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Cover photo

*Aulacigaster neoleucopeza* (Diptera: Schizophora)

Photo by Dr. Craig M. Brabant
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New Records of *Aulacigaster neoleucopeza* Mathis and Freidberg (Diptera: Schizophora: Aulacigastridae) from Wisconsin

Daniel K. Young1*, and Craig M. Brabant1**

**Abstract**

In Wisconsin, *Aulacigaster neoleucopeza* was previously known from but a single Dane County record dating from April 1951. We report one specimen captured with a flight-intercept trap on private property in Lafayette County, five specimens recovered from Lindgren funnel and Malaise traps at the Hemlock Draw, Nature Conservancy Preserve in Sauk County, and 659 specimens from Malaise traps at the Quincy Bluff State Natural Area in Adams County. The specimens were taken from mid-April 1998, late April to mid-May 2014, and early to mid-April 2010, respectively.

As presently understood, sap flies (Aulacigastridae) comprise a small acalypterate, schizophorid fly family whose common name refers to the fact that many species of *Aulacigaster* Macquart can be commonly found on tree wounds and slime fluxes where they feed and mate, and where females are known to oviposit. Most of the 55 species of *Aulacigaster* are distributed throughout Central and South America; three species are widely distributed across the Nearctic Region. The only other genus in Aulacigastridae is *Curiosimusca* Rung, Mathis and Papp with three species known from the Oriental Region (Malaysia, Thailand) (Rung et al. 2005).

According to Rung and Mathis (2011) and references cited therein, most published remarks relating to the natural history of *Aulacigaster* species pertain to members of the *leucopeza* species group, including *A. neoleucopeza* Mathis and Freidberg (Figs. 1–3). Larvae and adults are associated with sap flows from wounds and fermenting sap fluxes of deciduous trees. *Aulacigaster neoleucopeza* has been collected on wounds and fluxes from the following genera of deciduous trees: *Acer, Alnus, Pinus, Platanus, Populus, Quercus, and Salix* (Rung and Mathis, 2011). The senior author (DKY) has also observed specimens at a sap flow on *Morus rubra* (red mulberry) in northeastern Dane County, Wisconsin. Davis and Zack (1978) reared adults from larvae collected at sap flows associated with a wounded *Pseudotsuga menziesii* (Douglas fir).

Marshall (2012) summarized that “Female flies deposit their eggs in moist decaying sap, where the larvae develop as microbial grazers, breathing through a long, tail-like respiratory tube and long, thin spiracular lobes on the thorax.”

In the Neotropical Region, Rung and Mathis (2011) described species of the “bromeliae species group” whose larvae, where known, were discovered to develop in bromeliad phytotelmata. Larvae of these species are aquatic and are presumed to feed and develop on decaying organic matter typically associated with tank-syndrome bromeliads.

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Materials and Methods

Specimen Data and Specimens. Label data from new records reported below are presented verbatim. Line breaks on labels are denoted by a double slash (//). The specimens were field collected into 70–80% ethanol. However, since most Diptera are prone to excessive tissue distortion during the normal dehydration process associated with pinning, the HMDS technique (Nation 1983) was used in specimen preparation to minimize exoskeletal collapsing and shriveling.

All specimens of *A. neoleucopeza* reported herein are vouchered in the Insect Research Collection (WIRC) of the Department of Entomology, University of Wisconsin-Madison.

Figures. Images were captured by the second author (CMB) as TIFF files from a JVC KY-F75U digital camera attached to a Leica Z16 APO dissecting microscope with apochromatic zoom objective and motor focus drive, using a Syncroscopy Auto-Montage focus-stacking system. A series (or “stack”) of 40 images was captured and ZereneStacker Professional Edition software (Zerene
Systems LLC) was used to combine the stack into a final focus-stacked image. Specimens were illuminated with two gooseneck fiber-optic lighting units. Montaged images produced with ZereneStacker were post-processed using Photoshop CC 2015 (Adobe Systems Inc.) software to create the final figure plates.

Habitat images (Figs. 4–5) were taken by the senior author (DKY) using a Canon EOS Rebel T2i digital camera and depict two localities where the aulacigastrids were captured in Malaise traps. The sites are located in the Baraboo...
Hills of Sauk County, within the Hemlock Draw Preserve (TCN) in south-central Wisconsin (http://www.nature.org/ourinitiatives/regions/northamerica/united-states/wisconsin/placesweprotect/hemlock-draw.xml).

**Results and Discussion**

Previously, the only confirmed literature record for Aulacigastridae in Wisconsin is from a specimen in the National Museum of Natural History (1♂; USNM) (Rung and Mathis 2011). The specimen was collected by R. H. Jones on 29 April 1951 in Dane County.

The new records follow. One specimen of *A. neoleucopeza* was collected using a flight-intercept trap [USA: WI: Lafayette Co. // Wedel property; // ~3 mi. north of Argyle // 42°44'17"N/89°51'05"W // 5 Aug.–03 Sept. 2001 // Jeffrey P. Gruber; [second label] flight-intercept trap in // southern mixed hardwood // forest]. Two specimens were collected from a single, unbaited Lindgren funnel trap sample [USA: WI: Sauk Co. // Hemlock Draw; WGS84 // 43.365791°N/-89.94821°W // 17–20 April 1998 // Daniel K. Young // ex: Lindgren Funnel Trap]. A single specimen was collected from a Malaise trap sample [USA: WI: Sauk Co. // Hemlock Draw TNC // 43.36380°N/-89.94133°W // WGS84; 28.IV–05.V 2014 // Daniel K. Young; *Quercus* // *Prunus*; *Symplocarpus*]. One specimen was recovered from the same Malaise trap during the subsequent sampling period [USA: WI: Sauk Co. // Hemlock Draw TNC // 43.36380°N/-89.94133°W // WGS84; 05–14 May 2014 // Daniel K. Young; *Quercus* // *Prunus*; *Symplocarpus*]. The fifth specimen was recovered from a Malaise trap as well [USA: WI: Sauk Co. // Hemlock Draw TNC // 43.36447°N/-89.94067°W // WGS84; 05–14 May 2014 // Daniel K. Young; *Quercus* // *Prunus*; *Symplocarpus*]. The area of the *Populus* deadfall, results of a severe wind storm that moved through the area the previous season, provided more than ample habitat to support the types of wounds and sap flows consistent with microhabitats previously described in the literature, as noted above.

An additional bulk dipteran sample from another trap at the same site yielded another 172 specimens [USA: WI: Adams Co. // 43.86966°N/-089.87946°W // [WGS84]; Quincy Bluff TNC // 09–19 April 2010 // Daniel K. Young; ex: Malaise // trap in old *Populus* deadfall]. The area of the *Populus* deadfall, results of a severe wind storm that moved through the area the previous season, provided more than ample habitat to support the types of wounds and sap flows consistent with microhabitats previously described in the literature, as noted above.

In a recent paper describing a significant range extension for a very uncommon acrocerid fly (Woller et al. 2015) from the same Quincy Bluff site, the authors noted of salvaged bulk samples, “You never quite know what tasty morsels will be found within insect soup, so, by all means, dig in!” The Malaise traps providing the large Quincy Bluff series of *A. neoleucopeza* for this contribution, like the samples that were foundational to the acrocerid discovery, were originally employed for a beetle survey project by one of us (DKY) at Quincy Bluff. The present discoveries provide a plethora of ‘tasty morsels’ and further confirm the significance of databasing and maintaining bulk trap samples within our natural history collections.
Acknowledgments

Field research and travel funding support was provided in part through a block grant to the WIRC from the University of Wisconsin Natural History Museums Council, and in part from instructional funds associated with teaching a graduate-level, Advanced Taxonomy of Diptera course by the senior author at the University of Wisconsin-Madison. We also gratefully acknowledge the time and suggestions of our reviewers.

Literature Cited


Redescription of the female of *Oobius depressus* (Girault) (Hymenoptera: Encyrtidae), newly found in Michigan, U.S.A.

