and coarsely pitted transverse ridge dorsal to the mandible, the widespread and dense pits on the head dorsally, and the pits on the gena ventral to the genal ridge continuous with pits on the occiput.

FEMALE. Description

Color. Head and thorax black except for white spot extending from dorsal edge of eye to surface between genal ridge and outer edge of eye (Fig. C46.1); antenna black but 7 apical antennomeres reddish brown. Pronotum in dorsal view with small white spot on anterolateral corner. Legs black except yellow at extreme apex of femora, basal 0.2 of tibiae, and base of tarsomere 1 (Fig. C46.1). Wings very darkly tinted except for clear base of hind wing, veins black (including veins C and R, and vein 1r-rs near junction with stigma). Abdomen segment 1, lateral surface of tergum 2 and sternum 2 black; segments 2–10 reddish brown except for black apical section of sheath.

Head. Eye in lateral view (one specimen measured) with maximum height 1.23 times as long as maximum length, and maximum height of eye 0.51 times as long as maximum height of head (from transverse ridge on gena above mandible to top of head) (Fig. B5.6). Gena in dorsal view with maximum distance between outer edges hardly wider than maximum width between outer

edges of eyes (in frontal view, outer edges of eyes not intersecting genae, but very close to them), and in lateral view distance between outer edge of eye and genal ridge 0.42 times as long as maximum length of eye (Fig. B5.6). Transverse ridge above mandible broad, rounded and coarsely pitted (Fig. B5.20). Head in dorsal view with pits dense and widespread, but absent along weakly outlined furrow behind lateral ocelli, in lateral view pits numerous on gena ventral to level of eye and genal ridge, and pitted area of gena broadly connected to pitted area of occiput. Frons ventral to median ocellus impressed but not too clearly outlined, quite long, and smooth.

Thorax. Fore wing vein 3A reduced to a stump or absent. Abdomen. Median basin of tergum 9 with base (outlined by two lateral black longitudinal furrows) 0.8 times as wide as median length, with maximum width of basin 1.7 times as wide as median length, and basin 0.45 times as long medially as median length of cornus. Cornus constricted in dorsal view, its minimum width (at constriction) 0.85 times as wide as maximum width subapically. Sheath. Length 0.9 times as long as length of fore wing; basal section of sheath 0.4 times as long as apical section (Fig. B5.12); lateral surface of apical section with well defined ridge (as in Fig. B5.13, see insert). Ovipositor. Lancet with 31 annuli (first 14 annuli outlined but difficult to see); junction of basal and apical sections of sheath aligned between 4th and 5th annuli; major pits present on last 6 annuli before teeth annuli, and two preceding annuli with very small pits.

MALE. Unknown.

Type material

Holotype female (CNC), in perfect condition except left antenna broken and glued on label; labeled: [White] "6

mi.N.E. San Cristobal L. C., Chis. Mex. V.19 1969 H. E. Howden", [White & black frame] "Xeris tarsalis (Cr.) D. R. Smith 75", [Red] "HOLOTYPE Xeris tropicalis Goulet CNC No. 23908". Type locality: Mexico, Chiapas, San Cristobal de las Casas.

Origin of specific epithet

Xeris tropicalis is the southernmost record of *Xeris* and the specimen is clearly in a tropical region. The name *tropicalis* stress this aspect. The name is an adjective.

Host and phenology

The host of *X. tropicalis* is unknown but conifers are suspected. The single female was captured in mid May.

Range

Xeris tropicalis is only known from the type locality in southernmost Mexico (Fig. C41.3).



D. Additional Notes

1. Species excluded from the New World Siricidae

Sirex juvencus Linnaeus, 1758 has been commonly accepted as an established species in North America (Benson 1943, 1945 and 1963; Smith 1979). However, the species is not established though it has been intercepted at many sea ports in the United States and Canada. The species is a well known traveler; it also was often intercepted in New Zealand (FRNZ, NZAC and PANZ), Australia, and the Philippines. The range of S. juvencus in the Old World is said to extend from Europe to Asia, but we have seen specimens only from Europe. The few specimens seen by us and labeled with this name in Asia are not S. *juvencus*. In the New World, this species is clearly segregated on ovipositor pits size (pits size similar to those seen at middle of lancet in S. nitidus, but pits only slightly smaller on basal annuli) and flagellum color pattern. The main hosts of S. juvencus are various species of *Picea*. These hosts do not occur around most ports in eastern North America where the species has been intercepted.

A specimen from one interception in the United States was even described as a new species, *S. hirsutus* Kirby, 1882. Surprisingly, the male type (BMNH) is typical in all details with those of the European *S. juvencus*. Though this type specimen did not have a locality label, Kirby (1882: 380) believed that it was probably from "Georgia". If so, there was no host for *S. juvencus* on the coast that it could have reproduced on so it could not have become established. *Sirex hirsutus* is a NEW SYNONYM of the European *S. juvencus*.

Xeris spectrum has been commonly accepted as an established species in North America (Maa 1949, Ries 1951, Smith 1979, Schiff *et al.* 2006). However, it is not established, though it has been intercepted several times at various sea ports in the United States and New Zealand (specimens studied by us (FRNZ and USNM)). The range of *X. spectrum* extends from the Atlantic to the Pacific coasts in at least boreal regions of Eurasia (Maa 1949). The Nearctic species consists of two species, *X. caudatus* and *X. melancholicus*, and adults are distinguished from those of the *X. spectrum* complex by color pattern in both sexes and pit development on the ovipositor.

2. A name for the European "S. cyaneus"

The name *S. cyaneus* has long been used in Europe (Benson 1943) for a species presumed to be introduced from North America. The species does not match the North American *S. cyaneus* (see "Taxonomic notes" under *Sirex cyaneus* Fabricius). Based on ovipositor character states, the species is close to *S. nitidus* and *S.*

atricornis (see "Taxonomic notes" under *S. nitidus*) but does not match them or other Central European species of *Sirex*. Because the species is well represented in Central Europe and has been often intercepted at sea ports of North America and New Zealand, it is important to have a name for it. We studied about 40 specimens from SDEI, FRNZ, PANZ and USNM. We tried to find a described species within the range of *S. juvencus* and *S. noctilio* that matches the species (which is, in fact, European, not North American) and found three: *S. torvus* M. Harris, 1779: 96 + plate 28 (figure 1 under *Sirex*), *S. duplex* Shuckard, 1837: 631, and *S. leseleuci* Tournier, 1890: 200. *Sirex torvus* is the oldest name for the European "*S. cyaneus*".

For reasons mentioned above ("taxonomic notes under *S. cyaneus* and *S. nitidus*) and the probable loss of the syntypes from the collection containing *S. torvus* (Evenhuis 1997) [ICZN 75(d) (4)], a neotype for *S. torvus* is required [ICZN 75(a), 75(d) (3)]. Even though the original illustration (Fig. D2.1) and description of the female are sufficiently diagnostic to distinguish the species from other species in Central Europe, *S. torvus* is extremely similar to the subarctic European *S. atricornis* and the North American *S. nitidus*. The neotype female, here designated, is deposited in SDEI [ICZN 75(d) (6)]. It is labeled as follows:

[White and black outline] Schwäbische Alp Plettenberg bei Dottenhausen 7.VIII, 1976 Lauterbach leg.

[White label and black outline] Paururus \bigcirc noctilio F. 6.79 P. Westrich det. [White and black outline] Sirex cyaneus Fabr. E.Jansen det.' 93

[Red] NEOTYPE \bigcirc Sirex torvus M. Harris Des. H. Goulet, 2011

[ICZN article 75(d) (2)]. The neotype is perfect except for the broken off right flagellum. Its type locality is from Germany as entered above [ICZN 75(f)]. Because *S. torvus* females and males may be confused with two other Central European species of *Sirex* (*S. juvencus* and *S. noctilio*), they are distinguished from these briefly here to satisfy ICZN 75(b) (3). Females of *S. torvus* (Fig. D2.2, neotype) are distinguished from *S. juvencus* by their black antenna and long ovipositor sheath (M. Harris 1779), and from *S. noctilio* by their very long ovipositor sheath (length of sheath portion beyond apex of cornus as long as combined length of terga 9 and 10) (Chrystal 1928) [ICZN article 75(d) (1)].

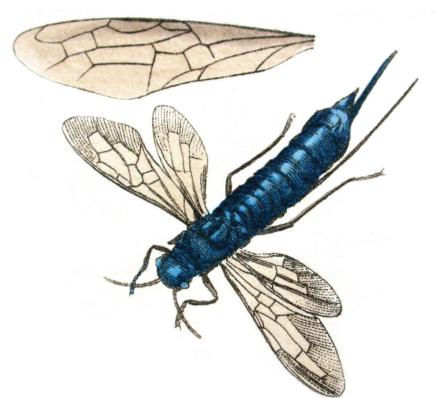
The synonymy is as follows:

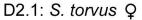
- *Sirex torvus* M. Harris, [1779]: 96, plate 28 [for publication year see Evenhuis 1997, and Blank *et al.* 2009].
- Sirex duplex Shuckard, 1837: 631. Syntypes: 43 males

and females (reared from *Pinus nigra* [now known as *Picea mariana* – information from P. Catling and G. Mitrow]), not seen. Shuckard's collection was auctioned off by T. Desvignes and J. C. Stevens in London in 1868 soon after Schukard's death (Horn *et al.*, 1990: 364). Syntype depository unknown and specimens assumed lost. NEW SYNONYM. Type

locality: "Cambridgeshire".

