24 January 2002
PROC. ENTOMOL. SOC. WASH.
104(1), 2002, pp. 174–194

A REVIEW OF THE SIRICID WOODWASPS AND THEIR IBALIID PARASITOIDS (HYMENOPTERA: SIRICIDAE, IBALIIDAE) IN THE EASTERN UNITED STATES, WITH EMPHASIS ON THE MID-ATLANTIC REGION

DAVID R. SMITH AND NATHAN M. SCHIFF

(DRS) Systematic Entomology Laboratory, PSI, Agricultural Research Service, U.S. Department of Agriculture, % National Museum of Natural History, Smithsonian Instituion, Washington, D.C. 20560-0168, U.S.A. (e-mail: dsmith@sel.barc.usda.gov); (NMS) U.S. Forest Service, U.S. Department of Agriculture, Southern Research Station, Center for Bottomland Hardwood Research, P.O. Box 227, Stoneville, MS 38776, U.S.A. (e-mail: nschiff@fs.fed.us)

Abstract.—Keys are presented for the five genera and 15 species of adult Siricidae and one genus and two species of their parasitoids of the family Ibaliidae that occur in or may be adventive in eastern United States. Siricid larvae are wood borers in conifers and broadleafed trees. Notes on their biology, fungal symbionts, distributions and host associations are given. Data from collections in the mid-Atlantic states include seasonal occurrence of both Siricidae and Ibaliidae.

Key Words: *Sirex, Urocerus, Tremex, Xerix, Eriotremex, Ibalia,* fungal symbionts

Worldwide, there are 85–100 species of Siricidae in two subfamilies and 11 genera (Smith 1978, 1993). The subfamily Tremicinae is associated with angiosperms and Siricinae with gymnosperms. The family is widespread in the deciduous and coniferous forests of the northern hemisphere, extending south to Cuba, northern Central America, New Guinea, Philippines, Viet Nam, northern India, and northern Africa; one genus with two species is Afrotropical. No Siricidae are native to Australia and South America.

All species for which larvae are known bore into weakened or dying trees (Middlekauff 1960, Smith 1979). Most species in their native range are considered to be of minor importance except for decreasing the value of lumber; however, introduced, exotic species can be very damaging. Because larvae of siricids feed and develop in wood, with several years required for their life cycle, they are commonly transported in lumber by commerce. Thus, non-native species may emerge in buildings constructed of lumber that originated in other parts of the country or from other nations. For example, *Sirex noctilio* (F.) is a European species that became a major pest of *Pinus radiata,* an American species, when *P. radiata* was planted in New Zealand and Australia (Gilbert and Miller 1952, Rawlings 1955, Gaut 1970). A major control effort in the 1960's and 1970's used parasitic nematodes to control *S. noctilio* (Bedding and Akhurst 1974). *Sirex noctilio* is now considered to be the most important threat to new *P. radiata* plantations in South Africa, Brazil, and Argentina (Stival et al. 1993; Iede et al. 1998; Tribe 1995, 1997). In the early 1970's, an Asian species, *Eriotremex formosanus* (Matsumura), was accidentally introduced

into the southeastern United States where it has spread rapidly (Smith 1975, 1996). It attacks hardwoods, including oaks, but it is not considered to be a major pest at this time. More recently, a Palearctic species, *Urocerus sah* (Mocsáry), was reported in New Hampshire (Smith 1987).

The Ibaliidae (Cynipoidea) are part of the parasitoid complex of Siricidae. We include them here because we recorded their presence in collections from the mid-Atlantic states and are able to present their seasonality in relation to that of their hosts.

Keys for the identification of the eastern United States species of Siricidae have been non-existent since Bradley's (1913) revision, although Smith (1987) published a key to North American *Urocerus,* and Stange (1996) gave a key to the six species of Siricidae in Florida. Johnson (1928) gave some notes on New England species and illustrated them, but he did not give a key to species. For the Ibaliidae, Liu and Nordlander (1992, 1994) published a revision of world and North American Ibaliidae. Here, we give keys for identification of the eastern U.S. Siricidae and Ibaliidae, summarize their distribution and hosts, and present seasonal activity of some species with emphasis on collections from the mid-Atlantic states.

General biology

Like other wood-boring insects, siricids do not make the enzymes that digest cellulose, the major energy source for wood feeders (Kukor and Martin 1983). To utilize cellulose, wood-boring insects live in symbiotic relationships with other organisms that produce cellulases (Buchner 1965, Francke-Grosmann 1939). Siricids use basidiomycetous wood-decay fungi to break down cellulose (Buchner 1928; Cartwright 1929, 1938). The relationship between siricids and these fungi is true symbiosis, as organisms derive benefit. The siricids gain the ability to utilize a large energy source, cellulose, and the fungus benefits because it is not only carried to a specific host tree, but it is also injected underneath the bark, past the tree's first line of defense. Female siricids, except in the genus *Xeris,* carry oidia (hyphal fragments) of the fungus in specialized, abdominal glands called mycangia that have ducts leading to the reproductive tract (Buchner 1928). When the wasp lays her eggs, oidia are also deposited. The fungus grows rapidly and secretes digestive enzymes onto the substrate. When the larvae hatch, they commence feeding on the fungus and digested wood. There is some disagreement about whether or not the insects actually consume the wood or feed on the fungi alone (Gilbertson 1984). In either case, however, wood is the ultimate source of energy for the larvae. Exactly how adult females acquire the fungus after the larvae pupate is also uncertain (Gilbertson 1984), but female larvae have specialized hypopleural organs (Parkin 1941, 1942; Stillwell 1965) that may play a role in scraping fungus from the tunnel walls which is then somehow incorporated into the mycangia.

Larvae take from one to three or more years to reach pupation and emerge as adults (Middlekauff 1960, Stillwell 1967, Smith 1993). Males are commonly reared but seldom seen in the field. They are occasionally seen in small groups at the tops of trees (Middlekauff 1960; Schiff, personal observation). In the western United States, many species are attracted to forest fires, where females lay eggs into charred trees. Forest fires are much less common in the eastern United States, and there are no data on eastern siricid species being attracted to fires in this region. Species of the genus *Xeris* do not appear to carry a wood decay fungus in mycangial glands; instead, they limit oviposition to substrates that have already been inoculated with a wood decay fungus by another species of siricid (Francke-Grosmann 1939, Fukuda and Hijii 1997).

Fungi

The identity of the fungal symbionts used by siricids has been complicated by both

the difficulty in inducing the fungi to produce fruiting bodies in vitro and in some cases by misidentifications of the siricids involved (Gilbertson 1984, Gaut 1970). The fungal symbionts of only two tremicine species have been identified: *Tremex columba* (L.) from North America and *Tremex longicollis* Konow from Japan, both of which harbor *Cerrena* (*Daedalea*) *unicolor* Bull. ex Fries (Stillwell 1964, Tabata and Abe 1995). The siricines use fungi in the genus *Amylostereum,* and there are three species worldwide: *A. chailettii* (Pers.: Fr.) and *A. laevigatum* (Fr.) that occur in the United States, and *A. areolatum* (Fr.) that is not known from the United States (Farr et al. 1995). All United States siricines whose symbionts have been determined (*Sirex cyaneus, S. nigricornis, S. edwardsii, S. longicauda, S. juvencus californicus, Urocerus albiconris, U. gigas flavicornis,* and *U. californicus*) use *A. chailettii* (see Gilbertson 1984 review). American isolates of fungus from *Sirex juvencus* have not been determined, but European examples use *A. areolatum* (Gaut 1970). If each siricid is faithful to a specific symbiont (Gaut 1970), then *Sirex juvencus* in America must use *A. areolatum,* and the fungus has simply not been found in the field as yet, or, the American *Sirex juvencus* is not the same as the European species. *Amylostereum areolatum* should also have been introduced with *Sirex noctilio,* its wasp symbiont, in places where that species was accidentally introduced.

Malaise Trapping and Virginia Species

This study is supplemented by material collected in Virginia and adjacent states over the past 18 years and specimens in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and Virginia Polytechnic Institute and State University, Blacksburg, Virginia (VPI).

Collections were made using Malaise traps which were set up and in continual use in different localities from approximately March through the first of November. Siricidae and Ibaliidae are not commonly collected this way, but enough have accumulated over the years of collecting to help verify what occurs in this region and indicate the seasonal activity of some species. Totals collected are 163 specimens of 5 species of Siricidae and 149 specimens of 2 species of Ibaliidae. The Siricidae are represented mainly by 133 specimens of *Tremex columba* (L.), associated with broad-leaved trees, and 126 specimens of its parasitoid, *Ibalia anceps* Say. The other Siricidae, 30 specimens of the genera *Urocerus* and *Sirex,* are associated with conifers, and 23 specimens of their parasitoid *Ibalia leucospoides* (Hockworth). All Siricidae collected in Malaise traps were females.

Seven species of Siricidae and two species of Ibaliidae occur in Virginia. We have been able to verify several exotic species, e.g., *Sirex longicauda* Middlekauff, but there are undoubtedly others. Another non-native species is *Eriotremex formosanus* (Matsumura), an introduced species in southeastern U.S. which has been found in extreme southeastern Virginia.

Materials and Methods

The keys are valid for eastern United States, east of the Rockies, and eastern Canada. Species not native to this region but are possible adventives in imported lumber are included. There are no confirmed collections of *Sirex noctilio* from eastern U.S., but it is included it in the key because the species has a history of introductions in other parts of the world and specimens are occasionally intercepted at ports-of-entry in the U.S.