Serguei V. Triapitsyn1, Toby R. Petrice2*, and Vladimir V. Berezovskiy1

Abstract

A female of *Oobius depressus* (Girault) (Hymenoptera: Encyrtidae), collected in a modified Malaise trap in the canopy of a black locust tree, *Robinia pseudoacacia*, at Rose Lake State Wildlife Area in Bath Charter Township, Clinton Co., Michigan, U.S.A., is re-described and illustrated. This species was previously known only from the type series of headless specimens of both sexes from the type locality in Morristown, Henry Co., Illinois, U.S.A. These type specimens were from a single cohort of locust borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae), eggs collected and reared over one hundred years ago. An updated taxonomic key to females of native and introduced species of the genus *Oobius* Trjapitzin, which now includes *O. depressus*, is provided.

Recently, Triapitsyn et al. (2015) revised the Nearctic species of the genus *Oobius* Trjapitzin (Hymenoptera: Encyrtidae), which are egg parasitoids of Buprestidae and Cerambycidae (Coleoptera). Two members of this genus, *O. agrili* Zhang & Huang and *O. longoi* (Siscaro), have been introduced into the U.S. as classical biological control agents of *Agrilus planipennis* Fairmaire (Buprestidae) and *Phoracantha semipunctata* (Fabricius) (Cerambycidae), respectively (Hanks et al. 1995, Bauer et al. 2015). Another potential biological control agent of *A. planipennis*, *O. primorskyensis* Yao & Duan, has been imported into quarantine in Newark, Delaware, U.S.A. from the Far East of Russia; it is currently in culture, but has not yet been released as it is still being evaluated for host-specificity and other bionomic factors (Yao et al. 2016). Nearctic species of *Oobius* are poorly studied, and their importance as natural enemies of native wood-boring beetles, including a number of pests of forest and ornamental trees, is unclear. One species, *O. depressus* (Girault), was not included by Triapitsyn et al. (2015) in the taxonomic key to Nearctic females because its identity was at that time unclear without knowing the details of its female antennal characters.

*Oobius depressus* was described from the type series of three females and two males reared from eggs of the locust borer, *Megacyllene robiniae* (Forster) (Cerambycidae), on 8 December 1914 in Morristown, Henry Co., Illinois, U.S.A. (Girault 1916). There is no record of this species being re-collected since. The original description of *O. depressus* is poor and without any illustrations; unfortunately, the slide with the heads and fore wings of each sex (Girault 1916) could not be found in the National Museum of Natural History, Washington, District of Columbia, U.S.A. (USNM) and is presumed lost. To facilitate recognition of

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this species, Triapitsyn et al. (2015) provided illustrations of the scutellum and habitus of the female (without head and antennae) in dorsal view.

The uncertain identity of *O. depressus* required attention considering its potential importance as a natural control agent of locust borer, a serious pest of black locust, *Robinia pseudoacacia* L., that limited plantings of this valuable tree (Linsley 1964, Solomon 1995). Comprehensive identification tools are also important for *Oobius* species to ensure correct identification of *O. agrili* when evaluating its establishment and impacts at release sites throughout the expanding range of *A. planipennis* (Bauer et al. 2015). Therefore, we attempted to collect this species for the first time in 100 years since its original rearing, and allow the inclusion of *O. depressus* in an updated key to the females of the described Nearctic species of *Oobius* (Triapitsyn et al. 2015). For that, we had to have at least one female specimen of this species with intact antennae, because antennal characters are used in the relevant couplets of the key.

**Material and Methods**

**Collecting.** Linsley (1964, p. 83) summarized the following about the habits of locust borer adult: “In the fall when the goldenrod is in full bloom, the adults are found feeding on the pollen of this plant. They lay the eggs beneath the bark scales of black locust, the young larvae hatching before the leaves fall and overwintering in the outer corky bark”. Because eggs of *M. robiniae* are very difficult to find, especially parasitized ones, and adult female beetles apparently visit black locust trees only for a short time to oviposit, we attempted to collect adult locust borers and egg parasitoids using a canopy insect trap, a modification of a Malaise trap that has both bottom (good for capturing wood-boring and other arboreal Coleoptera) and top (good for capturing micro-Hymenoptera and other insects) collection jars. One such trap, manufactured by Sante Traps (Lexington, Kentucky, U.S.A.; description is available at www.santetraps.com), was hung in the canopy of a live black locust tree, surrounded by many other conspecific trees, at Rose Lake State Wildlife Area in Bath Charter Township, Clinton Co., Michigan from 15 August to 28 October 2015 (Fig. 1). Both collection jars were filled with 90% ethanol that was emptied and re-filled periodically (about every 15–20 days); collected samples were stored in a freezer at -18°C until shipped to the Entomology Research Museum, University of California, Riverside, California, U.S.A. (UCRC). There, the samples were sorted by V. V. Berezovskiy under a dissecting microscope.

Also, S. V. Triapitsyn and Michael White of Chicago, Illinois, made a short collecting trip on 23 August 2015 to the type locality of *O. depressus* in Morristown. Unfortunately, no black locust trees could be located there or in the proximal vicinity.

**Taxonomic study.** The specimen documented in this study was critically point dried, point-mounted, and labeled. It was then measured, photographed, dissected, and slide-mounted in Canada balsam, followed by examination under a Zeiss Axioskop 2 plus compound microscope using Nomarski differential interference contrast optics. Stereomicroscopic images were taken and compiled using Auto-Montage by Syncroscopy.

Terms used for morphological features are those of Gibson (1997). Abbreviations used are: F = antennal funicle segment; mps = multiporous plate sensillum or sensilla on the antennal flagellar segments (= longitudinal sensillum or sensilla or sensory ridge(s) of other authors). Body length was measured exclusive of the exserted part of the ovipositor.
Results

Only one parasitoid specimen belonging to the genus *Oobius*, fortunately a female, was found (in the bottom jar sample dated 6 October 2015) in the samples collected by the canopy insect trap. It matched perfectly both the original description of *O. depressus* and the illustrations of this species in Triapitsyn et al. (2015). It is re-described and illustrated below. Based on the useful information obtained, this species is included in the updated taxonomic key to females of the Nearctic species of *Oobius* that follows its redescription.

Also, it is interesting to note that only one specimen of the locust borer, a male, was collected in the same canopy trap (on 31 August 2015). This voucher specimen was pinned, labeled, and deposited in the UCRC.

*Oobius depressus* (Girault, 1916)

Figs. 2–8

Habrolepoidea depressa Girault 1916: 343–344. Lectotype female [USNM], examined (Triapitsyn et al. 2015).

*Oobius depressus* (Girault): Triapitsyn et al. 2015: 36–37 (taxonomic history, information on the type material, discussion), 41 (illustrations).

**Material examined.** U.S.A., Michigan, Clinton Co., Bath Charter Township, 42°47’55.5”N 84°22’50.8”W, 259 m, 6.x.2015, T. R. Petrice [1 female, UCRC (UCRC ENT 383312)].

Redescription. FEMALE (non-type specimen from Michigan). Body (Figs 3, 4) notably flattened, shining black; with some slight violet reflections on mesoscutum and scutellum; propodeum partially whitish; antenna dark brown to black; fore wing venation brown to dark brown except stigmal vein contrastingly lighter (light brown); legs mostly dark brown except apical half or so of protibia and pretarsus light brown.

Frontovertex and scape striate, pronotum weakly reticulate, mesoscutum and axilla with faint mesh-like sculpture [very difficult to see both in an alcohol-preserved and a dry-mounted specimen], scutellum almost smooth. Pubescence on head and mesosoma mostly light-colored; scutellum also with a pair of longer, fine, subapical setae.

Head (Fig. 6) very short (much wider than long), with ocelli in a very obtuse triangle, posterior ocellus touching eye margin. Occipital margin narrowly rounded. Transfacial and inner orbital sutures present. Mandible with 2 acute and 1 rather truncate teeth (Fig. 2); palpal formula 4-3.