- *Sirex Leseleuci* Tournier, 1890: 200. Syntypes presumed lost, not seen. NEW SYNONYM. Type locality: "Douarnenez, France".
- Sirex cyaneus; Benson, 1943: 38 (not Fabricius, 1781: 419).







D2.2: S. torvus Q

E. Mitochondrial DNA results

1. Introduction

Although a large part of this work is a classical morphological revision of the New World Siricidae, DNA barcoding analysis was used to identify potential new species and develop a method to identify siricid larvae.

DNA barcoding as used here was originally proposed by Hebert et al (2003) as "a new approach to taxon identification." They postulated that if we wished to identify extant biodiversity we needed a faster, easier system than classical morphological methods and proposed that animal species could be uniquely identified by an approximately 600 base pair DNA sequence (barcode) of the mitochondrial Cytochrome Oxidase 1 gene. The advantages of barcode analysis included that it was fast, inexpensive, the characters are relatively uniform and unbiased, the analysis is quantitative, it can be used on all life stages, and it requires no specialized taxonomic experience or knowledge.

Since the proposal of Hebert et al. in 2003, barcodes have been used to identify animals including birds, fish and arthropods, discover cryptic species and associate life stages (Hajibabaei et al. 2006, Hebert et al. 2004, Hebert et al. 2004A, Hogg and Hebert 2004, Ball and Armstrong 2006, Smith et al. 2006, Ward 2005). However, as more studies were published, theoretical and practical difficulties were used to challenge the use of DNA barcodes alone for new species identification and classification (summarized in Rubinoff et al. 2006). These issues included heteroplasmy, where more than one mitochondrial haplotype is present in an individual (Frey and Frey 2004); numts (Lopez et al. 1994) where a nuclear pseudogene of mitochondrial origin was sequenced instead of the mitochondrial gene itself (Song et al. 2008, Pamilo et al. 2007, Koutroumpa et al. 2009); hybridization or indirect selection resulting from organisms like Wohlbachia mediating mitochondrial introgression in closely related species (Whitworth et al. 2007, Linnen and Farrell 2007, 2008); effects related to the biology of mitochondria such as reduced population size, maternal inheritance and limited recombination; and, finally, how much genetic distance should be used to delimit species (see Rubinoff et al. 2006 and the references therein). These limitations made it very difficult to use DNA barcoding as an easy alternative to classical or more sophisticated molecular methods for identifying new species. However, DeSalle (2006) in a rebuttal to Rubinoff et al. (2006) made a distinction between "species discovery" and "species identification." He argued that using barcodes alone for species discovery was indeed rife with difficulties, but that once a set of barcodes was established for a group of

species, unidentified specimens could be identified with the caveat that some specimens might not be resolvable. He suggested that a novel barcode sequence should be viewed as only a new species hypothesis to be tested and verified with more established methods. Although this resolution does not solve the challenge of how to recognize the vast number of undescribed species in the world, with our combined morphological and barcoding approach, it should allow us a means to identify adults and thus immature stages of New World Siricidae.

As with many groups of Hymenoptera, there are no morphological keys to immature stages of Siricidae, for several mostly practical reasons. First, until recently, there has been no pressing need for morphological keys to siricid larvae. Sirex noctilio, the most significant siricid pest, has only been an economic pest in conifer plantations in the Southern Hemisphere where there were no native woodwasps to confuse it with (Hoebeke et al. 2005). Second, rearing larvae from trees is costly and time consuming. Locating, harvesting and storing infested trees is labor intensive and because many species of woodwasps take up to several years to attain maturity it is quite time consuming and thus expensive. Third, until this manuscript, most woodwasps were not considered to be particularly host specific and because many species can attack the same host it was not easy to associate specific larvae with reared adults.

The primary reasons to identify larvae are to recognize an infestation of a pest species and to prevent further introductions of exotic species. As the larval stage is present for 11 months and adults are only present for a few weeks it would be advantageous to be able to identify larvae immediately using molecular methods (hours or days) rather than wait as much as a year or more until identifiable adults can be reared. Because DNA is the same for all life stages, a molecular technique that identifies adults will also identify immature life stages.

2. Results of DNA analysis

The 622 specimens of woodwasps sequenced were resolved into 31 taxa including 28 taxa of Siricidae (603 sequences) and one taxon each of Xiphydriidae (*Xiphydria mellipes*, 3 sequences), Syntexidae (*Syntexis libocedrii*, 12 sequences) and Orussidae (*Orussus thoracicus*, 4 sequences) (Fig. E2.1). Complete consensus sequences, 658 base pairs, were obtained for 29 of the 31 taxa ultimately resolved. The consensus sequences for *Sirex obesus* and *Sirex* near *californicus* were only 613 and 615 base pairs, respectively. Of the 622 specimens sequenced, 476 (76.5 %) were complete sequences; of the rest, 88 specimens were greater in length than 600 base pairs, 48 were longer than 300bp. Length of sequence

for individual specimens is recorded under each species description. All species except *Sirex obesus* and *Sirex* near *californicus* had at least one specimen with a full length sequence.

Although all 622 specimens were unambiguously assigned to the correct family, genus and species taxon according to the siricid family revision proposed here, when this work was started, under the former classification (summarized in Smith 1979, Smith and Schiff 2002, Schiff et al. 2006), barcoding results generated several new species level hypotheses. In two cases, one in Xeris and one in Sirex, pairs of what were considered to be good species or subspecies were found to share identical barcodes. What were formerly classified as Sirex nigricornis and S. edwardsii are now listed as S. nigricornis and what were formerly listed as Xeris spectrum townesi and X. morrisoni indecisus are now listed as X. indecisus. Further, two pairs of subspecies, X. morrisoni morrisoni and X. morrisoni indecisus, and Urocerus gigas gigas and U. gigas flavicornis were easily separated using barcodes and are now elevated to species as Xeris indecisus, X. morrisoni, Urocerus gigas and U. flavicornis, respectively. DNA barcodes also hypothesized or supported several new taxa. Sirex abietinus was a single novel sequence until the species was characterized morphologically and more specimens were obtained and sequenced. Xeris melancholicus was initially recognized by its unique barcode and then characterized morphologically. Sirex obesus was identified morphologically and then, when fresh

specimens were obtained and sequenced, supported by barcodes. Two other taxa, *Sirex* near *nitidus* and especially *Sirex* near *californicus* are recognized by barcodes but have not been assigned species names because we have been unable to find supporting morphological characters with so few specimens.

The neighbor-joining tree of consensus sequences of each taxon (Fig. E2.1) showed well-delimited taxa. Separate neighbor-joining trees (Figs. E2.2 to E2.5) for individual specimens of small groups of species showed low intra-specific and high inter-specific divergence with no overlap between species. Percent identity and divergence for consensus sequences of all taxa are presented in Table E2.6. The greatest divergences were between families of woodwasps (30-40%). Anaxyelidae was most divergent from the others (34.1%-45.5%)followed by Orussidae (30.5%-42.6%) and Xiphydriidae (30.5%–40.3%). Within the Siricidae, the genera were well defined with percent divergences in the 20s-30s and within genera as low as 1.7% to the 20s. Divergences for the closest pairs of taxa were 1.7% for Sirex nitidus and S. near nitidus, 2.2% for Xeris indecisus and X. morrisoni, 2.8% for Urocerus gigas and U. flavicornis, 3.3% for Xeris caudatus and X. melancholicus, 4.6% for Sirex abietinus and S. varipes, 5.1% for Sirex californicus and S. near californicus and approximately 3.7% for Sirex cyaneus and S. nitidus or S. near nitidus. Of these least divergent pairs the smallest and largest divergences were for pairs that lacked morphological support.