Recorded distributions and host plants are from the literature and examined specimens. The following are given for each species: distribution (state/province from which recorded); Virginia records; collection records (from Malaise trapping in Maryland, Virginia, and West Virginia); hosts (as recorded); and remarks.

Records in the collections sections are cited only by county. Specific data are as

Fig. 1. *Sirex nigricornis* (arrow points to cornus).

follows: MARYLAND: Allegheny Co., Green Ridge State Park.; Prince George's Co., Beltsville Agricultural Research Center. VIRGINIA: Clarke Co., University of Virginia Experimental Farm and State Arboretum of Virginia, 2 mi S Boyce; Essex Co., 1 mi SE Dunnsville; Fairfax Co., near Annandale; Louisa Co., 4 mi S Cuckoo; Loudoun Co., nr. jct. of Sycolin Road and Goose Creek. WEST VIRGINIA: Hardy Co., 3 mi NE Mathias, 38°55′N, 78°49′W; Tucker Co., Fernow Experimental Forest, south of Parsons.

Literature references to original descriptions and synonymies are found in Smith (1978, 1979). Only significant or subsequent literature is presented here.

The use of pits on the lancet for species separation were first used by Viitasaari (1984) and Viitasaari and Midtgaard (1989). The size, form, and location of the lateral ridges and pits may be significant for species identification. They are used here mainly to separate *Sirex noctilio* from the native North American species of *Sirex*.

Males are more difficult to separate than females. Use caution in the keys to males since color variation may be more extensive than we have observed.

Results

Siricidae

Key to Genera of North American Siricidae

1. Hindtibia with two apical spurs; antenna with 18 or more segments, usually more than 22 2
– Hindtibia with one apical spur; antenna with more than 22 segments in *Xeris*, less than 22 segments in *Tremex* and *Eriotremex* 3
2. Head usually with large white spot behind each eye; female cornus long and slender, constricted at base (Fig. 2); male hindtarsus slender, first segment 4 or more times longer than broad, commonly 5–6 time longer, second and third segments 2 times or more longer than broad (Fig. 6) . . . . . *Urocerus*
– Head black; female cornus short, triangular, not constricted at base (Figs. 1, 3, 4); male hindtarsus stout, laterally flattened, first segment 4 times or less longer than broad, second and third segments triangular, slightly longer or about as long as broad (Fig. 5) . . . . . *Sirex*

3. Antenna with 15–21 segments; head without genal carina behind eyes; female ovipositor shorter than forewing; hindwing with anal cell 4
– Antenna with 23 or more segments; head with a genal carina behind each eye (Figs. 7, 8); female ovipositor longer than forewing; hindwing without anal cell . . . . . *Xeris*
4. Antenna with 14–15 segments; body without long golden hairs . . . . . *Tremex*
– Antenna with 20–21 segments; body with long golden hairs . . . . . *Eriotremex*

Comments.—Use of the white spot behind each eye to separate *Urocerus* and *Sirex* is commonly used in keys but is not infallible. Although most specimens can be separated by this, a series of *Urocerus cressoni* from Virginia varies from an entirely black head to some with a distinct white spot. Examination of the shape of the female cornus and the male hind tarsus should be checked for determination. The more slender, more rounded hindtarsus (Fig. 6) of *Urocerus* vs. the stout, laterally flattened hindtarsus (Fig. 5) of *Sirex* males is a good character for the eastern species.

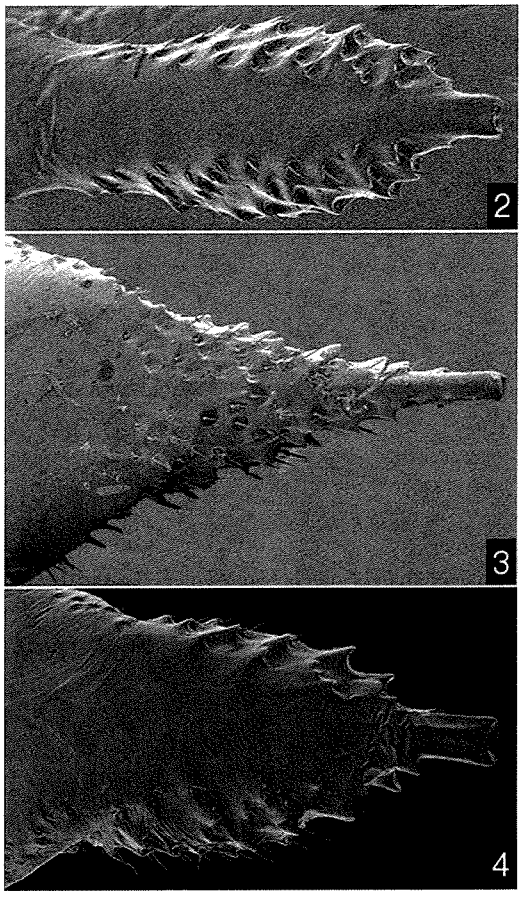
Subfamily Siricinae

Genus *Sirex* Linnaeus

The most recent key is to the species of California by Cameron (1967). Two species, *S. edwardsii* and *S. nigricornis,* are widespread in eastern U.S. *Sirex cyaneus* is northern but extends south in the Appalachians to North Carolina, *S. juvencus* is northern and transcontinental, *S. behrensii* has only been recorded from Virginia and emerging from imported wood in Florida, and two species, *S. areolatus* and *S. longicauda,* are adventive in the eastern states emerging from wood.

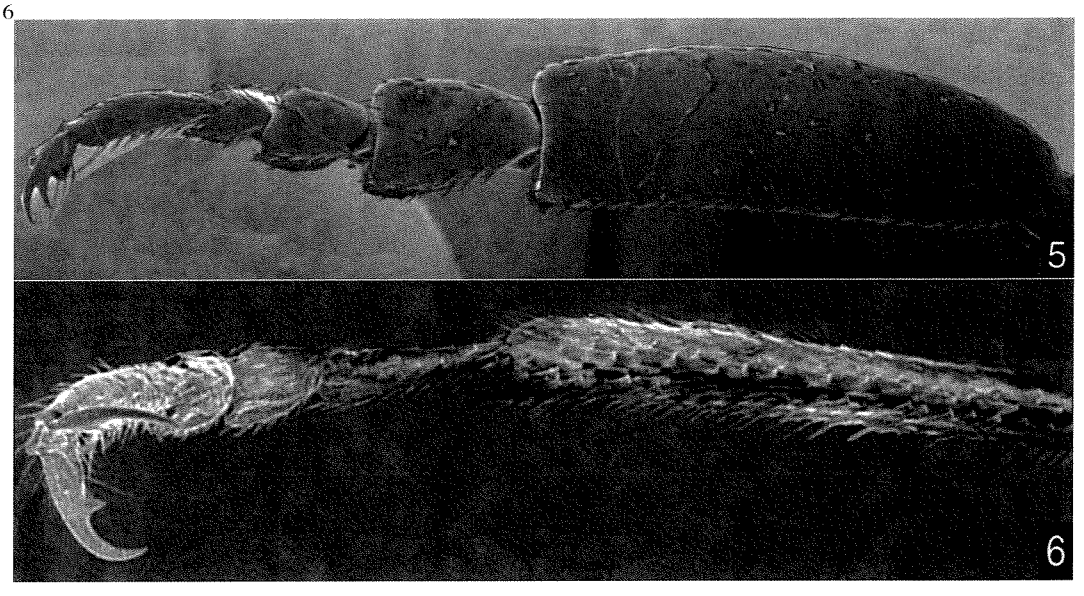
Key to Species

1. Female 2
– Male 9
2. Ovipositor longer than forewing 3
– Ovipositor shorter than forewing 4
3. Tibiae and tarsi red . . . *longicauda* Middlekauff
– Legs entirely black or blue black . . . . . *areolatus* (Cresson)
4. Abdomen mostly red, but may be infuscated to black at base, laterally or ventrally 5



Figs. 2–4. Female cornus. 2, *Urocerus cressoni.* 3, *Sirex cyaneus.* 4, *Sirex longicauda.*

– Abdomen entirely black or blue black 6
5. Legs black, only tarsi reddish brown; wings darkly, uniformly infuscated (Fig. 1) . . . . . *nigricornis* (Fabricius)
– Legs with tibia and tarsi reddish brown; wings hyaline, forewing with fuscous band below stigma and fuscous apical margin . . . . . *behrensii* (Cresson)
6. Legs black . . . . . *edwardsii* Brullé
– Legs largely orange 7
7. Apical tarsal segment black; sawsheath (valvula 3) shorter than oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to base of radial cell; mesopleuron densely punctured, in the middle with interspaces mostly smaller than punctures (Fig. 9); pits of lancet large and close together (Fig. 11); antenna black . . . . . *noctilio* (Fabricius)
– Tarsi yellow to orange; sawsheath (valvula 3) as long as or longer than oblong plate (valvula 2); length of ovipositor as long as distance



Figs. 5–6. Hindtarsus. 5, *Sirex edwardsii*. 6, *Urocerus cressoni*.

from base of wing to beyond base of radial cell; punctures at middle of mesopleuron farther apart, with shining flat interspaces mostly broader than punctures (Fig. 10); pits of lancet small and far apart (Fig. 12); antenna black or brown at base 8

8. Sawsheath (valvula 3) longer than oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to apex of radial cell; antenna black . . . *cyaneus* (Fabricius)

– Sawsheath (valvula 3) equal to oblong plate (valvula 2); length of ovipositor as long as distance from base of wing to middle of radial cell; basal segments of antenna often reddish brown . . . . . *juvencus* (Linnaeus)

9. Abdomen red, with only basal 1 or 2 segments black 10

– Abdomen black at both base and apex, black at apex may be only on dorsum or venter of apical segment 12