Antenna (Fig. 5) inserted slightly below lower eye margin. Radicle a little more than 0.2x total scape length, rest of scape 4.2x as long as wide, narrowing apically. Pedicel longer than any funicle segment, about 2.0x as long as wide, and shorter than the combined length of F1–F3. F1 and F2 about as long as wide and subequal, F3 a little longer than F1 or F2 and slightly wider than long, F4–F6 subquadrate and subequal to each other; F1 and F2 without mps, F3 with 1 mps, F4 with 3 or 4 mps, F5 with 4 mps, and F6 with 5 mps. Clava 2.3x as long as wide, as long as combined length of F4–F6 plus about half length of F3; claval segments obliquely divided; first (basal) claval segment with 4 mps, second with 5 mps, and third with 4 (or, possibly, with as many as 5) mps; apical claval segment obliquely truncate ventrally.

Mesosoma (Fig. 7) shorter than gaster. Mesoscutum about 1.5x as wide as long. Scutellum somewhat depressed, wider than long, shorter than mesoscutum.

Wings (Fig. 8) not abbreviated, fore wing extending beyond apex of gaster. Fore wing about 2.1x as long as wide, hyaline; marginal setae very short; disc densely setose, linea calva interrupted posteriorly by a row of setae, filum
spinosum present (2 spine-like setae). Hind wing about 3.4x as long as wide, hyaline; longest marginal seta about 0.1x maximum wing width.

Mesotibial spur slightly shorter than mesobasitarsus.

Ovipositor (Fig. 7) occupying about 0.6x length of gaster, exerted beyond gastral apex by about 0.1x total ovipositor length; ovipositor length:metatibia length ratio 1.5:1. Outer plate of ovipositor with 1 subapical seta.

Measurements (mm, as length or length:width, taken from the slide-mounted specimen unless stated otherwise). Body (of the dry-mounted specimen prior to slide-mounting): 1.238; head (of the dry-mounted specimen prior to slide-mounting): 0.132; mesosoma: 0.547; gaster: 0.707; ovipositor: 0.492. Antenna: radicle: 0.07; rest of scape: 0.233; pedicel: 0.079; F1: 0.03; F2: 0.03; F3: 0.036; F4: 0.051; F5: 0.051; F6: 0.052; clava: 0.183. Fore wing: 0.984:0.461; hind wing: 0.738:0.215.

**MALE.** Known and described (Girault 1916) but not illustrated.

**Diagnosis.** Among the Nearctic species of *Oobius*, *O. depressus* differs from *O. whiteorum* Triapitsyn, known from Pennsylvania, U.S.A. from eggs of *Agrilus anxius* Gory (Coleoptera: Buprestidae) on European white birch trees, *Betula pendula* Roth (Triapitsyn et al. 2015), to which it is somewhat similar, by a relatively more flattened body (Fig. 4) and by a larger body size in females. According to Girault (1916), the body length of *O. depressus* is 1.15 mm (our specimen is a little larger), whereas females of *O. whiteorum* are at most 0.75 mm. Also, F1 through F3 progressively increase in width in *O. depressus*, whereas these three funicular segments are subequal in both width and length in *O. whiteorum*; the ovipositor is 1.5x length of metatibia in the former and 1.3x length of metatibia in the latter species. *Oobius depressus* is particularly similar to another Nearctic species, *O. dahlsteni* (Trjapitzin) from California, U.S.A., which was well described by Trjapitzin (1971) and more recently was illustrated by Triapitsyn et al. (2015), and whose host(s) is/are unknown; these two taxa differ mainly in the proportions of the female antennal segments, as indicated in the key below.

*Oobius depressus* cannot be possibly confused with *O. primorskyensis* which has all legs with tarsi 4-segmented (Yao et al. 2016), in case of its possible release and establishment in North America.

**Distribution.** U.S.A.: Illinois (Girault 1916) and Michigan (new record).

**Host.** *Megacyllene robiniae* (Forster) (Cerambycidae) (Girault 1916 [as *Cyllene robinia*]).

**Updated key to the described Nearctic species of *Oobius*, females**
[both native and introduced, modified from Triapitsyn et al. (2015)]

1  Tarsi 4-segmented ........................................*O. agrili* Zhang & Huang
   – Tarsi 5-segmented .................................................................2

2(1)  Clava entire.............................................*O. nearcticus* (Trjapitzin)
   – Clava 3-segmented .........................................................................3

3(2)  Body length (dry-mounted specimens) at most 0.53 mm; mps only on F6 .................................................*O. minusculus* Triapitsyn & Petrice
   – Body length (dry-mounted specimens) at least 0.66 mm; mps on F6 and other funicle segments .......................................................4

4(3)  Mps on F5 and F6 .........................................*O. buprestidis* (Gordh & Trjapitzin)
   – Mps at least on F4-F6........................................................................5

5(4)  Linea calva “open” posteriorly, uninterrupted by row of setae
.................................................................*O. longoi* (Siscaro)
– Linea calva interrupted posteriorly by a line (or lines) of setae ........ 6

6(5) F5 and F6 each notably longer than F4 (F4 0.8x length of F5) .......................................................... O. whiteorum Triapitsyn
– F5 and F6 each subequal in length to F4 (F4 more than 0.9x length of F5) .................................................. 7

7(6) Pedicel shorter than combined length of F1-F3; clava as long as combined length of F4-F6 plus about half length of F3 (Fig. 5) .................................................. O. depressus (Girault)
– Pedicel longer than combined length of F1-F3; clava about as long as combined length of F2-F6.................... O. dahlsteni (Trjapitzin)

Acknowledgments

We thank Michael White for his kind help in collecting efforts, Leah S. Bauer (USDA Forest Service, Northern Research Station, Lansing, Michigan) and Erin Morris (Michigan State University, East Lansing, MI) for review of the manuscript prior to its submission, and Douglas Yanega (UCRC) for confirming the identity of the locust borer. Two anonymous reviewers made several useful suggestions towards improvement of the manuscript.

Literature Cited


A Synopsis of the Cimicoidea (Heteroptera) of Michigan

Daniel R. Swanson1,2*

Abstract

An overview of the 20 species of Cimicoidea (Anthocoridae, Cimicidae, Lasiochilidae, Lyctocoridae) found in Michigan is presented, along with identification keys, distribution maps, and relevant literature. Five new state records for the following species, representing three of the four cimicoid families found in Michigan, are presented: Oeciacus vicarius Horváth (Cimicidae: Cimicininae), Cimexopsis nycalis List (Cimicidae: Haematosiphoninae), Amphiareus obscuriceps (Poppius) (Anthocoridae), Cardiastethus borealis Kelton (Anthocoridae), and Lyctocoris stalii (Reuter) (Lyctocoridae).

Cimicoidea is a superfamily of small predaceous or parasitic true bugs comprising 111 species in 39 genera in the United States and Canada (updated from Froeschner 1988a, b; Henry 1988). Excepting the infamous Cimex lectularius Linnaeus, most are relatively inconspicuous and often overlooked, owing in part to their small size (most under 5 mm) and cryptic habitats, and this trend is reflected in collections and in print, despite the fact that many are both common and abundant. Their minute size also makes them difficult to identify correctly. Another consequence is frequent pagility: these insects may be easily transported unknowingly by humans, and the percentage of non-native species in the United States, especially in Anthocoridae, rivals that of any other heteropteran group (Lattin 2007).

At present, the literature concerning the Michigan cimicoid species remains disparate. O’Brien (1983, 1988) listed references for the terrestrial arthropods of Michigan and several contain information relevant to the group. Three partial faunal checklists contain cimicoid records: Townsend (1890) reported “an unnamed anthocorid...taken on garden soil” in the vicinity of Constantine (Saint Joseph County), Pettit (1901) reported the common bed bug from a biological station in Chatham ( Alger County), and Hussey (1922) reported an unidentified species of Anthocoris (Fallén) from lights near the Warren Woods (Berrien County). Two other references provide parasitological records: Lawrence et al. (1965) and Dood and Kurta (1982) discussed some of the ectoparasites taken on mammals found in the state. Lattin (1999a) provided a recent reference focusing on a collection of two species of anthocorids made in Oceana County.

In an effort to gather together this information and present a macroscopic treatment of the superfamily, I herein present the results of my study of the Cimicoidea of Michigan, my sixth synoptic family-level contribution to the heteropteran fauna of the state.