TAXA		1 Eri. formanosus	2 Oru. thoracicus	3 Sir. abietinus	4 Sir. areolatus	5 Sir. behrensii	6 Sir. californicus	7 Sir. cyaneus	8 Sir. longicauda	9 Sir. near californicus	10 Sir. near nitidus	11 Sir. nigricornis	12 Sir. nitidus	13 Sir. noctillio	14 Sir. obesus	15 Sir. varipes	16 Sir. xerophilus	17 Syn. libocedrii	18 Tre. columba	19 Tre. fusicornis	20 Uro. albicornis	21 Uro. californicus	22 Uro. cressoni	23 Uro. flavicornis	24 Uro. gigas	25 Uro. taxodii	26 <i>Xer. melancholichus</i>	27 Xer. caudatus	28 Xer. indecisus	29 Xer. morrisoni	30 Xip. mellipes	31 Xoa. matsumurae	
	31	72.0	62.6	76.3		8.3			78.1	77.1				78.9	75.2					71.6				77.5 2	77.2 2	74.8	73.7 2			73.9 2	65.5		31
Percent Identity	30 3	3.1 72	68.7 62	67.5 70	6.6 70	7.3 78	5.2 78	4.0 70	68.1 78	65.0 77	4.670	7.6 75	4.9 7	6.1 78	64.6 75	7.9 7	6.0 75	8.8 6	4.4 77	1.7 7	9.0	7.5 70	5.2 75	8.7 77	8.4 7			4.7 74	97.9 63.1 74.0	63.2 73	6	35.2	30 3
	29	9.0 6	63.5 6	6.16	4.8 6	4.36	5.4 6	6.4 6	2.2 6	6.1 6	6.3 6	4.66	6.4 6	4.5 6	5.7 6	8.16	3.7 6	4.76	8.5 6	7.96	5.1 6	5.4 6	5.8 6	5.5 6	5.46	3.66	8.06	8.4 6	7.9 6	9	39.7	27.0 3	29
	28	8.7 6	3.5 6	76.0 76.1	5.5 7	5.17	5.87	6.6 7	75.1 72.6 72.2	77.4 75.9 76.1	5.4 7	4.2 7	5.8 7	75.8 73.9 74.5 66.1	5.0 7	7.5 7	3.7 7	64.1	57.6 6	70.7 67.5 67.9 61.7	4.9 7	5.47	5.7 7	4.8 7	91.5 76.3 76.6 74.6 75.4 68.4	74.9 73.4 73.6 63.2	96.8 88.1 88.0 64.1	88.0 88.4 64.7 74.8	6	2.2	0.3 3	6.82	28
	27	58.5 6	63.5 63.5	76.7	78.0	77.1	76.47	75.77	75.17	77.47	76.1	76.7	77.1	75.87	76.0	78.1	76.1	52.96	72.3 6	70.7 €	76.3	75.47	74.9	75.47	76.67	74.9	96.8	8	12.5		37.5 40.3	26.8 26.8	27
	26	66.7	62.7	76.6	77.1	76.6	75.8	76.0	74.2	77.2	76.3	76.7	76.6	75.4	76.2	78.3	75.8	62.0	71.7	70.1	76.0	75.2	74.8	75.4	76.3	74.2		3.3	11.9	12.1	38.0	27.4	26
	25	68.5	64.4	77.1 74.9 76.6 76.7	7.7.7	74.8	76.3	74.6	77.5 75.8 74.2	75.4	75.4	76.4	75.4	77.4	77.5 75.7 76.2 76.0 75.0 75.7	75.4	74.9	63.4	67.6	65.0	90.3	90.3	89.5	97.3 91.5 75.4 75.4 74.8 75.5 68.7	91.5		25.7	24.8	27.5	27.3	39.0 38.0	25.5	25
	24	72.6[72.3]70.5[72.5]70.2]62.3[75.8]76.1[71.9]70.8]70.7[71.3]71.1]68.5]66.7]68.5]68.7]69.0]63.1	64.9 64.6 64.9 66.0 65.5 64.4 62.7	77.1	.4 86.6 85.9 82.7 85.1 84.2 64.7 73.4 68.8 80.2 78.3 79.5 79.6 79.9 77.7 77.1 78.0 75.5 74.8 66.6 76.3	.0[84.3]85.7[84.3]84.8[85.3]63.7]72.8]71.3]78.6[78.3]76.3]78.4]78.9]74.8]76.6]77.1]75.1]74.3[67.3]78.3	.1 88.1 88.8 89.4 90.0 86.5 65.3 73.4 69.1 77.1 78.3 76.4 78.0 77.2 76.3 75.8 76.4 75.8 75.4 65.2 78.1	.0 96.4 89.5 87.4 89.1 88.3 64.7 72.9 68.8 78.0 75.8 76.9 77.5 76.9 74.6 76.0 75.7 76.6 76.4 64.0 76.9	77.5	89.691.290.787.264.973.269.477.477.176.378.577.675.477.2	88.6 98.3 90.0 87.1 88.6 88.3 64.4 72.9 70.1 78.6 76.9 78.4 78.7 78.1 75.4 76.3 76.1 75.4 76.3 64.6 76.9	89.2 88.0 85.5 88.1 90.4 65.7 74.5 70.5 78.4 79.0 78.0 78.9 78.7 76.4 76.7 76.7 74.2 74.6 67.6 75.4	90.9 86.8 89.4 88.6 65.0 73.4 70.1 78.1 76.7 78.0 78.0 77.4 75.4 76.6 77.1 75.8 76.4 64.9 77.1	86.890.188.065.076.672.078.978.778.079.979.977.475.4		87.5 65.0 74.6 72.2 77.5 78.4 77.1 78.1 78.0 75.4 78.3 78.1 77.5 78.1 67.9 77.1	63.8 72.9 69.9 77.1 76.6 75.2 76.7 75.8 74.9 75.8 76.1 73.7 73.7 66.0 75.8	62.9 58.8 65.7 64.9 63.4 64.9 64.6 63.4 62.0 62.9 64.1 64.7 68.8 61.7	76.1 68.5 69.8 67.6 69.6 69.9 67.6 71.7 72.3 67.6 68.5 64.4 72.0	67.3 67.6 67.3 68.1 65.0 70.1	91.291.893.092.990.376.076.374.975.169.076.6	92.693.992.790.375.275.475.475.467.576.6	92.9 93.3 89.5 74.8 74.9 75.7 75.8 65.2 75.2	97.3		8.9	22.9 25.7	.8 23.0 24.7 24.5 22.5 24.8 40.3 29.5 29.5 23.2 24.4 24.6 24.4 22.7 24.8	25.9	24.8	33.3 33.1	22.8 23.2 25.5 27.4	24
	23	71.3	66.0	77.7	579.6	3 78.4	178.0	977.5	82.2 82.7 65.3 73.6 70.1 76.9 75.7 75.4 77.2	3 78.5	18.7	78.9	78.0	79.9	77.2 78.1 76.3 78.1	78.1	276.7	164.9	69.6	67.3	93.0	693.9	92.9		2.8	1 8.9	30.6 22.9 24.4 24.6 24.2	524.4	525.9	124.8	33.3	t 22.8	23
	22	8 70.7	5 64.5	77.7 76.7	3 79.5	376.3	3 76.4	8 76.5	7 75.4	1 76.3	978.4	078.0	7 78.0	7 78.0	1 76.3	477.1	575.2	9 63.4	867.6	3 67.€	291.8	92.6		. 7.6	. 7.1	3 11.4	424.6	424.€	1 24.6	1 24.4	36.8 40.3 32.6 34.3 37.2	22.8 24.4	22
	21	970.8	964.0	777.2	2 78.3	678.3	1 78.3	075.8	975.2	4 77.	676.9	4 79.(176.	978.	2 78.	5 78.4	1 76.0	7 64.9	5 69.8	3 67.3	91.2		5 7.7	6.4	t 7.4	1 10.3	924.4	224.4	5 25.	3 25.	634.3	2 22.8	21
	20	171.	7 64.	74.5 71.6 77.7	880.	378.	177.	878.	176.	4 77.	178.	5 78.	1 78.	078.	777.	277.	977.	8 65.	168.	69.3	3	9 9.1	7 8.6	5 7.2	7 7.4	22.623.624.624.839.032.935.10.1	622.	5 23.	025.	2 25.	332.	23.624.641.927.929.323.2	20
	8 19	.8 76.	.7 59.7	.571.	.4 68.	.871.	.4 69.	.9 68.	.670.	.2 69.	.970.	.5 70.	.4 70.	.672.	88.3 85.0 63.8 73.1 68.7	.672.	.969.	.958.	76.	4	.2 30.3	.832.	.832.	.632.	23.4 37.5 29.6 31.7	.935.	.730.	.5 29.	.034.	.633.	.840.	.929.	8 19
	7 18	.3 75.	65.6 65.2 64.7	.774	.773.	.772	.3 73.	.772	.373.	.973.	.472	.774	.073	.076	.873.	.074	.872	62	.7	.5 24.4	.531	.029.	.831	.5 29.	.5 29.	.032	.329.	.329	.234	.732	.136	.927	17 18
	16 17	.2 62	665	664	.2 64	6.3 63	5.5 65	3.64	2.7 65	.2 64	3.64	.4 65	.6 65	3.0 65	0.0	.5 65	63	0.0	.039	0.145.5	.536	.737	.438	.737	.437	.839	.641	.840	.438	.5 37	32.9 35.0 34.1	.641	16 1
	15 1	2.5 7(4.7 65	5.4 85	5.184	4.885	0.086	9.188	2.2 82	0.787	8.688	8.190	9.4 88	0.188	8.3 85	87	2.6	8.539	5.227	8.330	2.3 22	1.5 22	2.924	2.3 22	22.1 23	4.624	2.124	2.5 24	2.7 27	2.3 27	2.935	3.624	15 1
	14]	0.5 72	2.8 64	88.6 95.4 85.6 64.7	2.7 8:	4.38	9.4 90	7.4 89	82.7 82	1.29(7.18	5.5 88	6.8 89	6.8 9(8	11.4	4.7 11	9.53	6.32:	0.92	1.62	0.72	2.3 22	0.9 22	1.42	3.62	3.9 22	4.5 2	4.82	4.1 2	6.83	24.7 2.	14 1
	13	2.37	6 64.6 66.6 62.8 64.7		5.98	5.78	8.88	9.58	82.18	9.69	0.08	8.08	0.98	8	12.5	9.7 1	1.7 1	37.5 37.5 39.5 38.5 39.0	4 26.3 22.5 26.3 25.2 27.0 39.7	27.9 30.9 28.3 30.1	20.3 21.6 22.3 22.5 36.5 31.2	22.5 20.7 20.7 21.5 22.7 37.0 29.8 32.9	20.9 21.3 22.3 22.9 24.4 38.8 31.8 32.7	.9 21.5 19.7 20.9 22.3 22.7 37.5 29.6 32.5	21.5 19.3 21.4	2.62	4 22.8 24.3 23.9 22.1 24.6 41.3 29.7	4.7 2	5.5 2	4.92	9 36.0 34.0 36.8	21.22	13
	12	72.6	54.66	89.8 90.1	36.68	34.3 8	38.1 8	96.4 8	82.7 8	.5 89.3 8	98.3	39.2 8	6	8.9	12.7 1	8 10.3	1.7	37.5 3	26.3 2	.4 29.2 2	20.7 2	22.5 2	20.92	21.5 1	21.5 1	24.42	22.8 2	23.0 2	23.62	23.0 2	36.03	23.2 2	12
	11	4	65.	87.7	85.4	85.08	85.18		83.7	2	88.6		10.8	11.1	14.1		9.8	5		29.4	21.3	20.3	5	20.9		24.2	23.4	23.8	26.8	26.1	32	24.2	11
	10	72.8	65.0	89.2	85.3 87.8 84.7 87.4 85	83.4 86.9 83.4 83.9 85	89.1 82.7 95.0 87.8 85.	96.4 88	83.0	89.4		11.3	1.7	9.9	12.3	11.0 11.	11.9	38.5	26.7	29.9 29.	22.6 20.9 22.8 22.4 20.3 21.3	22.5	20.5	22.2 22.2 23.2 21.5 20.7 20.	20.7 21	24.7	23.4	24.0	24.7	23.6	36.5	23.2	10
	6	70.7	65.4	90.4	84.7	83.4	95.0	90.1	83.1		10.7	12.6	17.6 10.9	18.0 10.7	8.0	9.2	13.0	39.0	27.4	31.3	22.4	23.1	23.8	21.5	22.6 22.4 22.5 22.2	25.3 24.2 24.7	23.3	23.3	24.7	24.7	36.6	23.0 23.7	6
	8	71.6	65.3	82.4	87.8	.86.9	82.7	82.7		17.8	17.2	16.6	17.6	18.0	11.9 16.9	18.0	17.8	37.2	27.4	30.5	22.8	24.2	24.6	23.2	- 22.5	24.2	26.6	25.9	28.6	29.0	33.1	23.0	×
	7	9 73.1	3 65.3	89.7		5 83.4	89.1	0	2 17.4	10.1	3 3.8	2 12.C	9 3.7	5 10.3		l 10.6	5 12.0	2 38.7	27.2	331.3	5 20.9	7 23.6	5 22.6	22.2	5 22.4	3 25.3	3 24.2	3 25.1) 23.6	5 23.6	5 36.7) 23.2	٢
	9	6 73.9	1 66.3	7 88.9	85.9 83.7	83.6	2	7 11.(3 18.2	4 5.1	3 12.3	9 15.2	7 11.9	14.2 14.0 11.5	3 10.4	7 10.1	7 13.5	0 38.2	2 27.2	4 31.8	1 22.6	3 21.5	0 23.5	3 22.2	5 22.6	3 23.8	8 24.8	3 24.3	3 25.(5 25.5	3 36.5	2 23.0	9
	ŝ	673.	66.6 63.1	3 84.7	85.	2	5 17.	916.	913.	15.3 17.4	7 16.	5 14.0	6 15.	2 14.0	9 15.	9 15.	5 14.	739.	827.	32.2 29.4	921.	121.	1 23.0	921.	920.	8 25.	1 23.	5 23.	3 25.	3 26.	35.6 34.3	623.	S
	4	73.3 71.6 73.6 73.9 73.1 71.6 70.7 72.8 71	.1 66.	84.3	.5	.7 14.	.016.	.3 14.	17.4 11.9 13.3	4 15.	37.2 10.6 12.7 16.3 12.3 3.8 17.2 10.7	.4 14.	37.0 10.1 13.6 15.7	7 14.	37.9 10.8 16.9 15.3 10.4	4.6 14.9 15.7 10.1 10.6 18.0	.6 15.	.2 37.	.727.	.2 32.	36.7 21.9 19.9 21.1	22.5 22.1 21.3 21.7 23.6 24.2 23.1 22.5 20.3	.021.	22.8 20.9 21.3	22.5 19.9 20.5	38.0 24.4 22.8 25.3 23.8	23.4 23.1 23.8 24.8 24.2 26.6 23.3 23.4	.622.	.825.	.626.	.835.	24.0 24.6 23.2	4
	3	.273.	63.1	.7	.5 15.5	.7 15.	.7 11.	.710.	.717.	0.9.4	.2 10.	.2 12.	.010.	2 9.7	.910.		.5 14.	.738.	.025.	.1 29.2	.721.	.722.	.5 23.	.722.	.5 22.	.024.	.223.	.2 23.	.5 23.	.5 23.	.5 33.8	.324	3
	1 2	60.2	42.6	27.5 37.7	29.4 34.5	26.8 37.7 15.7 14.2	26.4 35.7 11.0 16.5 17.2	27.036.710.314.916.7111.0	29.6 35.7	29.8 36.0	27.5 37.	28.7 34.2 12.4 14.5 14.9 15.2 12.0 16.6 12.6 11.3	27.5 37.	27.9 34.2	29.4 37.	28.3 36.4	29.7 35.5 14.6 15.5 14.7 13.5 12.0 17.8 13.0 11.9 9.8 11.7 11.7 14.7 12.6	41.0 36.7 38.2 37.7 39.0 38.2 38.7 37.2 39.0 38.5 36	24.8 37.0 25.7 27.8 27.2 27.2 27.4 27.4 26.7 24	25.2 42.1	27.8 36	29.7 36.7	28.5 36.5 23.0 21.1 23.0 23.5 22.6 24.6 23.8 20.5 21	28.8 35.7	28.5 36.5	31.5 38.	34.6 39.2	31.9 38.2 23.6 22.5 23.3 24.3 25.1 25.9 23.3 24.0 23	31.238.523.825.325.325.325.023.628.624.724.726.823.625.524.822.727.438.234.034.025.525.124.625.925.925.927.511.9	30.8[38.5]23.6[26.3]26.5[25.5]23.6[29.0]24.7[23.6[26.1]23.0]24.9[24.1]22.3[27.5]37.7[32.6[33.2]25.3[25.1]24.4[24.8[24.8[27.3]12.1]11.9	39.7 30.5	29.1 40.3	1 2
		1	2 42	3 27	4 29	5 26	6 26	7 27	8 29	9 29	10 27	11 28	12 27	13 27	14 29	15 28	16 29	17 41	18 24	19 25	20 27	21 29	22 28	23 28	24 28	25 31	26 34	27 31	28 31	29 30	30 39	31 29	
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Table 2.6. Percent identity between species of sequenced Siricidae and one taxon in three related families (Orussidae, Syntexidae and Xiphydriidae).