10. Femora, tibiae and tarsi red; antenna pale at base; wings hyaline . . . . . *behrensii* (Cresson)

– Hindleg black or black with femur red; midleg black; antenna black; wings yellowish 11

11. Hindleg black, apical 2 tarsal segments yellowish . . . . . *nigricornis* (Fabricius)

– Hindleg with femur red, tibia and tarsus black . . . . . *cyaneus* (Fabricius)

12. Legs entirely black (abdominal segments 2–7 orange; wings hyaline, stigma of forewing black) . . . . . *areolatus* (Cresson)

– Legs partly reddish brown to orange 13

13. Femora and rest of hindleg black 14

– Femora orange; apical 2–3 hindtarsal segments orange 15

14. Abdominal segments 5 and 6 and sometimes part of 7 orange; wings yellow, stigma of forewing yellow . . . . . *edwardsii* Brullé

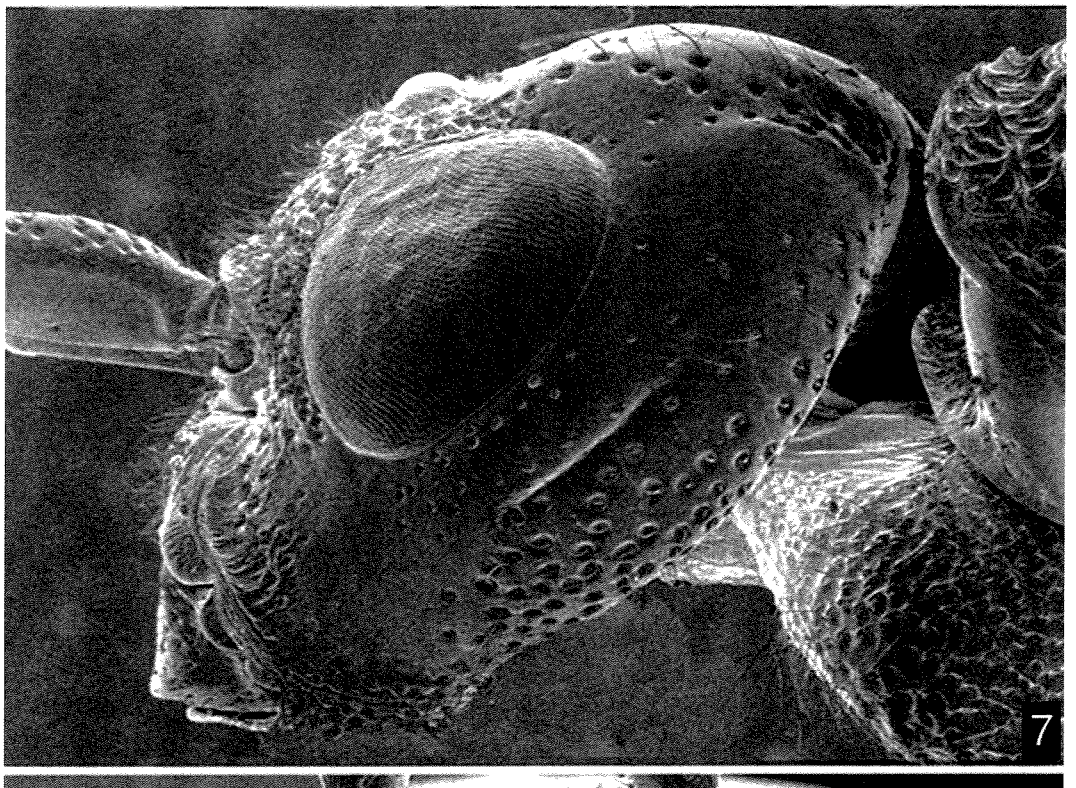
– Abdominal segments 3–7 and sometimes 8 orange; wings clear, hyaline, stigma of forewing black . . . . . *longicauda* Middlekauff

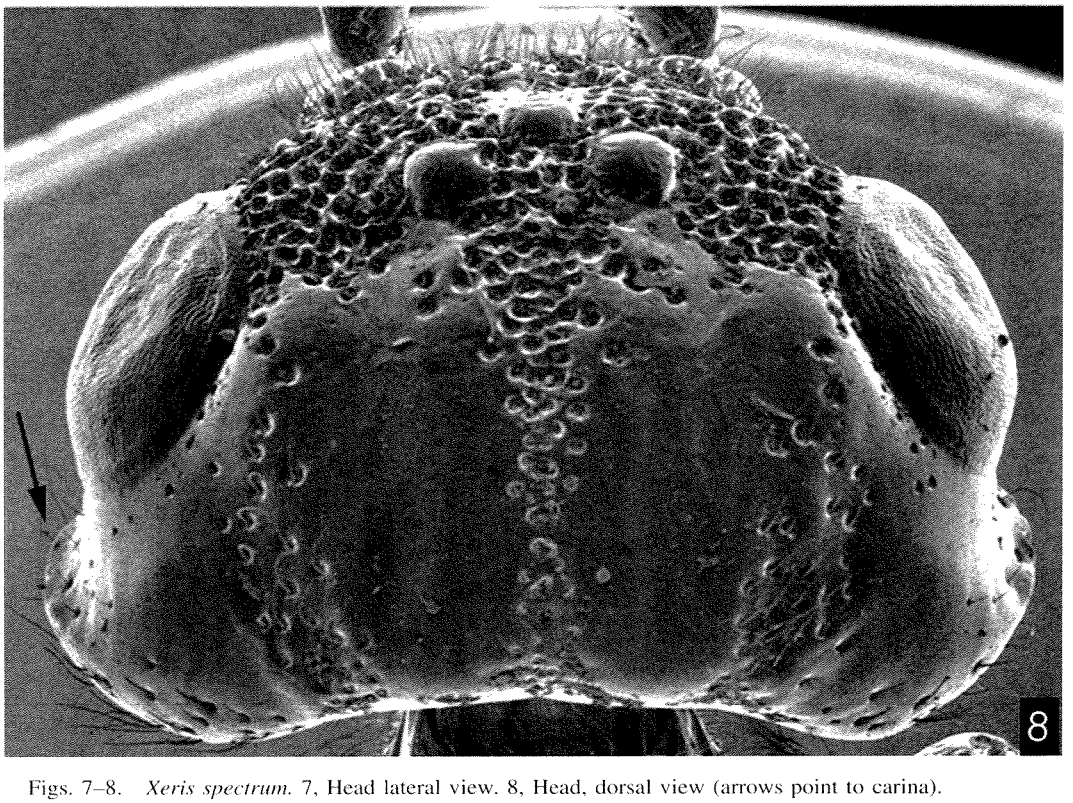
15. Basal antennal segments orange; apical tarsal segments yellow to orange; punctures of mesopleuron separated by flat, shining interspaces, usually broader than punctures (Fig. 10) . . . . . *juvencus* (Linnaeus)

– Antenna black; apical two tarsal segments blackish; punctures of mesopleuron close together, interspaces usually shorter than punctures (Fig. 9) . . . . . *noctilio* (Fabricius)

Sirex areolatus (Cresson)

Distribution.—Alabama, Arizona, Arkansas, British Columbia, California, Colorado, Florida, New Mexico, Oregon, Virginia, Washington (Middlekauff 1960, Smith 1979). The Florida specimens emerged from fir wood imported from western United States (Stange 1996). In Alabama, specimens were "found boring into sheet rock inside home," and in Arkansas, "ex sheet rock." It was found in Kauai, Hawaii "ex cedar wall."





Figs. 7–8. *Xeris spectrum*. 7, Head lateral view. 8, Head, dorsal view (arrows point to carina).

Virginia records.—Cape Henry, IX-13023, J.N. Knull, bald cypress (1 female, 2 males); Cape Henry, 9-9-24, W.S. Fisher (1 male).

Hosts.—*Cupressus macrocarpa, Juniperus occidentalis, J. scopulorum, Liobocedrus decurrens, Pinus contorta, P. jeffreyi, P. lambertiana, P. radiata, Psuedotsuga menziesii, Sequoia sempervirens, Taxodium distichum, Thuja* sp. Commonly attacks redwood, cypress, and cedars; found less frequently on pines (Middlekauff 1960, Smith 1979).

Remarks.—The only eastern records known for this species are from Virginia and Florida. The Virginia collections appear authentic and are probably not from imported wood. Inasmuch as *S. areolatus* commonly attacks redwood, cypress, and cedars and is found less frequently on pines (Middlekauff 1960), this species could be established on baldcypress in the East. De Leon (1952) recorded it from *Sequoia sempervirens* in California, and Westcott (1971) from *Juniperus occidentalis* in Oregon.

Sirex behrensii (Cresson)

Distribution.—California, Idaho, Nevada, Oregon, Washington.

Hosts.—*Cupressus macrocarpa, Pinus jeffreyi, P. lambertiana, P. ponderosa, P. radiata,* Japanese pine (Middlekauff 1960, Smith 1979).

Remarks.—This species has been found in Ohio emerging from imported lumber: "Cleveland O., ex plaster wall."

Sirex cyaneus Fabricius
(Fig. 3)

Distribution.—Alabama, Alaska, Alberta, British Columbia, California, Colorado, Georgia, Idaho, Illinois, Kansas, Maine, Michigan, Minnesota, Montana, Nebraska, New Brunswick, New Hampshire, New Jersey, Newfoundland (Labrador), Nevada, New Mexico, New York, North Carolina, Nova Scotia, Oregon, Quebec, Utah, Washington, West Virginia, Wyoming (Middlekauff 1960, Smith 1979).