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Materials and Methods

Methods parallel previous installments of this series (Swanson 2011, 2012a, b, 2013, 2015):

The cimicoid holdings of the two major university collections in southern Michigan were examined. County records were compiled, identification keys were modified, and the existing natural history information, both Michiganian and extralimital, was summarized. The minuscule size of the focus organisms, through the phenomena mentioned above, skews the biodiversity to a level of underrepresentation. This nature, particular for this group of Heteroptera, necessitates a brief discussion of species that might occur but are currently unknown in the state; this section follows the primary species accounts.

The identification of the 793 specimens included in this study was rendered or confirmed by the author, and all specimens reside in one of the collections listed below, unless otherwise noted. Collection dates indicate the earliest and latest adults examined and refer specifically to specimens collected in Michigan. In the instances where provided, label data are not transcribed verbatim, but complete locality information is included. Any additions, changes, or interpretive elements provided by the author are shown in brackets. Locations of Michigan counties from which specimens were collected are depicted in Figure 1.

Figure 1. The counties of the State of Michigan.
The taxonomy of the group has undergone several recent changes at various ranks that affect species found in Michigan. I have incorporated the synonymization of Dufouriellini and tribal re-assignment of Dufouriellus, as proposed by Carpintero and Dellapé (2008). I also have incorporated the genus-level changes proposed in Carpintero’s (2014) revision of the Lasiliochilinae of the Western Hemisphere, although I have not adopted his suprageneric classification. This is because the familial composition of Cimicoidea was not formally tested in a phylogenetic manner, and the support for the previous hypothesis of relationships, i.e., Schuh and Štys (1991), was not adequately addressed. Instead, I have retained Lasiochilidae as a separate family, as per Schuh and Štys (1991) and Schuh and Slater (1995).

The habitus plates (Figs. 2, 3) are intended to provide a visual reference for species not often seen because of their small habitus or host affinities. However, as many of the species greatly resemble each other in appearance, comparison with the plates will not serve as a replacement for keying out specimens.

In the keys, certain characters are occasionally set apart using brackets. These brackets signify that the contrasting character is not in that particular couplet but appears in one of the immediately successive couplets attained through the opposite lead.

Collections are designated as follows: Daniel R. Swanson, personal collection (DRS); Albert J. Cook Arthropod Research Collection, Michigan State University, East Lansing, Michigan (MSUC); and University of Michigan Museum of Zoology Insect Collection, Ann Arbor, Michigan (UMMZ).

Results and Discussion

Superfamily CIMICOIDEA

Cimicoidea comprises six families in the Nearctic region: Anthocoridae, Cimicidae, Curaliidae, Lasiochilidae, Lyctocoridae, and Polyctenidae. It is thought that the group remains united by the hemelytral membrane possessing 4–5 free veins (rarely with one long closed cell) (Schuh and Štys 1991); however, the varying form of the hemelytra presents problems for this hypothesis, and the single species of Curaliidae lacks veins in the hemelytral membrane altogether. Most are either arthropophagous predators or hematophagous ectoparasites of warm-blooded vertebrates, with a few rare phytophagous exceptions (Schuh and Slater 1995). They occupy a wide range of habitats, from flowers and fruiting bodies to subcorticular substrates to nidicolous and synanthropic sites. In some groups, mating takes place via a process known as traumatic insemination, in
Figure 3. Anthocoridae, Lasiochilidae, and Lyctocoridae of Michigan, dorsal habitus.
which the male stabs a sclerotized copulatory structure through the abdominal wall of the female to deposit his sperm (Schuh and Slater 1995).

The positions of this superfamily and its constituents have shifted repeatedly, but modern analyses place the group as highly derived within Cimicomorpha (Schuh 1986, Schuh and Štys 1991, Schuh and Slater 1995, Schuh et al. 2009). Lasiochilidae and Lyctocoridae have been elevated to family status from within the Anthocoridae: Schuh and Štys (1991) indicated that recognizing Cimicidae and Polyctenidae as separate families required the same treatment for the aforementioned groups. Thus, most pre-1991 literature treated Lasiochilidae and Lyctocoridae under Anthocoridae, and this paraphyletic concept will be referred to hereafter as Anthocoridae sensu lato or the “anthocoroids” (an informal, rather than taxonomic, term). More recently, Carpintero’s (2014) revision proposed returning Lasiochilidae to a subfamily of Anthocoridae. Additionally, Curaliidae was originally thought to be the sister-group of the Old World family Velocipedidae (Schuh et al. 2008), but molecular evidence used in a total-evidence phylogeny placed the taxon within Cimicoida (Schuh et al. 2009).

Four of the six Nearctic families are present in Michigan. Polyctenidae, or the bat bugs, and their chiropteran hosts, do not occur in the state (Froeschner 1988b; Kurta 2008). The single species of Curaliidae is known only from Florida and Louisiana (Schuh et al. 2008). Within the other four families, 20 species in 14 genera are found in Michigan (Table 1).

Families of Cimicoidea are rarely treated together, except in systematic studies, as the three “anthocoroid” families (Anthocoridae, Lasiochilidae, and Lyctocoridae) share similar natural histories and differ comparatively more from the two hematophagous families (Cimicidae and Polyctenidae). Thus, literature relevant to the family-groups is presented under the headings for Cimicidae and Anthocoridae. The following key to the cimicoid families has been modified from Schuh and Slater (1995), supplemented with Schuh et al. (2008). Separating Lyctocoridae and Anthocoridae may be difficult, and the discussion under the Lyctocoridae heading, as well as the habitus plate (Fig. 3), will facilitate recognition of that family.

Table 1. List of the Michigan Cimicoidea.

<table>
<thead>
<tr>
<th>Anthocoridae</th>
<th>Lasiochilidae</th>
</tr>
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<tbody>
<tr>
<td>Amphiareus obscuriceps (Poppius, 1909)</td>
<td>Dilasia fuscula Reuter, 1871</td>
</tr>
<tr>
<td>Anthocoris confusus Reuter, 1884</td>
<td>Lyctocoris stalii (Reuter, 1871)</td>
</tr>
<tr>
<td>Anthocoris dimorphicus Anderson and Kelton, 1963</td>
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<tr>
<td>Anthocoris musculus (Say, 1831)</td>
<td>Lyctocoridae</td>
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<tr>
<td>Callidodis temnostothoides (Reuter, 1884)</td>
<td></td>
</tr>
<tr>
<td>Cardiastethus borealis Kelton, 1977</td>
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<tr>
<td>Cardiastethus luridellus (Fieber, 1860)</td>
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</tr>
<tr>
<td>Dufouriellus ater (Dufour, 1833)</td>
<td></td>
</tr>
<tr>
<td>Elatophilus inimicus (Drake and Harris, 1926)</td>
<td></td>
</tr>
<tr>
<td>Orius diespeter Herring, 1966</td>
<td></td>
</tr>
<tr>
<td>Orius insidiosus (Say, 1831)</td>
<td></td>
</tr>
<tr>
<td>Tetraphleps canadensis Provancher, 1886</td>
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<tr>
<td>Xylocoris cursitans (Fallén, 1807)</td>
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<table>
<thead>
<tr>
<th>Cimicidae</th>
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<tbody>
<tr>
<td>Cimex adjunctus Barber, 1939</td>
</tr>
<tr>
<td>Cimex brevis Usinger and Ueshima, 1965</td>
</tr>
<tr>
<td>Cimex lectularius Linnaeus, 1758</td>
</tr>
<tr>
<td>Cimexopsis nyctalis List, 1925</td>
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<tr>
<td>Oeciacus vicarius Horváth, 1912</td>
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</tbody>
</table>
Key to the North American families of Cimicoidea

<p>| | | | |</p>
<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Hemelytra always staphylinoid, in the form of small pads, or absent; ocelli absent; frequently ectoparasitic</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>1'</td>
<td>Hemelytra usually well developed, occasionally brachypterous; ocelli present; rarely, if ever, ectoparasitic</td>
<td>3</td>
<td>Meso- and metatarsi 4-segmented; hemelytra absent; ctenidia present; compound eyes absent; permanent ectoparasites of bats [not present in Michigan]</td>
</tr>
<tr>
<td>2</td>
<td>All tarsi 3-segmented; hemelytra present, small and pad-like; ctenidia absent; compound eyes present, small; temporary ectoparasites of mammals and birds</td>
<td>3</td>
<td>Pronotum under-developed, short, ring-like, exposing mesonotum [not present in Michigan]</td>
</tr>
</tbody>
</table>

Family CIMICIDAE Latreille, 1802

Cimicidae, commonly known as the bed and bat bugs (the latter name also is used for the Polyctenidae), is a family of blood-feeding parasites, with members notorious throughout the world and easily recognized by the flattened, ovoid habitus and staphylinoid wing pads. There are 15 species in 8 genera found in America north of Mexico (Froeschner 1988a). Most are nidicolous and therefore, synanthropic in the case of humans. Insemination occurs traumatically. Unlike the other cimicoids in this treatment, members of this group exhibit negative phototaxis, quickly fleeing when exposed to bright lights. Schaefer (2000a, 2000b) discussed the economic effects of the cimicids, both as ectoparasites and occasional adventitious biters.