3. Discussion

The most important question when deciding to use a new technique to identify species is: does the technique unambiguously identify specimens of each species correctly 100% of the time? In the case of using DNA barcodes to identify New World Siricidae the answer is yes but it was difficult to get to this answer because the Siricidae was in need of revision when the project was started. Our simultaneous morphological and barcoding analyses are in almost complete agreement. Unique barcodes exist for all morphologically distinct species for which we could obtain sequences. However, two of the morphologically distinct species, Sirex californicus and S. nitidus, each appear to harbor a cryptic taxon that is only recognizable by DNA barcode. The question remains: are these cryptic taxa good species? It is possible they could be artifacts of barcoding such as heteroplasmy or numts or it may be they are very good cryptic species and we have been unable as yet to discover morphological or behavioral support for them. To reduce the risk of heteroplasmy we directly sequenced double stranded PCR products. If there were rare haplotypes they would be masked by the most common haplotype. If there were two or more common haplotypes there would have been double peaks and the sequences would have been difficult to read. To reduce the possibility of having amplified numts we isolated samples from mitochondrial rich tissue and we inspected translated sequences to look for artifacts common in numts such as stop codons, insertions and deletions. There were no stop codons, insertions or deletions in any of the samples except for Orussus thoracicus which was missing one codon, in frame. We do not believe this is indicative of a nuclear mitochondrial pseudogene however, as the same codon is absent in three other Orussus species (data not presented). Either, all four Orussus species have the same pseudogene which is amplified preferentially over the mitochondrial gene, which seems unlikely, or the missing codon reflects a genuine difference between Orussus and all the other woodwasps. Although we believe the cryptic taxa are probably valid species, until we can examine more specimens and do further analyses we have chosen to leave the cryptic taxa unnamed. Despite the utility of barcodes for identifying Siricidae we still believe new species require a morphological description.