Hosts.—*Abies balsamea, A. concolor, A. fraseri, A. grandis, A. lasiocarpa, A. magnifica, Larix laricina; Picea engelmanni, P. glauca, P. sitchensis, Picea* sp., *Pinus contorta, P. ponderosa, Pseudotsuga menziesii, Tsuga heterophylla* (Middlekauff 1960, Kirk 1975, Smith 1979).

Remarks.—This species is known as the "blue horntail." No specimens have been collected in Virginia, but *S. cyaneus* probably occurs in higher elevations in the Appalachians between New York and North Carolina (Amman 1969) where its hosts, *Abies* and *Picea,* occur.

Johnson (1930) recorded hundreds of emergences from balsam fir, *Abies balsamea,* in Randolph, N.H., from July 29 to August 29. He discussed variation in size and color. Forty-one specimens emerged from a section of the tree 11″ long and 4¾″ in diameter. Also, several specimens of *Ibalia* emerged. Amman (1969) reared *S. cyaneus* from Fraser fir in North Carolina. Blackman and Stage (1918), reporting it as *S. abbotii,* reared it from *Larix laricina* in New York.

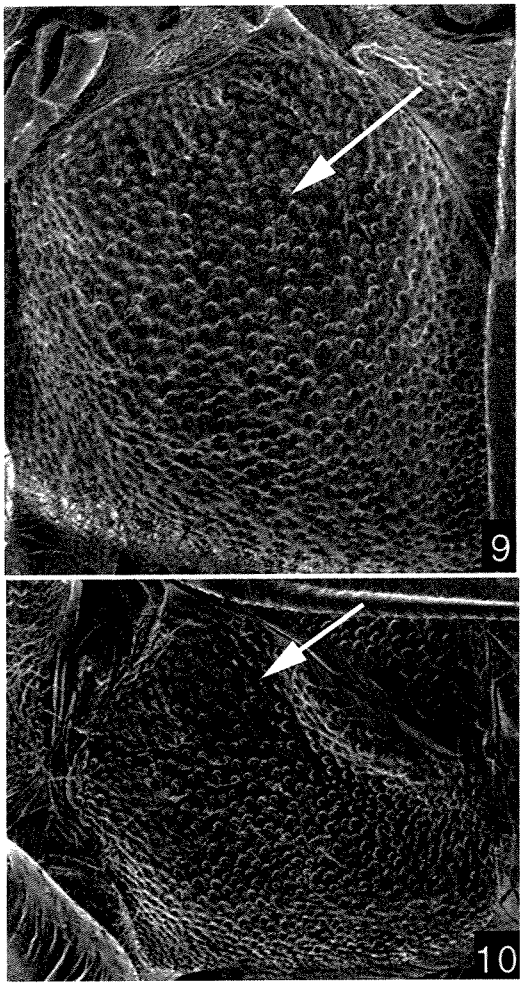
The life history was reported on by Chrystal (1928, 1930) and Chrystal and Meyers (1928). It has often been confused with, or sometimes considered a subspecies of, *S. juvencus.*

Sirex edwardsii Brullé
(Figs. 5, 16)

Distribution.—Alabama, Arkansas, District of Columbia, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, North Carolina, Oklahoma, Quebec, Saskatchewan, South Carolina, Texas, West Virginia, Wisconsin, Virginia. The Louisiana record is from Chapin and Oliver (1986).

Virginia records.—Lynhaven Inl., City of Virginia Beach, X-27-43; Virginia Beach, *Pinus,* Hopk. 69202; W. Minor Hills, Falls Church, pine, Hopk. 11339a1; Montgomery Co., Oct. 2, 1964; Blacksburg, X-11-47.

Collection records.—VIRGINIA: Essex Co., X-24–XI-17-95 (1).



Figs. 9–10. Mesopleuron. 9, *Sirex noctilio.* 10, *Sirex juvencus.* Arrows point to area where density of punctures differ.

Hosts.—*Picea abies; Pinus echinata, P. elliottii, P. palustris, P. rigida, P. strobus, P. virginiana* (Kirk 1974, Smith 1979).

Remarks.—This species was recorded as *Sirex abbotii* by Kirk (1974). In Essex Co., where one specimen was collected, only two species of pines were present (*Pinus virginiana* and *P. taeda*).

Sirex juvencus (Linnaeus)
(Figs. 10, 12)

Distribution.—Eurasia; British Columbia, New Brunswick, Newfoundland (insular and Labrador), New Jersey, Nova Scotia, Yukon Territory.

Hosts.—*Abies balsamea, A. lasiocarpa, Larix* sp., *Picea* sp., *Pinus contorta.*

Remarks.—Benson (1962) first recognized that *S. juvencus* occurs in North America, recording it from "Labrador and Newfoundland (? introduced)." Subsequently, specimens have been identified as *S. juvencus* from across North America, and it is believed to be widespread. Its distinction from *S. cyaneus* and *S. californicus* (Ashmead) is not clear, but we have separated *S. juvencus* and *S. cyaneus* in the key using traditional characters pending a thorough study of this complex.

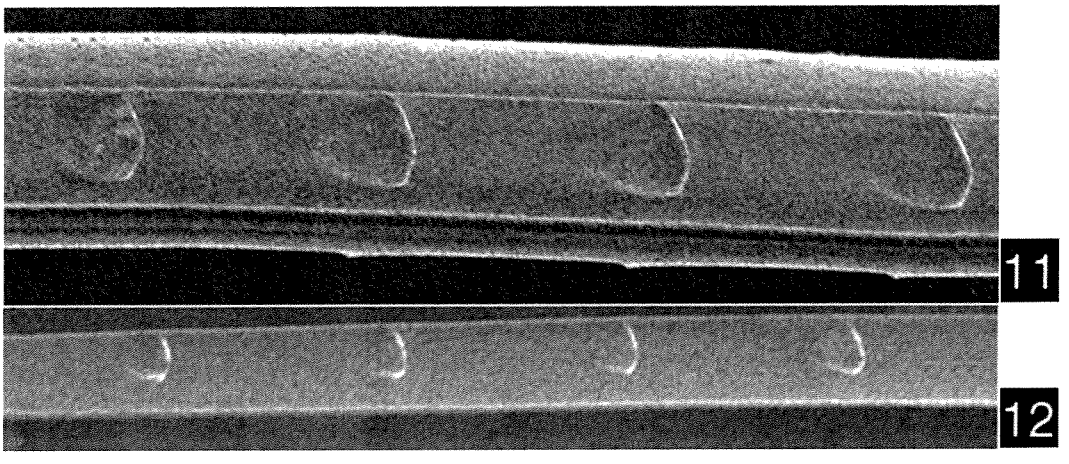
Both *S. juvencus* and *S. cyaneus* can be separated from *S. noctilio,* the three species most likely to be confused, by the much smaller pits on the lancet (Fig. 12; *S. noctilio,* Fig. 11). *Sirex juvencus* and *S. cyaneus* also differ by the size of the pits, with those of *S. cyaneus* being much smaller (breadth of pit less than a third of diameter of ovipositor), but this distinction is not as evident (see Viitasaari and Midtgard 1989).

Sirex longicauda Middlekauff
(Fig. 4)

Distribution.—California, Colorado, Idaho, Kansas, Montana, Nebraska ("emerg. wood in new home;" probably west coast wood), Nevada, New Mexico, Ohio (?), Oregon, Utah, Virginia, West Virginia (Monongalia Co., ex 2 × 4's in new house, lumber cut in Pacific Northwest). Adventive in eastern states emerging from lumber. The records from Kansas, Ohio, and Virginia are probably from imported lumber.

Virginia records.—Campbell Co., Lynchburg, 6-31-64 (1). This specimen is at VPI&SU. Probably emerged from building materials imported from western United States, though this is not given on the labels.

Hosts.—*Abies concolor, A. magnifica; Pinus ponderosa, Pseudotsuga menziesii* (Kirk 1975, Smith 1979).



Figs. 11–12. Pits on lancet. 11, *Sirex noctilio.* 12, *Sirex juvencus.*

Remarks.—So far as is known, this species is not established outside its native range in western North America.

Sirex nigricornis Fabricius
(Figs. 1, 16)

Distribution.—Alabama, Arkansas, District of Columbia, Florida, Georgia, Florida, Louisiana, Maryland, Massachusetts, Mississippi, North Carolina, Ohio, Pennsylvania, Quebec, Saskatchewan, South Carolina, Texas, Virginia, West Virginia, Wisconsin (Kirk 1974, Smith 1979).

Virginia records.—Falls Church, Oct. 14, 1970, Oct. 28, 1916; Virginia Beach, Nov. 11, 1907; Norfolk, 1909; Lurray, Page Co., X-5-13; Lynhaven Inl., City of Virginia Beach, X-27-43; Montgomery Co., X-6-61.

Collection records.—VIRGINIA: Essex Co., IX-29–X-27-92 (1).

Hosts.—*Picea* sp., *Pinus clausa, P. echinata, P. palustris, P. rigida, P. strobus, P. taeda, P. virginiana* (Kirk 1974, Smith 1979).

Remarks.—Webster (1895) received specimens, called the "black horned horntail," reported as being numerous on peach and apple trees in Tennessee. He was probably referring to *S. nigricornis.*

Sirex noctilio (Fabricius)
(Figs. 9, 11)

Distribution.—Eurasia; introduced and established in Australia, New Zealand, Brazil, Uruguay, Argentina, and South Africa.