Usinger’s (1966) magnum opus, with its wealth of information, remains the most important taxonomic reference for Cimicidae; the key below is modified from that work. Froeschner (1988a) provided the most recent catalog for the species found in America north of Mexico, and Ryckman et al. (1981) did the same for the Western Hemisphere (although several taxa have been described since its publication).

Two of the three subfamilies found in the Nearctic region are represented in Michigan (Primicimicicinae are known only from Texas), and 5 species in 3 genera are found in the state.
Key to the Cimicidae of Michigan

1 Bristles of lateral pronotal margins smooth on outer sides; metasternum a somewhat compressed rounded lobe between metacoxae (Haematosiphoninae); [bristles of pronotal margin distinctly shorter than width of eye; ectoparasites of chimney swifts].................. Cimexopsis nyclalis

1' Bristles of lateral pronotal margins minutely serrate on outer sides; metasternum forming a flattened plate between metacoxae (Cimicinae)........................................................................................................ 2

2 (1') Body clothed with pale slender bristles; second antennomere not more than two-thirds length of interocular space; width of pronotum less than 1.5 times width of head; [bristles of pronotal margin subequal to or slightly longer than width of eye; ectoparasites of swallows]

.................................................................................... Oeciacus vicarius

2' Body clothed with relatively short stout bristles; second antennomere subequal to interocular space; width of pronotum at least 1.5 times width of head (Cimex)........................................................................... 3

3 (2') Longest bristles of pronotal margin subequal to or shorter than width of eye; metafemur usually more than 2.6 times as long as greatest width; female with paragenital sinus (opening on posterior margin of fifth sternite) narrowly cleft on right side at spermalege; hosts: humans, bats, chickens.................................................. Cimex lectularius

3' Longest bristles of pronotal margin much longer than width of eye; metafemur usually less than 2.6 times as long as greatest width; female with paragenital sinus roundly emarginate on right side; hosts: bats........................................................................................................ 4

4 (3') Longest bristles of metatibia longer than width of tibia; width of pronotum 1.1 mm................................................. Cimex brevis

4' Longest bristles of metatibia shorter than or subequal to width of tibia; width of pronotum usually 1.2 mm or more........... Cimex adjunctus

Subfamily CIMICINAE Latreille, 1802

Genus CIMEX Linnaeus, 1758

Cimex adjunctus Barber, 1939. (Figs. 2, 4).—This member of the pilosellus group, commonly known as the eastern bat bug, was reported from Michigan by Dood and Kurta (1982); the record apparently was overlooked by Froeschner (1988a). The specimens examined by the former authors were taken from the big brown bat (Eptesicus fuscus (Palisot de Beauvois)) and Indiana bat (Myotis sodalis Miller and Allen) (Dood and Kurta 1982). Usinger (1966) indicated that C. adjunctus also has been taken on the following chiropteran hosts in other states in the eastern and central United States: the little brown bat (Myotis l. lucifugus (LeConte)) in Indiana and Vermont, silver-haired bat (Lasionycteris noctivagans (LeConte)) in Nebraska, and evening bat (Nycticeius humeralis (Rafinesque)) in Alabama, Florida, Kentucky, North Carolina, South Carolina, and Texas. Each of these bats is known from Michigan (Kurta 2008), and examination of their roosts may yield additional records of C. adjunctus in the state. Reeves (2001) discussed the bionomics of this species in South Carolina. 1 specimen examined. Collection date is given only as “summer”.

Cimex brevis Usinger and Ueshima, 1965.—Also a member of the pilosellus group, this species was reported from Michigan by Usinger (1966) who recorded it from “Ontario, Michigan” on 2 September; this record was included by Froeschner (1988a). Like Dood and Kurta (1982), I have been unable to find a location corresponding to Ontario in Michigan, and it seems possible that
this references the southeast corner of the state where Michigan abuts the Canadian province. Additionally, the specimen is not explicitly stated to have come from *Myotis l. lucifugus* as indicated by Dood and Kurta (1982); the host record actually referred to a specimen from Carbondale, Illinois. However, *M. l. lucifugus*, as mentioned above, is found in Michigan and probably acts as a host for *C. brevis* in the state. Usinger (1966) did not indicate a depository for the Michigan specimen. No specimens examined. Collection date is 2 September.

*Cimex lectularius* Linnaeus, 1758. (Figs. 2, 5).—The common bed bug was reported from Michigan by Townsend (1890) (as *Acanthia lectularia*). Label data from Michigan specimens indicate this species was taken in the “U of M dorms...brought in...by a coed” in 1961; it also was found in a public library in 1921. Despite the paucity of records indicated on the map (Fig. 5), which contains only entomological literature records and specimens I have examined, this species, one of the “few truly cosmopolitan insects” (Usinger 1966), undoubtedly occurs widely throughout the state. Furthermore, its presence in an area may go unnoticed for some time, and once detected, eradication is difficult and comes with no guarantee of permanence. It should come as no surprise that a vast amount of time and energy has been devoted to the study of this notorious insect, and in this regard, I have adopted Usinger’s (1966) view: “The literature on *lectularius* is so extensive and repetitious that a full treatment here would serve no useful purpose.” However, Usinger (1966) and Schaefer (2000a) provided bibliographies containing much literature relevant to *C. lectularius*. Furthermore, the State of Michigan (2011) compiled links to many useful resources, and the Michigan Department of Community Health and Michigan Bed Bug Working Group (2010) recently authored an extensive online manual concerning the public health aspects of this species. 16 specimens examined. Collection dates from 20 April to 22 November.

*Cimex pilosellus* (Horváth, 1910).—Lawrence et al. (1965) reported *C. pilosellus* taken from a *Myotis* species in Iron County, and this record came at a time when the intricate relationships of the *pilosellus* complex were becoming apparent (Usinger and Ueshima 1965). Subsequently, Dood and Kurta (1982) pointed out that *C. pilosellus* is a western species (as indicated by Usinger 1966)
and rightly suggested that the record probably referred to either *C. adjunctus* or *C. brevis*. Thus, this record and *C. pilosellus* are excluded from the cimicid fauna of Michigan.