One of the reasons barcoding was so useful in revising the North American Siricidae is because it is color blind. Prior to this study, abdomen and leg color were often used as simple diagnostic characters for siricid species (Middlekauf 1960, Smith and Schiff 2002, Schiff *et al.* 2006). However, identical DNA barcodes supported by morphological characters suggested that pairs or groups of what were considered to be good species based on abdomen color were really single species. In

this study there were three examples, Sirex nigricornis, Xeris indecisus and Tremex columba. In the first two examples, each species has two female color morphs with either red (the former Sirex nigricornis and the former *Xeris morrisoni indecisus*) or black (the former Sirex edwardsii and the former Xeris spectrum townesi) abdomens. In the third example, females of T. columba have one of three color morphs associated with wing color differences. These color morphs were recognized as separate species until Bradley (1913) lumped them together, a position supported by the current barcode results. Whereas it is easy to understand why such dramatic characters would be considered diagnostic for species, this study demonstrates that abdomen color can be misleading. Interestingly, in the original description Brullé suggested that the only difference he saw between Sirex edwardsii and Sirex nigricornis was that the abdomen was blue and he even suggested that it might just be a variety of Sirex nigricornis. Genetic control of abdomen color must be fairly loose in Symphyta because there are several examples of different color morphs in at least four different families. Species with both red and black abdominal color morphs have been recorded in the Xiphydriidae (Xiphydria tibialis Say, in Smith 1976), Xyelidae (Macroxyela ferruginea (Say), in Smith and Schiff 1998), Tenthredinidae (Lagium atroviolaceum (Norton), in Smith 1986) and, Siricidae (present study). Barcodes were also useful in resolving leg color morphs. Sirex californicus, S. nitidus and S. noctilio each have pale and dark leg color morphs. At least for Sirex californicus and S. nitidus both color forms have the same barcode. We have no sequences for the dark color morph of Sirex noctilio. Ironically, abdomen and leg color are still useful characters for identifying woodwasps (e.g., Sirex varipes) but this work shows that they should not be used as sole diagnostic characters. Instead, they should be combined with other characters, as we do here, to lead to a diagnosis.

To identify any stages of woodwasps using barcodes, a novel sequence should be aligned with the 31 consensus sequences reported here (See appendix 3) using Clustal V and then visualized in a neighbor-joining tree using appropriate software. The novel sequence should align very closely with the branch of its congener. The range of intra-specific variation is represented in the species trees (Figs. E2.2 - E2.5) and it should be easy to recognize if a species falls outside its expected range. Determining a species threshold limit for barcode data of unknown taxa is quite controversial (Rubinoff et al. 2006). Hebert et al. (2003) originally proposed that a 2-3% difference would be sufficient to separate animal species. At that level, we might not be able to separate Sirex nitidus from the cryptic taxon S. near nitidus, or two pairs of closely related but morphologically distinct species, Urocerus flavicornus

from U. gigas and Xeris morrisoni from X. indecisus. Later, Hebert et al. (2004A) proposed a threshold that was 10 times the mean intraspecific variation for the group under study. This new threshold addresses the diagnostic value of the relationship of interspecific to intraspecific variation but still presupposes a level of species uniformity. Both of these thresholds could be problematic if we were trying to separate species from a sea of unknowns; fortunately, we are trying to identify unknowns by comparison to a relatively well sampled database of recognized species. Unknown sequences will either match one of the known species or become a new hypothesis to be evaluated with morphological or other methods. Although all the species represented here are well delimited, it is possible that barcodes for newly recognized, closely related species could overlap and this database would not be able to resolve them.

We believe the consensus tree (Fig. E2.1) is robust because of the species sampling that went into it. We obtained representatives of each species from as much of the geographic and temporal ranges as possible, as can be seen in the specimens for molecular studies section under each species description. Although sampling can never be complete, multiple samples across the range are a more cogent representation of the species variation then a single specimen from one location in its range.

4. Conclusion

The combination of classical morphological and DNA barcoding methods have allowed us to revise New

World Siricidae and develop a DNA database that will enable identification of most New World siricid larvae. Each morphological species has a corresponding welldelimited barcode. Two species appear to have a cryptic taxon which we have chosen to keep unnamed because they lack morphological support. Our work demonstrates that barcodes are a useful addition to other taxonomic methods, especially for tasks such as associating life stages.

Outgroups studied and illustrated in consensus tree (Fig. E2.1):

Orussus thoracicus

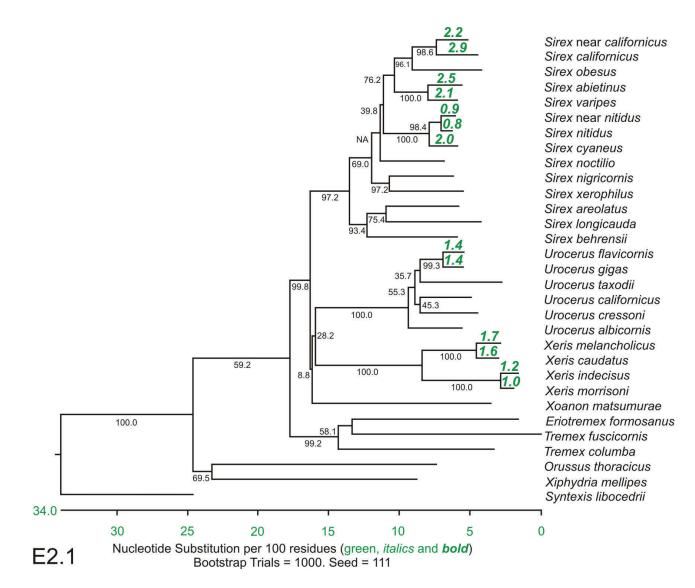
USA. California: 2005, *CBHR 35*, 655; 2005, *CBHR 306*, 655; 2005, *CBHR 307*, 655; 2005, *CBHR 308*, 655.

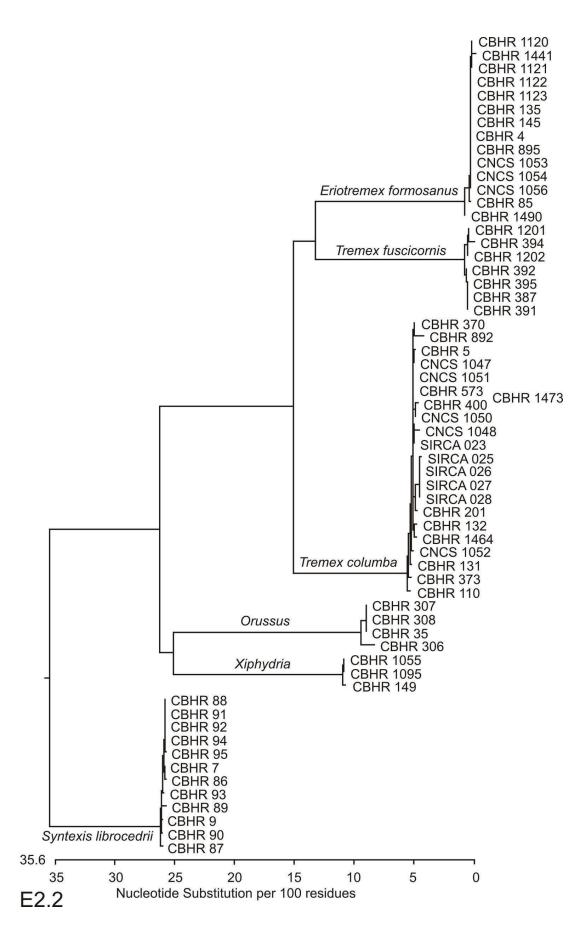
Syntexis libocedrii:

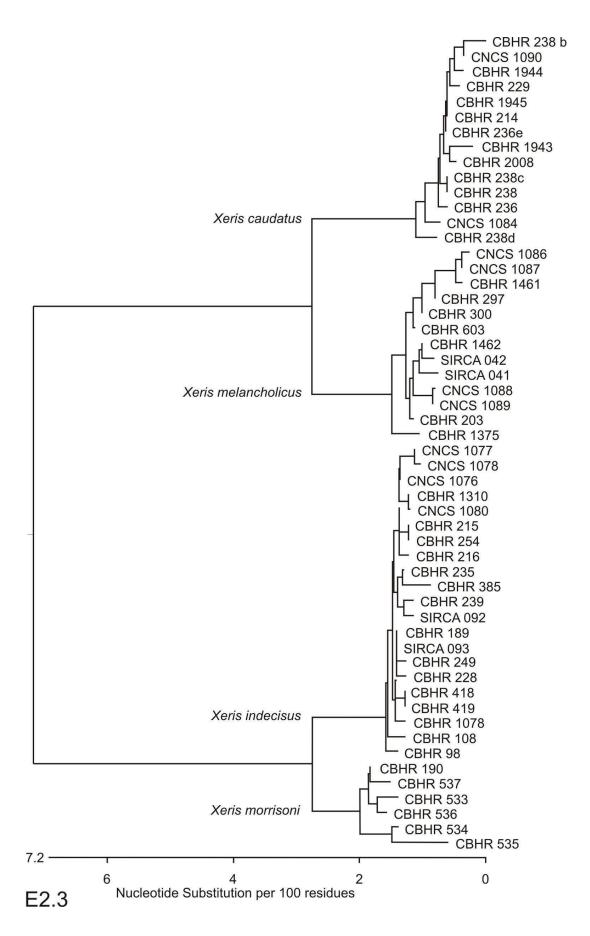
USA. California: 2005, *CBHR 86*, 658; 2005, *CBHR 87*, 658; 2005, *CBHR 88*, 658; 2005, *CBHR 88*, 658; 2005, *CBHR 99*, 658; 2005, *CBHR 91*, 658; 2005, *CBHR 92*, 658; 2005, *CBHR 93*, 658; 2005, *CBHR 94*, 658; 2005, *CBHR 95*, 658. **Oregon**: 2003, *CBHR 7*, 658; 2003, *CBHR 9*, 658.