Hosts.—*Abies* spp., *Larix* spp., *Picea* spp., *Pinus radiata, Pinus* spp., *Pseudotsuga menziesii.*

Remarks.—There is a questionable record for this species in North America by Benson (1962) from "Manitoba (? introduced)." No other information is available and we have not seen confirmed records except the Wyoming record by Smith (1979) from a specimen in the USNM which is labeled "Old Faithful, Yellowstone, Wyo., VIII/26.25, Satterthwait collector." We will not consider this species established in North America until there are more confirmed records. It has been intercepted occasionally in wood and dunnage at ports-of-entry in the United States. This species is a major pest of pine plantations where it has been accidentally introduced (see references in Introduction). We have included it in the preceding key so it can be distinguished from native North American species, and it will be helpful to identifiers at ports-of-entry.

Genus *Urocerus* Geoffroy

Smith (1987) gave a key to North American species. Two species, *Urocerus cressoni* and *U. taxodii,* are widespread in the East, though the latter is seldom collected; one species, *U. albicornis,* is northern and extends south in the Appalachians to North Carolina; one species, *U. gigas flavicornis,* is transcontinental in northern U.S. and Canada; and *U. sah,* an introduced species, has been recorded only from New Hampshire.

Key to Species

1. Female 2
– Male 6
2. Wings black; antennal flagellum partly white with some basal and/or apical segments black 3
– Wings yellow, only apical margins may be slightly blackish; antenna yellow, scape and pedicel may be black 5
3. Abdomen mostly red, sometimes basal and/or apical segments blackish . . . . . *cressoni* Norton
– Abdomen black, only cornus may be orange . . 4
4. Cornus orange, contrasting with black abdomen; fore- and midlegs usually all black . . . . . *taxodii* (Ashmead)
– Cornus black; basal half of tibiae and basal half of tarsi of each leg whitish yellow . . . . . *albicornis* (Fabricius)
5. Yellow on head continuous across top, at most separated by a narrow black line at center of postocellar area; pronotum and upper half of mesepisternum yellowish orange (legs mostly yellow with hindfemur and apical two-thirds of hindtibia black) . . . . . *sah* (Mocsáry)
– Yellow on head separated into a spot on each side by a black band usually as broad as distance between eyes; thorax black . . . . . *gigas flavicornis* (Fabricius)
6. Head mostly yellow to yellow orange; wings yellowish (legs usually with hindfemur and apical two-thirds of hindtibia black; apical abdominal segment may be black) . . *sah* (Mocsáry)
– Head largely black, with a broad black band separating yellow spots on each side of head; wings blackish or hyaline 7
7. Abdomen reddish, may be black at base, but basically unicolorous; wings black 8
– Abdominal segments 1 and 2 or 1 to 3, and 7 to apex black, segments 2 or 3 to 7 red to orange; wings hyaline 9
8. Legs black . . . . . *cressoni* (Norton)
– Fore- and midtibiae and tarsi dark orange; basal third of hindtibia and basal half of hindbasitarsus white . . . . . *taxodii* (Ashmead)
9. Hindbasitarsus 4.0–5.5 × longer than broad . . . . . *gigas flavicornis* (Fabricius)
– Hindbasitarsus 6.5–8.0 × longer than broad . . . . . *albicornis* (Fabricius)

Urocerus albicornis (Fabricius)

Distribution.—British Columbia, California, Georgia, Idaho, Louisiana, Michigan, Minnesota, Missouri, Montana, New Brunswick, Newfoundland, New Mexico, New York, North Carolina, Nova Scotia, Ontario, Oregon, Pennsylvania, Rhode Island, Virginia, Washington, West Virginia.

Virginia records.—Montgomery Co., VIII-8-74; Arlington, VI-10-1952; Washington Co., Bristol, 7-24-72.

Hosts.—*Abies amabilis, A. balsamea, A. fraseri, A. lasiocarpa; Larix laricina, L. occidentalis; Picea engelmanni, P. mariana, P. sitchensis; Pinus* spp.; *Pseudotsuga menziesii; Thuja plicata; Tsuga heterophylla* (Smith 1978).

Remarks.—Some of the Virginia records may represent emergence from imported lumber or firewood in buildings; the species is probably native to only the higher elevations. For the life cycle, see Belyea (1952). Amman (1969) reared this species from Fraser fir, *Abies fraseri,* in North Carolina. Blackman and Stage (1918) reared it from *Larix laricina* in New York and gave notes on its life history; it was found in dying or recently felled conifers.

Urocerus cressoni Norton
(Figs. 2, 6, 16)

Distribution.—Florida, Georgia, Iowa, Minnesota, Nebraska, New Brunswick, North Carolina, Nova Scotia, Ohio, Ontario, Quebec, Virginia, Wisconsin.

Virginia records.—Falls Church, IX-2-17; Montgomery Co., VIII-9-1974.

Collection records.—VIRGINIA: Essex Co., VII-27–VIII-9-91 (1), VIII-27–IX-16-91 (1); VII-3–16-96 (1); VII-17–VIII-2-96 (2); VII-18–VIII-1-97 (4); VIII-2–18-97 (2); IX-9–X-6-97 (2); VII-4–21-98 (3); VIII-22–IX-11-98 (3); IX-12–X-5-98 (1);

VII-17–VIII-2-99 (3); VIII-3–20-99 (3). Fairfax Co., IX-16–22-90 (1).

Hosts.—*Abies balsamea, A. fraseri; Picea* sp.; *Pinus rigida, P. taeda* (Kirk 1974, Smith 1979).

Remarks.—Most all collections in Essex Co., VA, were from traps in or adjacent to mixed coniferous hardwood forests. The predominant conifers were *Pinus taeda* and *P. virginiana.* All collections were from July to early October (Fig. 16). Sixteen of the 26 specimens from this collection had no white behind the eyes or a very small and faint white spot slightly lighter than the black on the rest of the head; thus, they could be confused with *Sirex* if the female cornus and male hind tarsus are not checked carefully.

Bradley (1913) recognized several varieties based on the amount of red on the abdomen and wing darkness: (1) abdomen entirely red and wings dark fuliginous; (2) basal six dorsal segments of abdomen dark brown; and (3) abdomen red with a black band on the third, fourth, and fifth dorsal segments. All specimens collected would belong to variety (2), except three had the basal 5 segments black, one had the basal 7 segments black, and one had only the basal 3–4 segments black. In a number of specimens, there is a central red mark on the second segment.

Amman (1969) reared this species from Fraser fir, *Abies fraseri,* in North Carolina.

Urocerus gigas flavicornis (Fabricius)

Distribution.—Alaska, Alberta, Arizona, California, Colorado, Idaho, Montana, New Mexico, Northwest Territories, Ontario, Oregon, Washington, Wyoming, Yukon Territory.

Hosts.—*Abies concolor, A. lasiocarpa, Larix occidentalis, Picea engelmanni, P. sitchensis, Pinus contorta, Pseudotsuga menziesii* (Middlekauff 1960, Kirk 1975).

Remarks.—The North American form is considered a subspecies of the Eurasian *Urocerus gigas* (Linnaeus). It is transcontinental in Canada, but we have not seen specimens from eastern United States.

Urocerus sah (Mocsáry)

Distribution.—North Africa, Asia Minor and the Near East, southern Russia; New Hampshire.

Hosts.—Probably *Abies* spp., *Picea* spp., *Pinus* spp.

Remarks.—This species was first recorded in North America by Smith (1987) from several specimens taken in New Hampshire. No other specimens have been discovered. It is close to the European *Urocerus augur* (Klug) and sometimes has been treated as a subspecies of it.

Urocerus taxodii (Ashmead)
(Fig. 16)

Distribution.—District of Columbia, Florida, Mississippi, Missouri, Virginia.

Virginia records.—City of Virginia Beach, Cape Henry, VI-8-24.

Collection records.—VIRGINIA: Essex Co., V-14–24-91 (1).

Host.—*Taxodium distichum* (Smith 1979).

Remarks.—It was unusual to find a specimen in Essex Co., VA. No *Taxodium* were anywhere near the trap in which it was collected.

Genus *Xeris* Costa

Xeris spectrum (Linnaeus)

(Figs. 7, 8)

Distribution.—Holarctic; Alaska, Arizona, British Columbia, California, Colorado, Connecticut, Maine, Michigan, Montana, Nevada, New Brunswick, New Hampshire, Nova Scotia, Oregon, Utah, Washington.

Hosts.—*Abies concolor, A. lasiocarpa, Larix occidentalis, Picea engelmanni, P. pungens, Pinus contorta, P. ponderosa, Pseudotsuga menziesii. Pinus contorta* is the favorite host in California (Middlekauff 1960, Kirk 1975).

Remarks.—This species is transcontinental in Canada and northern United States.

The most southern records in the East are Connecticut and Michigan. Adults of this species mate at the highest points on mountain tops. Many specimens were hand collected at the top of Mount Rigaud, Quebec (H. Goulet, personal communication).

Subfamily Tremicinae

Genus *Tremex* Jurine

Tremex columba (Linnaeus)

(Fig. 15)

Distribution.—Alabama, Arizona, Arkansas, California (one record from Riverside Co.), Colorado, Connecticut, Georgia, Florida, Illinois, Indiana, Iowa, Kansas, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Montana, Nebraska, New Brunswick, New Jersey, New Mexico, New York, Nova Scotia, Ohio, Ontario, Pennsylvania, Quebec, Tennessee, Texas, Utah, Virginia, West Virginia, Wisconsin, Wyoming (Middlekauff 1960, Smith 1979).

Virginia records.—Widespread throughout the state. We have seen specimens from the following: Appomattox Co., Arlington Co., Bedford Co., City of Norfolk, Clarke Co., Essex Co., Fairfax Co., Frederick Co., Giles Co., Hanover Co., Louisa Co., Loudoun Co., Montgomery Co., Nottaway Co., Roanoke Co., Smythe Co., Warren Co., Washington Co.