**Genus OECIACUS Stål, 1873**

*Oeciacus vicarius* Horváth, 1912. (Figs. 2, 6).—(NEW STATE RECORD). At the inception of this study, I set out to demonstrate the presence of the swallow bug in Michigan. This species was expected to occur in Michigan as it is known from Iowa, New York, and Ontario, among other states (Froeschner 1988a). Additionally, one of the various swallow species (Aves: Hirundinidae) that acts as a host for *O. vicarius* (Usinger 1966) occurs throughout Michigan (Sibley 2000). My first sojourn, attempted after the fledging and departure of the hosts, proved wildly successful. Label data as follows: MICHIGAN: Wayne Co., New Boston, Crosswinds Marsh, ex. nest of barn swallow (*Hirundo rustica*), 5 August 2012, 42.0958°N 83.4430°W, 630 ft., D. R. Swanson, #74, det. D. R. Swanson 2012 [257 males, 175 females] (DRS, UMMZ, MSUC). The specimens examined represent a single collection, all from 4 freshly vacated nests of the barn swallow (*Hirundo rustica* L.) collected by the author from the eaves of a pavilion. Only adults were collected, but all nymphal stages were present and their numbers easily equaled or exceeded the number of adults collected. The large number of individuals and variety of life stages in this collection is noted as typical for the species by Usinger (1966). Another cimicoid, *Dufouriellus ater* (Anthocoridae: Anthocorini), was collected from multiple nests infested with *O. vicarius*. It seems likely that examining the nests of the host in other parts of the state will reveal a more extensive Michigan distribution for *O. vicarius*. Myers (1928) and Loye (1985a, b) studied the life history and ecology, and other authors (Mills and Pletsch 1941, Foster and Olkowski 1968, Smith and Eads 1978, Eads et al. 1980, Kopachena et al. 2000, Brown and Brown 2005) addressed the parasitological aspects of this species. Hayes et al. (1977) and Rush et al. (1980) discussed the species’ role as a vector of viruses. Schaefer (2000a) also discussed the negative impact of this insect on humans as a result of the hosts vacating their nests for the year. 432 specimens examined. Collection date is 5 August.
Subfamily HAEMATOSIPHONINAE Jordan and Rothschild, 1912

Genus CIMEXOPSIS List, 1925

*Cimexopsis nyctalis* List, 1925. (Figs. 2, 7).—(NEW STATE RECORD). A single collection containing several Michiganian specimens of the chimney swift bug was discovered in the alcohol range of the UMMZ. Label data as follows: MICHIGAN: Washtenaw Co., Ann Arbor, 17 July 1974, R. B. Payne, det. T. E. Moore 1978 [4 males, 5 females, 2 nymphs] (UMMZ). An additional label in the vial indicates this sample comprises “less than half of [the] ectoparasites from 4 grown chimney swifts.” This species is known from Iowa, Illinois, Indiana, Minnesota, New York, Ohio, and Pennsylvania, among other states (Froeschner 1988a), and the sole host of this species, the chimney swift (*Chaetura pelagica* L. [Aves: Apodidae]) (Usinger 1966), is found in Michigan (Sibley 2000); thus, its occurrence in Michigan was expected. It seems probable that examining the nests of the hosts elsewhere in the state might reveal this species to be much more widely distributed in Michigan. Schaefer (2000b) briefly mentioned this species as an adventitious biter on humans. 11 specimens examined. Collection date is 17 July.

Family ANTHOCORIDAE Fieber, 1837

Members of Anthocoridae, commonly known as the minute pirate bugs or flower bugs, are small, typically predaceous insects found in a variety of habitats. These bugs are easily recognized by the presence of a cuneus, a feature uncommon among the Heteroptera but shared with Miridae and Microphysidae, as well as Lasiochilidae and Lyctocoridae. Anthocorids also possess ocelli, four-segmented antennae, a three-segmented rostrum, and a hemelytral membrane lacking closed cells, although these are not unique features, and the combination of characters also is shared with Lasiochilidae and Lyctocoridae. Wing polymorphism occurs in a few members of the group, although most known species are macropterous (Lattin 1999b). Little seems to be known about the life history and development of these small insects. Many species exhibit positive nocturnal phototaxis. Several studies have focused on the chemical ecology of this group, especially the attractiveness of certain plant compounds and arthropod pheromones to various anthocorid species; Lattin (1999b) summarized these studies. As mentioned in the Introduction, the small size of these insects allows easy dispersal by humans, and a large component of the species found in the United States are non-endemic (Lattin 2007). Lattin (1999b) treated the bionomics of the Anthocoridae sensu lato. Lattin (2000) discussed the positive economic impact of Anthocoridae as predators of pestiferous species, and many of the Michigan species are mentioned in some capacity. Schaefer (2000b) discussed the negative impacts of Anthocoridae sensu lato as adventitious biters.

Reuter’s (1871, 1884) systematic treatments were among the earliest for this group, and these contributions provided an important foundation for future work on the family in North America. Carayon (1972a) also studied the systematics of the group on a larger scale. Henry (1988) provided the most recent catalog for the taxa found in America north of Mexico, and 79 species in 23 genera are found in the region. Blatchley (1926) keyed the species of the eastern United States, but its outdated status and occasional erroneous information make it difficult to use. Herring (1976) provided a key to genera for the United States taxa; this is perhaps the most useful reference for identifying material to genus. Kelton (1978) treated the Anthocoridae sensu lato of Canada; all of the species found in Michigan, except *Amphiareus obscursiceps* and *Cardiastethus luridellus*, are treated there. Additionally, the framework of the following key is synthesized from these two works, supplemented with Schuh and Slater (1995). Because of the high level of non-endemic taxa present in North America, treatments of Old World species (i.e., Poppius 1909, Péricart 1972) also may prove useful.
The removal of Lyctocoridae has produced some taxonomic upheaval in the subfamilial and tribal positions, as other tribes still in Anthocoridae previously were placed under Lyctocorinae. I have followed Schuh and Slater (1995), in simply retaining the previous tribal placements and subsuming them all within the nominate subfamily. These groups will require further study to elucidate the tribal and intergeneric relationships within the family. Additionally, Carayon (1972a) and Henry (1988) gave authority for the nominate subfamilial and tribal taxa to Reuter [1884], who undoubtedly was instrumental in the introduction of these family-group names, but this authority is reserved for the author of the family (ICZN 1999), in this case Fieber [1837].

Each of the five tribes found in the Nearctic region is represented in Michigan, and 13 species in 9 genera are found in the state:

**Key to the Anthocoridae of Michigan**

1. Third and fourth antennomeres often filiform, usually thinner than base of second antennomere, with pilosity longer than twice diameter of segments (occasionally less conspicuous in *Cardiastethus*). ........... 2

1’ Third and fourth antennomeres distinctly fusiform, equal to or thicker than base of second antennomere (except *Dufouriellus*, which has pronotum with distinct midlongitudinal groove), with pilosity usually shorter than twice diameter of segments. ........................................... 6

2 (1) Ostiolar canal and evaporatorium long and sharply bent cephalad, with apex of canal reaching or nearly reaching anterior margin of metapleuron; third and fourth antennomeres filiform, very much thinner than second and provided with erect pilosity much longer than twice diameter of segment; protibia of male strongly dilated from base to apex, apical width more than twice, sometimes thrice basal width; male with protibial fossula spongiosa large and mesotibial fossula spongiosa conspicuously smaller; female with well-developed ovipositor (*Xylocorini: Xylocoris*). ................................................................. *Xylocoris cursitans*

2’ Ostiolar canal and evaporatorium not approaching anterior margin of metapleuron, except via accessory carina or if attaining anterior margin, then gradually evenly curved (*Cardiastethini: Cardiastethus*); third and fourth antennomeres slightly thinner than second and pubescence usually not more than twice diameter of segment; protibia of male less strongly dilated from base to apex, their apical width no more than twice basal width; fossula spongiosa greatly reduced or absent; female ovipositor often vestigial. ................................................................. 3

3 (2’) Ostiolar canal curved forward but ending in middle of tergite, neither attaining margin of metasternum nor joined by carina; rostrum reaching or surpassing mesocoxae; scutellum without circular depressions; male with glandular opening on fourth or fifth sternite (occasionally vestigial) (*Scolopini*) ......................................................... *Callioides tennostethoides*

3’ Ostiolar canal curved forward or essentially straight, attaining margin of metasternum or joined by carina that attains margin; rostrum short, usually not surpassing prosternum; scutellum often with circular depression on each side of middle; male without glandular opening on fourth or fifth sternite (*Cardiastethini*). ................................................................. 4

4 (3’) Ostiolar canal more or less straight and directed posterolaterally ................................................................. *Amphiareus obscuriceps*

4’ Ostiolar canal evenly curved cephalad (*Cardiastethus*). ................. 5
5 (4') Clavus, corium, and embolium light brown, strongly contrasting reddish-brown pronotum, scutellum, and cuneus; hemelytral membrane lightly fuscous. .................. *Cardiastethus borealis*