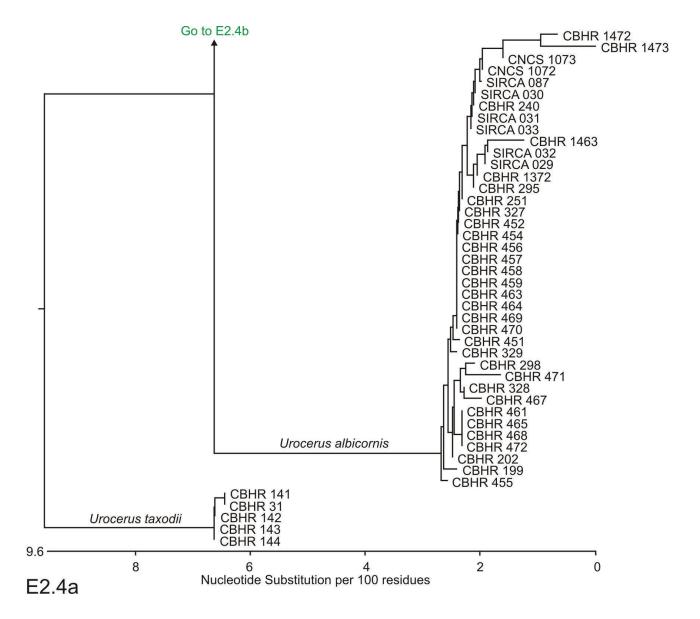
Xiphydria mellipes:

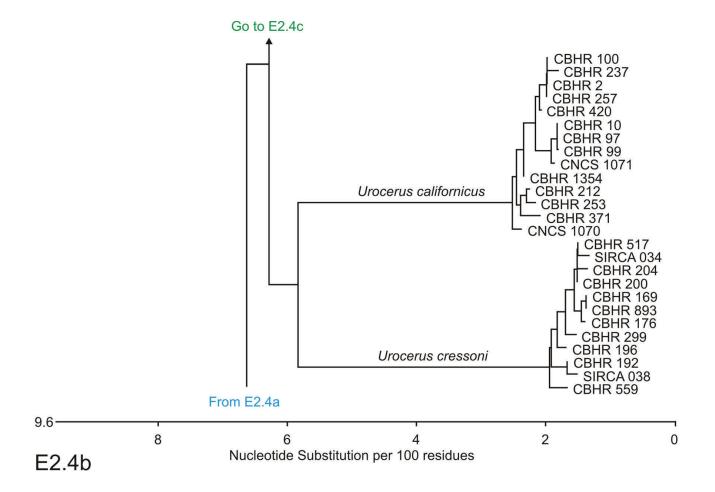
CANADA. Ontario: 2005, *CBHR 1055*, 658; 2005, *CBHR 1095*, 658. **USA. Wisconsin**: 2005, *CBHR 149*, 658.