Collection records.—MARYLAND: Prince George's Co. (4). VIRGINIA: Clarke Co. (12); Essex Co. (84); Fairfax Co. (7); Loudoun Co. (11); Louisa Co. (19). WEST VIRGINIA: Tucker Co. (3). See Fig. 15 for dates of collection.

Hosts.—*Acer* spp., *Ulmus* spp., *Quercus* spp., *Carya* spp., *Fagus grandifolia, Fagus* spp. (Smith 1979); *Celtis laevigata, Carpinus* sp. Also reared or collected from the following: apple, box elder, hackberry, pear, and sycamore (Middlekauff 1960). Probably in other angiospermous trees. Usually in dead or dying trees.

Remarks.—This species is known as the "pigeon tremex." Adults oviposit in dead or weakened deciduous trees or those dying as a result of disease or other cause. Feeding of larvae in the wood aids in the disintegration of trees. Stillwell (1967) noted a minimum two year life cycle in New Brunswick where the primary host was weakened or injured *Fagus grandifolia,* and occasionally *Acer saccharum.* Adult emergence and oviposition was from August to October, and 2–7 eggs were laid in each oviposition hole. Eggs hatched in 2–4 weeks or hatched the next May or June. Larvae tunnel in wood infected with the fungus *Daedalea unicolor,* a fungus associated with each stage of the female development. Stillwell (1965) also studied the hypopleural organs in larvae and the associated fungus. Eggs in absence of the fungus hatch but larvae do not develop past the first instar. Oviposition tunnels are at a right angle to the bark surface and 2–15 mm deep in the sapwood; eggs are laid at intervals along the tunnel. Several hundered eggs are deposited at intervals in the gallery. Packed sawdust and frass are in the galleries. Galleries may be 1–2 m long. Pupation is in the sapwood or up to 30 cm deep in the heartwood and may be oriented in any direction. The females may tunnel up to 1 m before emergence.

Laurent (1931) found numerous larvae in dead or nearly dead maple during May in Pennsylvania. From a cross section of trunk, 20″ long and 10″ in diameter, 96 males and 10 females emerged June 16–26; 7 males and 22 females from June 27 to July 6; 5 females and 1 female from July 7–16; and about the same number through August. There were no specimens after August. In all, 162 *Tremex* emerged.

Fattig (1949) observed *Megarhyssa* (Ichneumonidae) parasitoids in Georgia. From a dead tree, 86 specimens of *Megarhyssa* emerged during July. From July 29 to August 22, he collected 28 specimens of *T. columba.* He reported his observations on oviposition of the parasitoid.

Harrington (1887) gave some biological notes for *T. columba* on maple in Ontario.

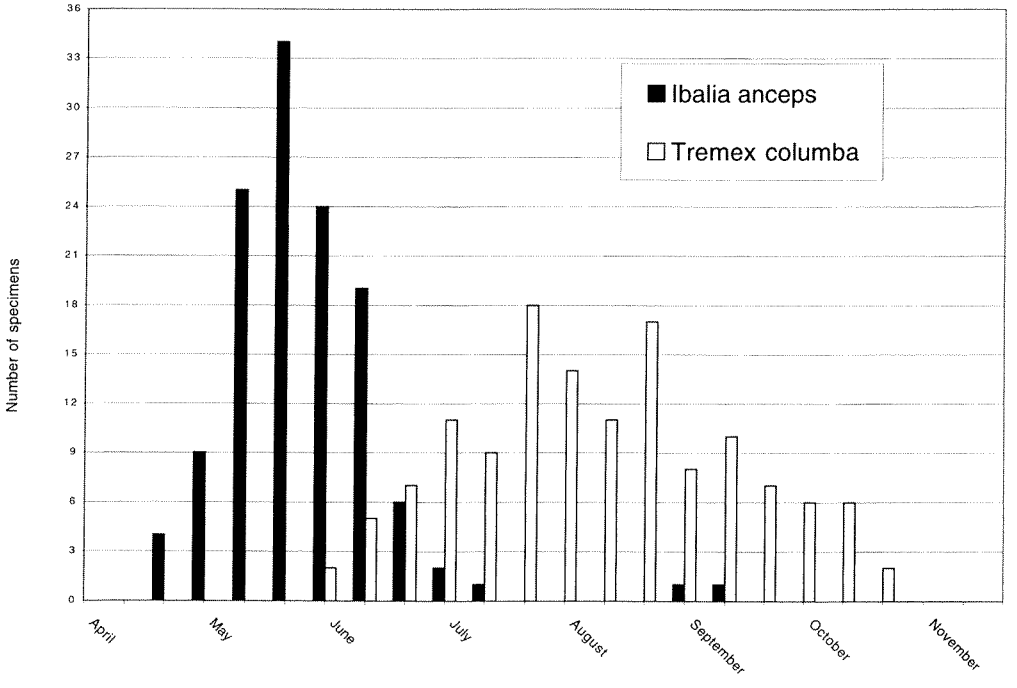


Fig. 15. Seasonal occurrence of *Ibalia anceps* and *Tremex columba* from collections in Maryland, Virginia, and West Virginia.

Collection records.—MARYLAND: Allegheny Co. (9); Prince George's Co. (28). VIRGINIA: Clarke Co. (9); Essex Co. (45); Fairfax Co. (4); Loudoun Co. (7). WEST VIRGINIA: Hardy Co. (7); Tucker Co. (17). All collections are from the end of April to the first of July with the peak flight time from mid-May to mid-June. The two records in September are from Allegheny Co. See Fig. 15 for flight times.

Host.—A parasitoid of *Tremex columba* in deciduous trees (Liu and Nordlander 1994).

Remarks.—Adult flight activity is limited to spring, whereas *Tremex columba* flies from July through October (Fig. 15). Since *T. columba* takes two or more years to complete its life cycle, the *Ibalia* possibly parasitizes the young larvae from eggs laid by the *Tremex* from the previous year.

Liu and Nordlander (1994) recognized variation in wing and body coloration of this species. The three predominate wing color forms are: (1) wings maculate with dark and almost clear areas; (2) same, but more or less dark; and (3) evenly dark. The first is the most common in the northeastern states, and all specimens collected appear to be of this form (Fig. 14).

Ibalia leucospoides (Hochworth)
(Fig. 16)

Distribution.—Europe; Alberta, Arizona, California, Colorado, Florida, Georgia, Idaho, Maine, Maryland, Michigan, Minnesota, Mississippi, New Brunswick, North Carolina, Oregon, Pennsylvania, South Carolina, Utah, Virginia, Washington, West Virginia.

Virginia records.—City of Virginia Beach, Cape Henry, IX-18-23.

Collection records.—VIRGINIA: Essex Co. IV-9–21-94 (1), IV-12–26-95 (2), X-24–XI-17-95 (1), IX-28–X-23-95 (1), VIII-19–IX-8-97 (1), IX-9–X-6-97 (3), X-7–31-97 (1), VIII-4–21-98 (1), VIII-22–IX-11-98 (2), IX-12–X-5-98 (3), X-6–XI-7-98 (1); Fairfax Co. VII-12–16-82 (1), VII-6-85

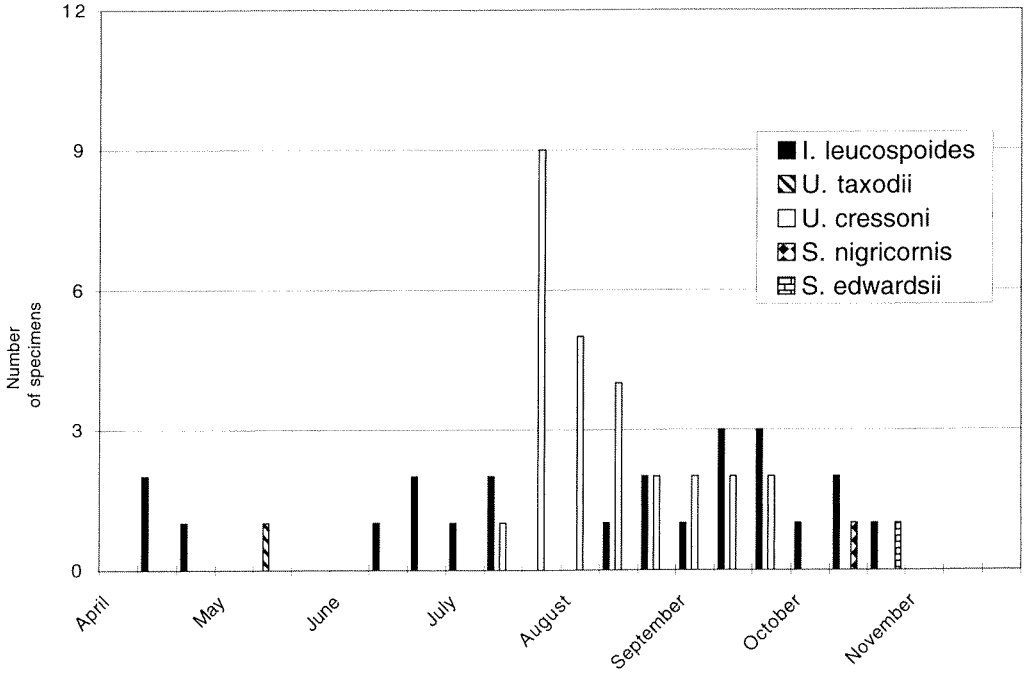


Fig. 16. Seasonal occurrence of *Ibalia leucospoides* and *Sirex edwardsii, S. nigricornis, Urocerus cressoni,* and *U. taxodii* from collections in Maryland, Virginia, and West Virginia.