5' Clavus and adjacent portion of corium dull, strongly contrasting otherwise shining dorsum; cuneus with vague fuscous vitta along apex adjacent to hemelytra membrane; hemelytral membrane uniformly fuscous or fumate, except narrow hyaline strip adjacent to apex of cuneus. .................. *Cardiastethus luridellus*

6 (1') Pronotum with distinct midlongitudinal groove, transverse groove absent; pronotal collar present, although often narrow. .............. 7

6' Pronotum with distinct transverse groove, midlongitudinal groove absent; pronotal collar present. ........................................... 9

7 (6') Pronotal collar narrow, poorly defined, not or only slightly transversely rugulose; tarsi with large pulvilli between claws; ostiolar canal evenly curved forward, reaching anterior margin of metapleuron as short accessory carina; pronotum frequently with distinct macrochaetae laterally; protibia of male spinulose on inner surface; fossula spongiosa absent in both sexes; eighth tergite of male asymmetrical, curved to left, paramere spiral; hemelytral membrane with two or three veins; generally smaller species, length less than 3 mm (Oriini: *Orius*) ..... 8

7' Pronotum collar generally large, distinct, sometimes transversely rugulose; tarsi devoid of pulvilli between claws; ostiolar canal short, not reaching anterior margin of metapleuron, except via long slender carina; macrochaetae of pronotum (and head) absent or indistinct; protibia of male not spinulose on inner surface; fossula spongiosa usually present on both males and females; eighth tergite of male only slightly asymmetrical, paramere falcate; hemelytral membrane with four veins, mesal one occasionally faint; generally larger species, length 3–5 mm (Anthocorini, in part) ........................................... 9

8 (7) Clavus usually mostly dark; flagellum of male paramere long and tapered, longer than cone. .............................................. *Orius diespeter*

8' Clavus mostly pale; flagellum of male paramere short and blade-like, not at all tapered or longer than cone. .................. *Orius insidiosus*

9 (7') Metacoxae widely separated; apex of metasternum truncate or rounded. ................................................................. *Elatophilus inimicus*

9' Metacoxae contiguous or nearly so; apex of metasternum triangular. ................................................................. 10

10 (9') Elytra densely punctured and heavily clothed with long pubescence; pronotal collar partially enclosed in anterior angles; head longer, anteocular portion at least equal to ocular-postocular portion; rostrum extending to middle of mesosternum; ostiolar canal not pale margined or joined to carina. .................. *Tetraphleps canadensis*

10' Elytra impunctate or extremely finely punctured, pubescence usually quite short and rather sparse; pronotal collar completely in front of anterolateral angles; head shorter, anteocular portion not as long as ocular-postocular; rostrum not or barely surpassing procoxae; ostiolar canal pale margined, straight, curved slightly forward at apex and joined to fine carina that reaches anterior margin of metapleuron (Anthocoris) ................................................................. 11

11 (10') Hemelytra appearing dull, mostly pruinose; male paramere with distinct preapical tooth. ............................................. *Anthocoris confusus*
Hemelytra entirely shining; male paramere lacking distinct preapical tooth................................................................. 12

Clavus entirely black; rostrum reaching beyond procoxae, penultimate rostral segment longer than cuneus.............. Anthocoris dimorphicus

Clavus partly pale; rostrum reaching only anterior margin of procoxae, penultimate rostral segment considerably shorter than length of cuneus .................................................. Anthocoris musculus

Subfamily ANTHOCORINAE Fieber, 1837

Tribe ANTHOCORINI Fieber, 1837

Genus ANTHOCORIS Fallén, 1814

Anthocoris confusus Reuter, 1884. (Figs. 3, 8).—This Palearctic species was reported from Michigan by Lewis et al. (2005). Anderson and Kelton (1963) first reported this species from North America, and Horton and Lewis (2009) discussed the distribution of this species in North America and provided characters for separating it from other congeners. Hill (1965) discussed the bionomics and ecology of this species in Scotland. Sands (1957) described the immature stages. Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. Hill (1957) provided a key to the North American species of Anthocoris, but Kelton’s (1978) more recent key to the Canadian species contains all those found in Michigan. 5 specimens examined. Collection date is 16 September.

Anthocoris dimorphicus Anderson and Kelton, 1963. (Figs. 3, 9).—This species was reported from Michigan by Lewis et al. (2005). Label data as follows: MICHIGAN: Huron County, Port Hope, ex Salix spp., 8 May 1965, J. & L. Donahue, det. T. Lewis 2004 [1 female] (MSUC). This label data is identical to three female specimens of Anthocoris musculus, suggesting the two species were taken syntopically. Although A. dimorphicus has both macropterous and brachypterous forms, other Anthocoris species are not known to have brachypter-
ous forms. Hill (1957) provided a key to the North American species of *Anthocoris*, but Kelton’s (1978) more recent key to the Canadian species contains all those found in Michigan. 1 specimen examined. Collection date is 8 May.

*Anthocoris musculus* (Say, 1831). (Figs. 3, 10).—Despite a comparatively large number of specimens examined, *A. musculus* was reported from Michigan only recently by Lewis et al. (2005). This species has been taken from willow (*Salix* sp.) in Huron, Isabella, Muskegon, and Newaygo counties and, as noted above, may occur syntopically with other species of *Anthocoris*. Lattin and Stanton (1992) discussed this species in association with lodgepole pine (*Pinus contorta* Doug. ex. Loud) in the western United States. Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. Hill (1957) provided a key to the North American species of *Anthocoris*, but Kelton’s (1978) more recent key to the Canadian species contains all those found in Michigan. 22 specimens examined. Collection dates from 27 March to 27 August.

**Genus DUFOURIELLUS** Kirkaldy, 1906

*Dufouriellus ater* (Dufour, 1833). (Figs. 3, 11).—This Old World species was reported from Michigan by Arbogast (1984) in a general list of New World collections housed in the NMNH; this record apparently was overlooked by Henry (1988). During my study, I examined the following corroborative material:

MICHIGAN: Clinton Co., Bath, 18 April 1964, R. Matthews collector, det. T. Lewis 2004 [1 female] (MSUC); Berrien Co., Galien, under bark, 1 April 1966, Toby Schuh collector, det. T. Lewis 2004 [2 males] (MSUC); Wayne Co., New Boston, Crosswinds Marsh, ex. nest of barn swallow (*Hirundo rustica*), 5 August 2012, 42.0958°N 83.4430°W, 630 ft., D. R. Swanson, #74, det. D. R. Swanson 2012 [3 males, 5 females, 4 nymphs] (DRS). The latter specimens were taken from four freshly vacated barn swallow (*Hirundo rustica*) nests built within the eaves of a single pavilion. These nests were heavily infested with *Oeciacus vicarius* (Cimicidae). Until now, *D. ater* was known chiefly as a predator under bark of decaying trees and in stored grains; no previous reports of nidicolous associations are known to me. It is presumed that these insects were feeding
on other tiny nest-inhabiting arthropods, rather than parasitizing the avian hosts. The extremely flattened habitus and bicolored hemelytral membrane (basal half pale translucent and apical half fuscous) are useful visual cues for recognizing this anthocorid. Péricart (1972) and Carpintero and DELLAPÉ (2008) redescribed the species. Arbogast (1984) studied the demography of this species, and Awadallah et al. (1981) studied the life history. Lattin (2000, 2007) also summarized the knowledge of this species in North America. Schaefer (2000b) briefly mentioned this species as an adventitious biter on humans. 11 specimens examined. Collection dates from 1 April to 5 August.

Genus ELATOPHILUS Reuter, 1884

Subgenus ELATOPHILUS Reuter, 1884

Elatophilus inimicus (Drake and Harris, 1926). (Fig. 12).—This species was reported from Michigan by Drake and Harris (1926) as Xenotracheliella vicaria Drake and Harris, a species described from a specimen in their personal collection and later synonymized by Kelton (1976b). This species has been taken on jack pine (Pinus banksiana Lamb.) (Kelton 1976b) and probably preys on species of Matsucoccus Cockerell (Coccoidea: Margarodidae) (Mendel et al. 1991, Lattin and Stanton 1993, Lattin 2000, Nelson et al. 2002). Kelton (1976b) reviewed the genus. The holotype of X. vicaria resides in the National Museum of Natural History, Washington, D.C. (NMNH), with the rest of Drake’s collection (Schuh and Slater 1995). No specimens examined. Collection date is 28 August.