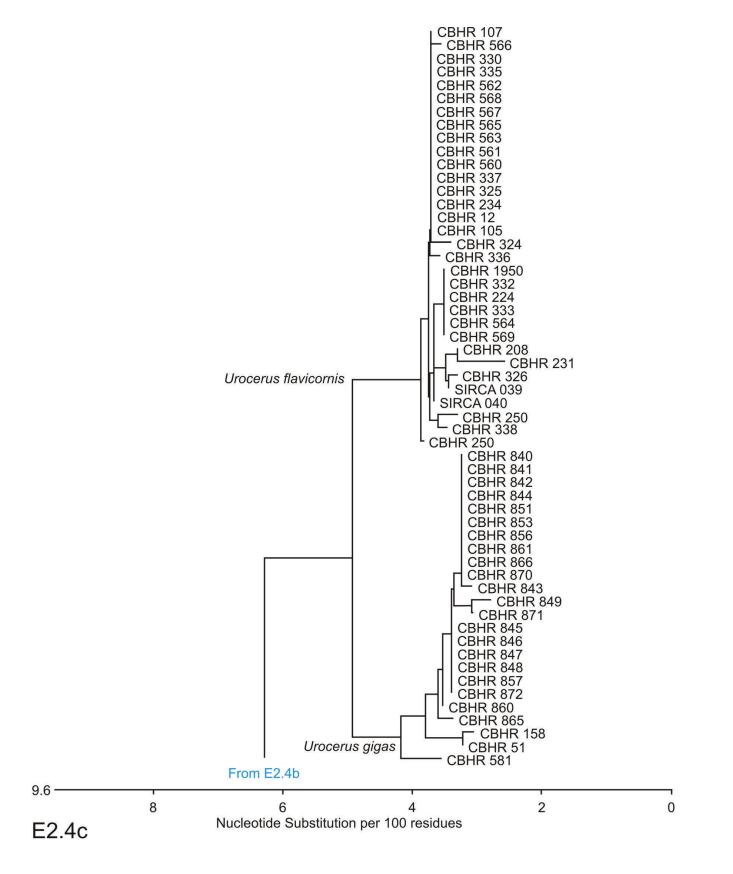


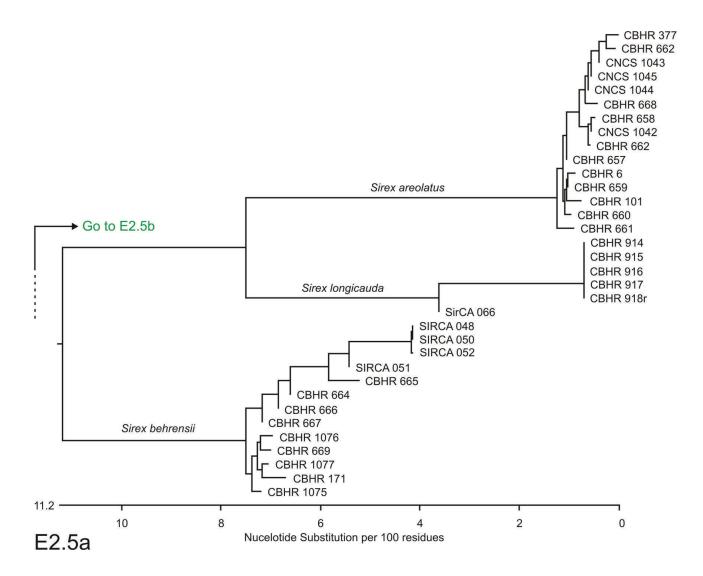


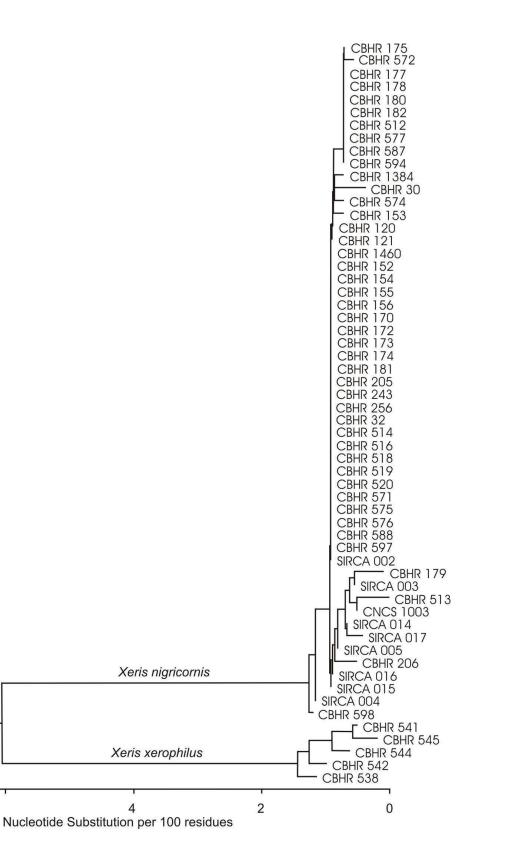










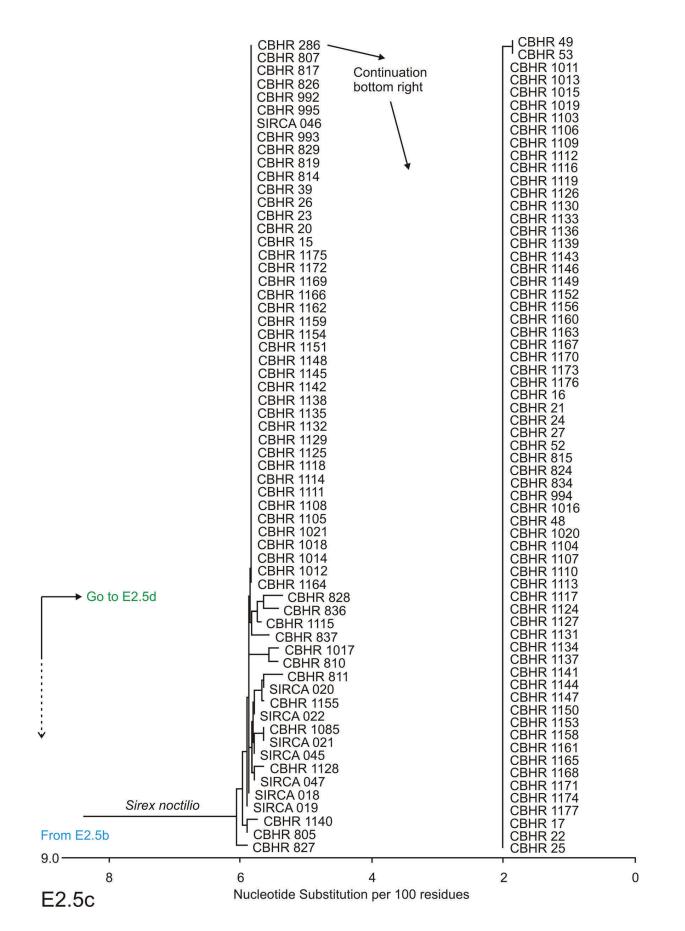




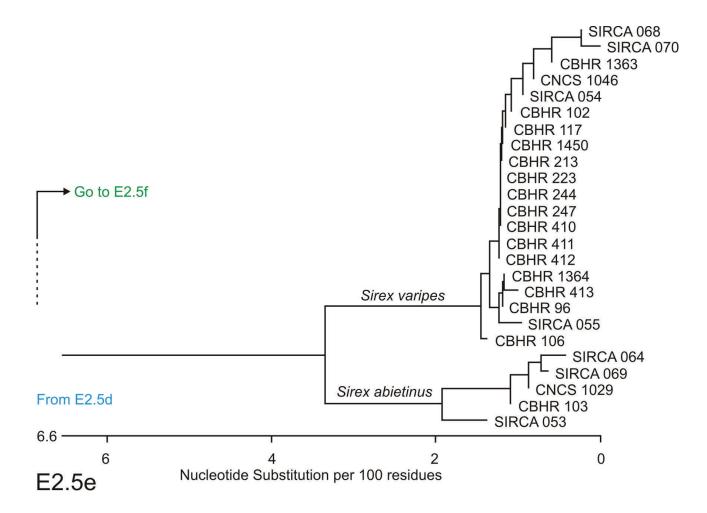
9.0-

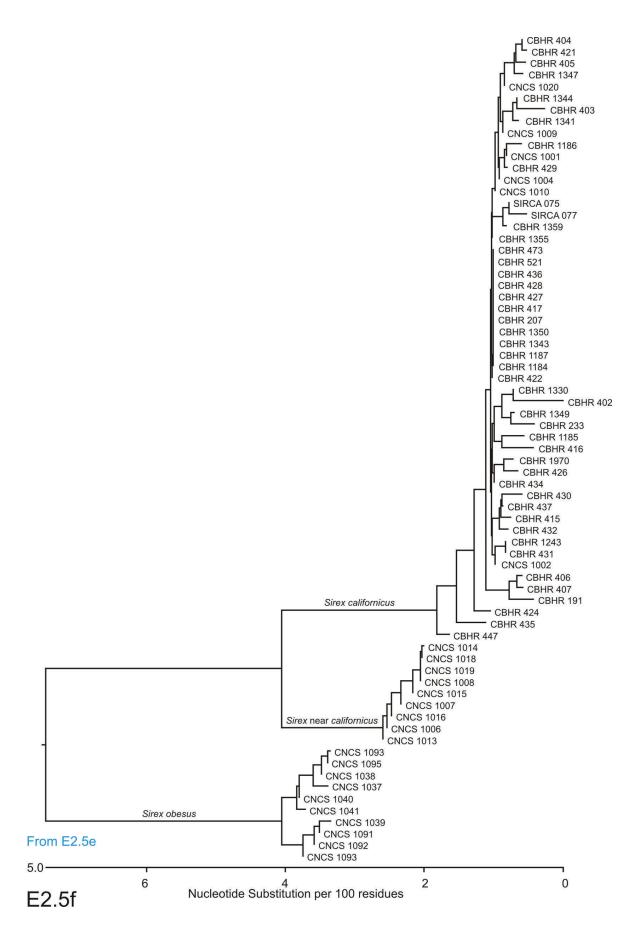
From E2.5a

Go to E2.5c



CBHR 1096
 CBHR 599





F. Acknowledgements

Many colleagues generously contributed various elements that helped us produce a comprehensive revision. We are most appreciative of and indebted for their support.

Systematic research is based on specimens stored in collections and looked after by conscientious colleagues. The quality of research is proportional to the number of specimens studied. We were fortunate to obtain a large number of them and are most thankful to the curators mentioned under "Materials and methods" that either facilitated our visit to their collection or sent us specimens on loan. With the establishment of Sirex noctilio in the Great Lake region, many surveys were carried out and long series of specimens were submitted to us for identification. We greatly appreciate the survey specimens of Siricidae generously given to us by H. Douglas (CFIA), D. Langor (NFRC), the late P. de Groot, K. Nystrom and I. Ochoa (GLFC), L. Humble and J. Smith (PFRC), J. J. Jones (Alberta), J. Kruze (USFS-AK), D. Miller (USFS-GA), C. Piché (MNRQ), J. Sweeney and J. Price (FRLC), and K. Zylstra (USDA). These fresh and clean specimens permit us to study the DNA of significant specimens and enriched our collections.

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Traditionally, only morphological features were studied from specimens in collections. Lately, DNA sequencing of properly preserved specimens has opened a new set of characters previously unavailable. Many of the submitted specimens were freshly collected and offered us the opportunity to extract information from DNA barcodes (cytochrome *c* oxidase 1 - CO1). This new tool in conjunction with the classical morphological approach gave us much confidence in our conclusions. We greatly appreciate having access to specimens properly preserved for DNA sequencing provided by H. Douglas (CFIA), V. Grebennikov (CFIA), D. Langor (NFRC), P. de Groot, K. Nystrom and I. Ochoa (GLFC), L. Humble and J. Smith (PFRC), and D. Miller (USFS– GA). We are also very grateful for support from the Government of Canada through Genome Canada and the Ontario Genomics Institute in support of the International Barcode of Life Project. This funding allowed staff at the Biodiversity Institute of Ontario under the leadership of P. Hebert to sequence more than 300 specimens of Siricidae, and covered the costs in the preparation and digitization of specimen data by J. Fernandez–Triana. We also appreciate the time spent by A. Smith and J. Fernandez–Triana explaining details of the results to HG.

We intended this work to be profusely illustrated. We had access to lots of dried adults, but we wanted to show how they looked when alive. Unless properly equipped, finding live specimens of Siricidae is often difficult. We therefore thank P. de Groot (GLFC), J. Sweeney and J. Price (FRLC), and K. E. Zylstra (USDA) for providing live specimens of some species of Siricidae or their parasitoids for live habitus images. We also appreciated movies of parasites and Siricidae provided by J. Read (CNC).

Adults of Siricidae are easily damaged so we were worried about borrowing type specimens. We tried to study types during our visit to various North American collections but we did not have the opportunity to visit European collections. To avoid having types sent by post, we studied the description and previous opinions about each type. Then, we decided if photos of a type would be enough to resolve its identity. Through the kindness of G. Hancock (HMUG), J. E. Hogan (OXUM), L. Vilhelmsen (ZMUC), we were able to get the necessary pictures taken.

Much information came from many colleagues. The following colleagues kindly spent time trying to find specimens of unusual species in their respective collections, providing information about types whereabouts, and hand carrying of such specimens. We are very grateful to C. P. D. T. Gillett (BMNH), H. Vardal (Swedish Museum of Natural History), Y. Bousquet (CNC), V. Grebennikov (CFIA), G. Hancock (HMUG), J. Karlson (Swedish Malaise Trap Project), J. Genaro (Toronto, Ontario), M. Sharkey (Kentucky), A. Shinohara (EIHU) for their efforts. Because of widespread surveys around the Great Lakes, we had access to records of numerous locations for each species. We greatly appreciate not only the data but the coordinates, allowing us to map rapidly the range of many species within the survey area. For this information we are indebted to R. Favrin and L. Dumouchel (CFIA), R. Hoebecke (CUIC), S. Long (CUIC), K. Nystrom (GLFC), and C. Piché (MNRQ). Preparing this paper for the internet involved new knowledge with new software programs. We are most grateful for the training provided by J. Read (CNC) to C. Boudreault (CNC), and her help in designing various templates. In addition we thank L. Bearss (CNC) for training C. Boudreault in the use of a mapping program.

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At completion of a large manuscript, it is very difficult to see one's own errors in the text. Despite our efforts we missed numerous punctuation, grammatical mistakes, overly long sentences, sentences with missing words, and duplication of part of sentences during copy and paste work. We are most thankful to reviewers, G. A. P. Gibson, J. T. Huber, S. A. Marshall, S. Blank, A. Liston, A. Taeger, R. A. Ochoa and T. J. Henry. We are especially thankful to J. T. Huber who read the text very critically three times. He rounded up most errors and insured a uniformity of style.