(1), VII-8–14-85 (1), IX-6–12-98 (1); Louisa Co. VI-29-85 (1), VI-8–19-89 (1), VI-22–VII-3-89 (1).

Hosts.—A parasitoid of woodwasps of the genera *Sirex, Urocerus,* and *Xeris* living in various conifers (Liu and Nordlander 1994).

Remarks.—Chrystal (1930) studied this species in Europe. Eggs are inserted in the egg of the host before hatching or on the first larval instar. They hatch after 2–3 months to a year later. The third stage leaves the interior of the host larva and starts to tunnel toward the surface of the log. Pupation is 5–6 weeks. The complete life cycle is not less than three years. Adults were found from August to October ovipositing in spruce and larch infested with *Sirex cyaneus.*

Kirk (1974) collected this species from trees infested with *Sirex edwardsii* (as *abbotii*) and *S. nigricornis* in Alabama, Georgia, South Carolina, and Florida. Infested trees included *Pinus virginiana, P. taeda, P. clausa, P. elliottii,* and *P. palustris.*

In the mid-Atlantic states, adults were collected from April to October, with most from August to October (Fig. 16). There was no clear, narrow emergence time as for *Ibalia anceps,* and correlations with the emergence times of the host siricids could not be determined.

Host List for Siricidae of Eastern United States

Abies amabilis Douglas ex J. Forges (Pacific silver fir).—*Urocerus albicornis.*

Abies balsamea (L.) Mill. (balsam fir).—*Sirex cyaneus, S. juvencus, Urocerus albicornis, U. cressoni.*

Abies concolor (Gord. & Glend.) Lindl. ex F.H. Hildebr. (white fir).—*Sirex cyaneus, S. longicauda, Urocerus gigas flavicornis, Xeris spectrum.*

Abies fraseri (Pursh) Poir. (Fraser fir).—

Sirex cyaneus, Urocerus albicornis, Urocerus cressoni.

Abies grandis (Douglas ex. D. Don) Lindl. (grand fir).—*Sirex cyaneus.*

Abies lasiocarpa (Hook.) Nutt. (subalpine fir).—*Sirex cyaneus, S. juvencus, Urocerus albicornis, Urocerus gigas flavicornis, Xeris spectrum.*

Abies magnifica A. Murray (California red fir).—*Sirex cyaneus, S. longicauda.*

Abies sp. (fir).—*Sirex noctilio, Urocerus sah.*

Acer negundo L. (boxelder).—*Tremex columba.*

Acer spp. (maple).—*Tremex columba.*

Carpinus sp. (hornbeam).—*Tremex columba.*

Carya spp. (hickory).—*Tremex columba, Eriotremex formosanus.*

Celtis laevigata Willd. (lowland hackberry).—*Tremex columba.*

Cupressus macrocarpa Hartw. ex Gordon (Monterey cypress).—*Sirex areolatus, S. behrensii.*

Fagus grandifolia Ehrh. (American beech).—*Tremex columba.*

Fagus spp. (beech).—*Tremex columba.*

Juniperus occidentalis Hook. (western juniper).—*Sirex areolatus.*

Juniperus scopulorum Sarg. (Rocky Mountain juniper).—*Sirex areolatus.*

Larix laricina (Du Roi) K. Koch (tamarack).—*Sirex cyaneus, Urocerus albicornis.*

Larix occidentalis Nutt. (western larch).—*Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.*

Larix sp. (larch).—*Sirex juvencus, S. noctilio.*

Libocedrus decurrens Torr. (incense-cedar).—*Sirex areolatus.*

Liquidamber styraciflua L. (sweetgum).—*Eriotremex formosanus.*

Picea abies (L.) Karst (Norway spruce).—*Sirex edwardsii.*

Picea engelmanni Parry (Engelmann spruce).—*Sirex cyaneus, Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.*

Picea glauca (Moench) Voss (white spruce).—*Sirex cyaneus.*

Picea mariana (Mill.) B.S.P. (black spruce).—*Urocerus albicornis.*

Picea pungens Engelm. (blue spruce).—*Xeris spectrum.*

Picea sitchensis (Bong.) Carr. (sitka spruce).—*Sirex cyaneus, Urocerus albicornis, U. gigas flavicornis.*

Picea sp. (spruce).—*Sirex cyaneus, S. juvencus, S. nigricornis, S. noctilio, Urocerus cressoni, U. sah.*

Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg. (sand pine).—*Sirex nigricornis.*

Pinus contorta Douglas ex Loudon (lodgepole pine).—*Sirex areolatus, S. cyaneus, S. juvencus, Urocerus gigas flavicornis, Xeris spectrum.*

Pinus echinata Mill. (shortleaf pine).—*Sirex edwardsii, S. nigricornis.*

Pinus elliottii Engelm. (slash pine).—*Sirex edwardsii.*

Pinus jeffreyi Grev. & Balf. (Jeffrey pine).—*Sirex areolatus, S. behrensii.*

Pinus lambertiana Dougl. (sugar pine).—*Sirex areolatus.*

Pinus palustris Mill. (longleaf pine).—*Sirex edwardsii, S. nigricornis.*

Pinus ponderosa Dougl. ex Laws. (ponderosa pine).—*Sirex behrensii, S. cyaneus, S. longicauda, Xeris spectrum.*

Pinus radiata D. Don (Monterrey pine).—*Sirex areolatus, S. behrensii, S. noctilio.*

Pinus rigida Mill. (pitch pine).—*Sirex edwardsii, S. nigricornis, Urocerus cressoni.*

Pinus strobus L. (eastern white pine).—*Sirex edwardsii, S. nigricornis.*

Pinus taeda L. (loblolly pine).—*Sirex nigricornis, Urocerus cressoni.*

Pinus virginiana Mill. (Virginia pine).—*Sirex edwardsii, S. nigricornis.*

Pinus sp. (pine).—*Sirex noctilio, Urocerus albicornis, U. sah, Eriotremex formosanus* (?).

Platanus occidentalis L. (sycamore).—*Tremex columba.*

Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir).—*Sirex areolatus, S. cy-*

aneus, S. longicauda, S. noctilio, Urocerus albicornis, U. gigas flavicornis, Xeris spectrum.

Pyrus sp. (apple, pear).—*Tremex columba.*

Quercus alba L. (white oak).—*Eriotremex formosanus.*

Quercus laurifolia Michx. (laurel oak).—*Eriotremex formosanus.*

Quercus nigra L. (water oak).—*Eriotremex formosanus.*

Quercus phellos L. (willow oak).—*Eriotremex formosanus.*

Quercus sp. (oak).—*Tremex columba, Eriotremex formosanus.*

Sequoia sempervirens (D. Don) Engl. (redwood).—*Sirex areolatus.*

Taxodium distichum (L.) Rich. (baldcypress).—*Sirex areolatus, Urocerus taxodii.*

Thuja plicata Donn ex D. Don (western redcedar).—*Urocerus albicornis.*

Thuja sp. (cedar).—*Sirex areolatus.*

Tsuga heterophylla (Raf.) Sarg. (western hemlock).—*Sirex cyaneus, Urocerus albicornis.*

Ulmus spp. (elm).—*Tremex columba.*

Acknowledgments

Most of the specimens on which this study is based are in the National Museum of Natural History, Smithsonian Institution, Washington, DC. We thank the curators of the following other collections examined: University of Arkansas, Fayetteville; Arizona State University, Tempe; University of Georgia, Athens; Iowa State University, Ames; University of Kansas, Lawrence; Mississippi State University, Mississippi State; University of Missouri, Columbia; Montana State University, Bozeman; Nebraska State Museum, Lincoln; University of New Hampshire, Durham; New Mexico State University, Las Cruces; Ohio State University, Columbus; Oregon Department of Agriculture, Salem; Oregon State University, Corvallis; Texas A&M University, College Station; Virginia Museum of Natural History, Martinsville; Virginia Polytechnic Institute and State University, Blacksburg; West Virginia University, Morgantown; University of Wyoming, Laramie.

We thank the following for allowing collections on their property: Mr. and Mrs. J. G. Kloke, Louisa and Essex counties, VA; T. J. Henry and D. R. Miller, Hardy Co., WV; R. Turner, Loudoun Co., VA; and M. E. Bowers, University of Virginia Blandy Experimental Farm and State Arboretum of Virginia, Clarke Co., VA. E. M. Barrows allowed study of his collections from Tucker Co., WV, and Allegheny and Garrett counties, MD. Cathy Anderson, Systematic Entomology Laboratory, USDA, took the scanning electron micrographs and arranged the plates.

Thanks are extended to the following for reviewing the manuscript: H. Goulet, Agriculture and Agri-Food Canada, Ottawa, and R. Ochoa and M. Pogue, Systematic Entmology Laboratory, USDA, Beltsville, MD, and Washington, DC, respectively.

Literature Cited

Amman, G. D. 1969. Annotated list of insects infesting bark and wood of Fraser fir. Journal of Economic Entomology 62: 249–250.

Bedding, R. A. and R. J. Akhurst. 1974. Use of the nematode *Deladenus siridicola* in the biological control of *Sirex noctilio* in Australia. Journal of the Australian Entomological Society 13: 129–137.

Belyea, R. M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Canadian Entomologist 84: 325–335.

Benson, R. B. 1962. Holarctic sawflies (Hymenoptera: Symphyta). Bulletin of the British Museum (Natural History) Entomology 12(8): 381–409.

Blackman, M. W. and H. H. Stage. 1918. Notes on insects bred from the bark and wood of the American larch—*Larix laricina* (Du Roc) Koch. Technical Publication No. 10 of the New York State College of Forestry at Syracuse University, 115 pp.

Bradley, J. D. 1913. The Siricidae of North America. Journal of Entomology and Zoology 5: 1–36, 5 plates.

Buchner, P. 1928. Holznahrung und Symbiose. J. Springer. Berlin.

———. 1965. Siricids, pp. 83–92. *In* Endosymbiosis of Animals with Plant Microorganisms. J. Wiley, N.Y. 909 pp. Revised English version.

Cameron, E. A. 1967. Notes on *Sirex juvencus californicus* (Hymenoptera: Siricidae), with a descrip-

tion of the male and a key to the California species of *Sirex*. Canadian Entomologist 99: 18–24.

Cartwright, K. St G. 1929. Notes on a fungus associated with *Sirex cyaneus*. Annals of Applied Biology 16: 182–187.

———. 1938. A further note on fungus association in the Siricidae. Annals of Applied Biology 25: 430–432.

Chapin, J. B. and A. D. Oliver. 1986. Records of *Eriotremex formosanus* (Matsumura), *Sirex edwardsii* Brullé, and *Neurotoma fasciata* (Norton) in Louisiana (Hymenoptera: Siricidae, Pamphiliidae). Proceedings of the Entomological Society of Washington 88: 190.

Chrystal, R. N. 1928. The *Sirex* woodwasps and their importance in forestry. Bulletin of Entomological Research 19: 219–247.

———. 1930. Studies of the *Sirex* parasites. Oxford Forestry Memoirs 11, 63 pp.

Chrystal, R. N. and J. G. Myers. 1928. The *Sirex* woodwasps and their parasites. Empire Forestry Journal 7: 145–154.

De Leon, D. 1952. Insects associated with *Sequoia sempervirens* and *Sequoia gigantea* in California. Pan-Pacific Entomologist 23: 75–91.

Farr, D. F., G. F. Bills, G. P. Chamuris, and A. Y. Rossman. 1995. Fungi on plants and plant products in the United States. 2nd Edition. APS Press, St. Paul, Minnesota, U.S.A., 1252 pp.

Fattig, P. W. 1949. Some observations on *Megarhyssa* (Hymenoptera, Ichneumonidae). Entomological News 60: 69–71.

Francke-Grosmann, H. 1939. Über das zusammenleben von Holzwespen (Siricinae) mit Pilzen. Zeitschrift für Angewandte Entomologie 25: 647–680.

Fukuda, H. and N. Hijii. 1997. Reproductive strategy of a woodwasp with no fungal symbionts, *Xeris spectrum* (Hymenoptera: Siricidae). Oecologia 112: 551–556.

Gaut, I. P. C. 1970. Studies of siricids and their fungal symbionts, Ph.D. Thesis, University of Adelaide, Australia. 166 pp.

Gilbert, J. M. and L. W. Miller. 1952. An outbreak of *Sirex noctilio* (F.) in Tasmania. Australian Forestry 16: 63–69.

Gilbertson, R. L. 1984. Chapter 6. Relationships between insects and wood-rotting basidiomycetes, pp. 130–165. *In* Wheeler, Q. and M. Blackwell, eds. Fungus-Insect Relationships, Perspectives in Ecology and Evolution. Columbia University Press, New York, 514 pp.

Harrington, W. H. 1887. Insects infesting maple trees. Seventeenth Annual Report of the Entomological Society of Ontario, 1887, pp. 22–23.

Iede, E. T., E. Schaitza, S. Penteado, R. C. Reardon, and S. T. Murphy, eds. 1998. Proceedings of a conference: Training in the control of *Sirex noctilio* by the use of natural enemies, Colombo, Brazil, November 4 to 9, 1996. Forest Health Technology Enterprise Team, Technology Transfer, Biological Control, Morgantown, WV, FHTET 98-13, 96 pp. (English); 101 pp. (Portuguese).

Johnson, C. W. 1928. The New England Siricidae or horntails. Bulletin of the Boston Society of Natural History, No. 49, pp. 3–7.

———. 1930. On the variation and abundance of *Sirex nitidus* Harris. Psyche 38: 281–282.

Kirk, A. A. 1974. Siricid woodwasps and their associated parasitoids in the southeastern United States (Hymenoptera: Siricidae). Journal of the Georgia Entomological Society 9: 139–144.

———. 1975. Siricid woodwasps and their associated parasitoids in the southwestern United States. Pan-Pacific Entomologist 51: 57–61.

Kukor, J. J. and M. M. Martin. 1983. Acquisition of digestive enzymes by siricid woodwasps from their fungal symbiont. Science 220: 1161–1163.

Laurent, P. 1931. Notes on *Tremex columba* Linn. (Hymen.: Siricidae). Entomological News 42: 67.

Liu, Z. and G. Nordlander. 1992. Ibaliid parasitoids of siricid woodwasps in North America: Two new *Ibalia* species and a key to species (Hymenoptera: Cynipoidea). Proceedings of the Entomological Society of Washington 94: 500–507.

———. 1994. Review of the family Ibaliidae (Hymenoptera: Cynipoidea) with keys to genera and species of the world. Entomologica Scandinavica 25: 377–392.

Middlekauff, W. W. 1960. The siricid wood wasps of California (Hymenoptera: Symphyta). Bulletin of the California Insect Survey 6(4): 59–77.

Parkin, E. A. 1941. Symbiosis in larval Siricidae (Hymenoptera). Nature 147: 329.

———. 1942. Symbiosis and siricid woodwasps. Annals of Applied Biology 29: 268–274.

Rawlings, G. B. 1955. Insect epidemics in *Pinus radiata* forests in New Zealand. New Zealand Journal of Forestry 7: 53–55.

Smith, D. R. 1975. *Eriotremex formosanus* (Matsumura), an Asian horntail in North America. United States Department of Agriculture, Cooperative Economic Insect Report 25(44): 851–854.

———. 1978. Suborder Symphyta (Xyelidae, Pararchexyelidae, Parapamphiliidae, Xyelydidae, Karatavitidae, Gigasiricidae, Sepulcidae, Pseudosiricidae, Anaxyelidae, Siricidae, Xiphydriidae, Paroryssidae, Xyelotomidae, Blasticotomidae, Pergidae). *In* van der Vecht, J. and R. D. Shenefelt, eds. Hymenopterorum Catalogus (nova editio). Dr. W. Junk B.F., The Hague, Holland, 193 pp.

———. 1979. Symphyta, pp. 3–137. *In* Krombein, K. V. et al., eds. Catalog of Hymenoptera in America North of Mexico. Vol. 1. Symphyta and Apocrita (Parasitica). Smithsonian Institution Press, Washington, D.C., 1198 pp.

———. 1987. *Urocerus sah* (Mocsáry) (Hymenop-

tera: Siricidae) new to North America and key to North American species of *Urocerus*. Proceedings of the Entomological Society of Washington 89: 834–835.

———. 1993. Systematics, life history, and diversity, pp. 3–32. *In* Wagner, M. and K. F. Raffa, eds. Sawfly Life History Adaptations to Woody Plants. Academic Press, 581 pp.

———. 1996. Discovery and spread of the Asian horntail, *Eriotremex formosanus* (Matsumura) (Hymenoptera: Siricidae), in the United States. Journal of Entomological Science 31: 166–171.

Stange, L. A. 1996. The horntails of Florida (Hymenoptera: Siricidae). Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Circular No. 376, 3 pp.

Stillwell, M. A. 1964. The fungus associated with woodwasps occurring in beech in New Brunswick. Canadian Journal of Botany 42: 495–496.

———. 1965. Hypopleural organs of the woodwasp larva *Tremex columba* (L.) containing the fungus *Daedalea unicolor* Bull. ex Fries. Canadian Entomologist 97: 783–784.

———. 1967. The pigeon tremex, *Tremex columba* (Hymenoptera: Siricidae), in New Brunswick. Canadian Entomologist 99: 685–689.

Stival, C. L. C., E. T. Iede, E. Schaitza, S. R. S. Penteado, and S. M. S. da Silva, eds. 1993. Conferencia Regional da Vespa da Madeira, *Sirex noctilio*, Na América do Sul, 1992, Florianópolis. EMBRAPA, Centro National de Pesquisa de Florestas, Curitiba, Brazil. 278 pp.

Tabata, M. and Y. Abe. 1995. *Cerrena unicolor* isolated from the mycangia of a horntail, *Tremex longicollis*, in Kochi Prefecture, Japan. Mycoscience 36: 447–450.

Tribe, G. D. 1995. The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa. Journal of the Entomological Society of Southern Africa 3: 215–217.

———. 1997. *Sirex* woodwasp expands its range. Plant Protection News, Bulletin of the Plant Protection Institute (Plantbeskermingsnuss) 49: 9–10.

Viitasaari, M. 1984. Sahapistiäiset 3. Siricicoidea, Orussoidea, ja Cephoidea. University of Helsinki, Department of Agricultural and Forest Zoology Reports 6, 66 pp.

Viitasaari, M. and F. Midtgaard. 1989. A contribution to the taxonomy of horntails with notes on the genus *Sirex* Linnaeus (Hymenoptera, Siricidae). Annales Entomologici Fennici 55: 103–110.

Webster, F. M. 1895. The black horned horntail, *Urocerus Nigricornis*. The Ohio Farmer, August 29, 1895, p. 177.

Westcott, R. L. 1971. New host and distribution records for three western wood-boring Hymenoptera (Syntexidae, Siricidae). Pan-Pacific Entomologist 47: 310.