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Species (source)	Number of specimens	Length of annulus 10 relative to diameter of ovipositor at annulus 10					
		Mean	St. Dev.	+2 S.D.	-2 S. D.	Min.	Max.
Sirex nitidus (QC)	32	1.54	0.13	1.81	1.29	1.27	1.85
Sirex nitidus (AK)	30	1.65	0.12	1.87	1.39	1.43	1.76
Sirex cyaneus (NB)	40	1.57	0.12	1.82	1.33	1.30	1.77
Sirex abietinus (BC)	26	2.06	0.15	2.37	1.75	1.85	2.05

Appendix 1: Statistical data

Table 1. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of annulus 10 between pits 9 and 10 relative to the diameter of the ovipositor at annulus 10.

Species	Number of specimens	Length of basal relative to apical sheath sections						
		Mean	St. Dev.	+2 S. D.	-2 S. D.	Min.	Max.	
Sirex longicauda	17	0.51	0.05	0.61	0.41	0.41	0.57	
Sirex areolatus	28	0.66	0.07	0.79	0.53	0.49	0.75	
Sirex behrensii	25	1.05	0.06	1.18	0.93	0.87	1.20	
Sirex nigricornis	30	1.26	0.09	1.45	1.07	1.07	1.44	
Sirex noctilio	30	1.170	0.06	1.28	1.05	1.06	1.31	
Sirex californicus	30	1.17	0.07	1.32	1.03	1.06	1.35	
Sirex varipes	53	0.98	0.03	1.05	0.91	0.87	1.09	
Sirex nitidus	30	1.04	0.06	1.17	0.91	0.89	1.21	
Sirex cyaneus	30	1.00	0.06	1.12	0.87	0.83	1.10	
Sirex abietinus	28	0.87	0.06	1.00	0.74	0.73	0.97	

Table 2. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the basal sheath section relative to the apical sheath section.

Species	Number of specimens	Length of sheath relative to length of fore wing						
		Mean	St. Dev.	+2 S. D.	-2 S. D.	Min.	Max.	
Sirex longicauda	17	1.10	0.08	1.41	1.25	1.16	1.39	
Sirex areolatus	28	0.84	0.09	1.21	1.03	0.82	1.23	
Sirex behrensii	25	0.68	0.04	0.82	0.75	0.69	0.855	
Sirex nigricornis	30	0.57	0.03	0.69	0.63	0.592	0.73	
Sirex noctilio	30	0.61	0.03	0.74	0.67	0.60	0.74	
Sirex californicus	30	0.58	0.05	0.79	0.69	0.55	0.78	
Sirex varipes	53	0.70	0.03	0.83	0.77	0.68	0.90	
Sirex nitidus	30	0.66	0.03	0.80	0.73	0.64	0.78	
Sirex cyaneus	30	0.71	0.04	0.86	0.79	0.71	0.88	
Sirex abietinus	28	0.65	0.07	0.95	0.80	0.63	0.97	

Table 3. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the sheath relative to the length of the fore wing.

Species (source)	Number of specimens	Length of apical relative to basal sheath sections					
		Mean	St. Dev.	+2 S.D.	-2 S. D.	Min.	Max.
Urocerus gigas	9	1.40	0.02	1.48	1.31	1.34	1.45
Urocerus flavicornis	20	1.32	0.10	1.51	1.12	1.16	1.46

Table 4. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of apical section of the sheath relative to that of the basal section of the sheath.

Species (source)	Number of specimens	Length of metatarsomere 2 relative to maximum height of metatarsomere 2					
		Mean	St. Dev.	+2 S.D.	-2 S. D.	Min.	Max.
Urocerus flavicornis	30	6.80	0.60	8.00	5.54	5.58	8.25
Urocerus albicornis	30	4.61	0.30	5.21	4.00	4.00	5.11
Urocerus gigas	21	5.38	0.45	6.27	4.50	4.5	6.27

Table 5. Mean, standard deviation (values for 1, +2 and -2) and range for the proportion of the length of the metatarsomere 2 relative to the maximum height of the metatarsomere 2.

Appendix 2: Revision to Schiff et al. (2006)

Schiff *et al.* (2006) published a key to genera and species of the North American Siricidae. Their excellent illustrations should help anyone without a reference collection trying to identify a specimen. However, the revisions below should first be made in the text.

Page 7, Figure 3 at centre is a Urocerus and at right a Xeris.

- Page 16, There are several problems with the key, and it should be avoided. For instance, in key couplet 7 the antennal color for *Sirex juvencus juvencus* does not work at all (this is *S. nitidus* or a European specimen of *S. juvencus*); in couplet 9, *Sirex juvencus californicus*, should be *S. californicus* (the pale legged form of the species is not considered in the key and would key to *S. cyaneus* in couplet 10), and *Sirex edwardsii* is the dark color form of *S. nigricornis*.
- Page 17, Figure 5 (top) is either S. cyaneus or S. nitidus.
- Page 27, Figure (left) the metatibia and metafemur are oddly colored (the species cannot be recognized); figure (right) is either a *S. nitidus* or *S. varipes* because of spot on the mesotibia and mesotarsomeres 1 and 2.
- Page 28. The figure is either *S. cyaneus* or *S. nitidus*.
- Page 29. The figure is S. nitidus (based on the visible portion of the ovipositor).
- Page 31. Sirex edwardsii is the dark color form of S. nigricornis.
- Page 35. *Sirex juvencus californicus* should be *S. californicus*. Females exist in two color forms. The dark form is as in figures on pp. 36 and 37. The pale form is not illustrated but it resembles *S. cyaneus* or *S. nitidus*.
- Page 39. The top figure is *S. cyaneus*, the left figure may be *S. cyaneus*, but it is not clear, the right figure is probably *S. juvencus* based on its antennal color pattern (a pattern that is almost never seen in North America). *Sirex juvencus* is not found in North America though it has been intercepted many times.
- Pages 40 and 41. The image is either *S. cyaneus* or *S. nitidus*.

Page 56. The key to species of *Urocerus* is good, but the species name of couplet 11 should be interchanged.

- Page 57. Figure 8. The caption should be reversed. The top image is *Urocerus albicornis* and the bottom image is *U. flavicornis*.
- Page 80. The key is not clear enough as it attempt to segregate only three species of *Xeris*. Two of the species, *X. morrisoni* and *X. spectrum*, are complexes of two and three species respectively. We now know of seven species of *Xeris* for the region. The figures are clear, however.
- Page 83. Xeris morrisoni indecisus should be replaced by X. indecisus. This is the pale color form of the species.
- Page 87. Xeris morrisoni morrisoni should be replaced by Xeris morrisoni.
- Page 91. The illustration is a male of the black form of Xeris indecisus, not of X. spectrum spectrum.
- Pages 92 and 93. Xeris spectrum spectrum is either X. melancholicus or X. caudatus.
- Pages 95 and 96. The illustrations are females of the black form of X. indecisus (X. spectrum townesi is a synonym).

Appendix 3: Disposition of Sequences

FASTA Sequences representing each of the 31 species of this study are deposited in Genbank and at the Center for Bottomland Hardwoods Research Web Site.

A set of zipped files can be downloaded from the CBHR site at the following URL: http://www.srs.fs.usda.gov/cbhr/products/downloads/2012_nms_SiricidFASTA.zip

The Genbank and Canadian accession numbers are as follows:

Sequence ID	Species name	Specimen code	Genbank accession number	Canadian collection specimen code
Seq1	Eriotremex formosana	CBHR4	JQ619784	
Seq2	Orussus thoracicus	CBHR35	JQ619785	
Seq3	Sirex abietinus	CBHR103	JQ619786	
Seq4	Sirex areolatus	CBHR377	JQ619787	
Seq5	Sirex behrensii	CBHR669	JQ619788	
Seq6	Sirex californicus	CBHR1184	JQ619789	
Seq7	Sirex cyaneus	CBHR610	JQ619790	
Seq8	Sirex longicauda	CBHR914	JQ619791	
Seq9	Sirex near californicus	CNCS1018	JQ619792	SIR 018
Seq10	Sirex near nitidus	CBHR555	JQ619793	
Seq11	Sirex nigricornis	CBHR30	JQ619794	
Seq12	Sirex nitidus	CBHR615	JQ619795	
Seq13	Sirex noctilio	CBHR815	JQ619796	
Seq14	Sirex obesus	CNCS1039	JQ619797	SIR 039
Seq15	Sirex varipes	CBHR104	JQ619798	
Seq16	Sirex xerophilus	CBHR541	JQ619799	
Seq17	Syntexis libocedrii	CBHR9	JQ619800	
Seq18	Tremex columba	CBHR5	JQ619801	
Seq19	Tremex fuscicornis	CBHR392	JQ619802	
Seq20	Urocerus albicornis	CBHR199	JQ619803	
Seq21	Urocerus californicus	CBHR2	JQ619804	
Seq22	Urocerus cressoni	CBHR169	JQ619805	
Seq23	Urocerus flavicornis	CBHR12	JQ619806	
Seq24	Urocerus gigas	CBHR842	JQ619807	
Seq25	Urocerus taxodii	CBHR31	JQ619808	
Seq26	Xeris caudatus	CBHR229	JQ619809	
Seq27	Xeris indecisus	CBHR216	JQ619810	
Seq28	Xeris melancholicus	CBHR300	JQ619811	
Seq29	Xeris morrisoni	CBHR190	JQ619812	
Seq30	Xiphydria mellipes	CBHR1055	JQ619813	
Seq31	Xoanon matsumurae	SIRCA188	JQ619814	SIR 193