Genus TETRAPHLEPS Fieber, 1860

Tetraphleps canadensis Provancher, 1886. (Fig. 13).—This species was reported from Michigan by Kelton (1966), although he did not note the depository of his examined material. This anthocorid has been taken on balsam fir (Abies balsamea L.), jack pine (Pinus banksiana Lamb.), white spruce (Picea glauca Moench.), and tamarack (Larix laricina Du Roi) in Canada (Kelton 1966). LATTIN and STANTON (1992) discussed this species in association with lodgepole...

**Tribe CARDIASTETHINI** Carayon, 1972

**Genus AMPHIAREUS** Distant, 1904

*Amphiareus obscuriceps* (Poppius, 1909). (Figs. 3, 14).—(*NEW STATE RECORD*). This presence of this Eurasian species in Michigan is demonstrated with the examination of several specimens from two temporally separated collecting events in each of two counties. Label data as follows: MICHIGAN: Clinton Co., E. State Road, 1 mile N. of Lansing, @ UV & white lights, 17 July 2003, G. L. Parsons coll., det. D. R. Swanson 2012 [1 female] (MSUC); idem. 22–24 July 2005 [1 female] (MSUC); Washtenaw Co., Ann Arbor, Nichols Arboretum, taken in dead leaf litter, 25 October 2009, 870 ft., 42.2806°N 83.7266°W, #214, D. R. Swanson, det. D. R. Swanson 2012 [1 male] (DRS); Washtenaw Co., Pittsfield, Pittsfield Preserve, Loop A, ex. small yellow flowers on trail edge in open field, 2 May 2012, 42.2103°N 83.7201°W, 890 ft., D. R. Swanson, #20, det. D. R. Swanson [1 male] (DRS). Henry et al. (2008) first reported this species in North America, based on specimens from fourteen eastern U.S. states, Washington, D.C., and Ontario; thus, it is not surprising to find *A. obscuriceps* in Michigan. Henry et al. (2008) also included a discussion of the dead leaf microhabitat of the species, and one of the Michigan collections made by the author corroborates this habitat affinity. Males may be easily separated from females by the presence of numerous spine-like setae on the distal three-fourths of the ventral face of the protibia. Yamada and Hirowatari (2003) and Yamada (2008) reviewed the taxonomy and keyed the genus in southern Asia. 4 specimens examined. Collection dates from 2 May to 25 October.

**Genus CARDIASTETHUS** Fieber, 1860

*Cardiastethus borealis* Kelton, 1977. (Figs. 3, 15).—(*NEW STATE RECORD*). Label data as follows: MICHIGAN: Midland Co., 22 July 1957, R. & K.
Dreisbach, det. T. Lewis 2004 [1 female] (MSUC). The profound convexity of the posterior pronotal margin is particularly distinctive in this species. In Canada, this species has been collected from Scotch pine (*Pinus sylvestris* L.), jack pine (*P. banksiana* Lamb.), and ponderosa pine (*P. ponderosa* Dougl. ex. Laws.) (Kelton 1977); the former two species occur in Michigan (Barnes and Wagner 2004). Lattin and Stanton (1992) discussed this species in association with lodgepole pine (*Pinus contorta* Dougl. ex. Loud) in the western United States. Difficulties in segregating this species from *C. luridellus* are summarized in the following account. 1 specimen examined. Collection date is 22 July.

*Cardiastethus luridellus* (Fieber, 1860). (Fig. 16).—This species was reported from Michigan by Lattin (1999a, 2007) where it was “collected from cluster of dead [black] oak leaves from fallen trees.” Lattin and LaBonte (2002) also reported taking this species in Oregon. Beyond these contemporary references, all earlier treatments merely repeated characters from the original description (Blatchley 1926, Torre-Bueno 1930) or catalogued its presence (Henry 1988). As a result, very little is known about this species, especially in comparison to species of *Cardiastethus* described in the second half of the twentieth century. Couplet 5 in the key provided reflects this trend and may be based on artificial characters. The specimen examined by Lattin resides in the Systematic Entomology Laboratory at Oregon State University (OSAC) (Lattin 1999a). No specimens examined. Collection date is 21 July.

**Tribe ORIINI Carayon, 1958**

**Genus ORIUS Wolff, 1811**

*Orius diespeter* Herring, 1966. (Figs. 3, 17).—This species was reported from Michigan by Lewis and Horton (2010), and Hussey’s (1922) record of the dark variety of *Triphleps insidiosus (=Orius tristicolor* (White, 1879)) is referred here. This anthocorid has been collected in a window pane trap in Oscoda County. Lewis and Horton (2010) clarified the confusion regarding this species and *O. tristicolor*; all records prior to that treatment should be considered suspect.
Ryerson and Stone (1979) provided a bibliography for *O. insidiosus* and *O. tristicolor*, although many of their records for the latter species actually may refer to *O. diespeter*. Lattin (2000) discussed the positive impacts of *O. tristicolor* as a predator of pestiferous arthropods, but these also may refer to *O. diespeter*. Herring (1966) discussed the subgenera of the Palearctic *Orius* species, and all of the species endemic to the Nearctic remain *incertae sedis* at the subgeneric level. Kelton (1963) provided a synopsis for the species known from north of Mexico at the time, and Herring (1966) keyed the species of the Western Hemisphere. 47 specimens examined. Collection dates from 7 June to 8 September.

*Orius insidiosus* (Say, 1831). (Figs. 3, 18).—This species, the most common "anthocoroid" in the state, was reported from Michigan by Hussey (1922) (as *Triphleps insidiosus*) as "[a]bundant on dog-fennel and other Compositae about the edges of the Warren Woods, and also taken in the dune region." This species has been collected in window pane traps in Montmorency and Oscoda counties, as well as from a Malaise trap in Monroe County. It has been taken on a beach in Berrien County and under bark in Washtenaw County. It has been collected from red clover (*Trifolium pratense* L.) in Ingham County, flowers of tickseed (*Coreopsis* sp.) in Washtenaw County, and common zinnia (*Zinnia elegans* Jacq.) in a home garden in Kent County. Ryerson and Stone (1979) provided a bibliography for *O. insidiosus* and *O. tristicolor* (but see notes above and below regarding the latter species). Isenhour and Yeargan (1981) studied the development and laboratory-rearing of *O. insidiosus*, and Kingsley and Har- rington (1981) studied the effect of temperature on development on this species. McPherson and Weber (1981) documented seasonal flight patterns of this species in North Carolina. Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. Schaefer (2000b) briefly mentioned this species as an adventitious biter on humans, and my own experiences attest this phenomenon, particularly among goldenrod (*Solidago* sp.) in the fall. Herring (1966) discussed the subgenera of the Palearctic *Orius* species, and all of the species endemic to the Nearctic remain *incertae sedis* at the subgeneric level. Kelton (1963) provided a synopsis for the species known from north of Mexico.
at the time, and Herring (1966) keyed the species of the Western Hemisphere. 220 specimens examined. Collection dates from 23 March to 1 October.

*Orius tristicolor* (White, 1879).—Until recently, this species has been considered part of the fauna of the eastern United States. Lewis and Horton (2010), however, showed that this species was confounded with *O. diespeter*; no specimens of *O. tristicolor* have been found east of Nebraska. Ryerson and Stone (1979) provided a bibliography for *O. insidiosus* and *O. tristicolor*, but, as noted above, many of their records for *O. tristicolor* actually may refer to *O. diespeter*. Therefore, this species should be excluded from the faunal list of Michigan species.

**Tribe SCOLOPINI Carayon, 1954**

**Genus CALLIODIS Reuter, 1871**

*Calliodis temnostethoides* (Reuter, 1884). (Figs. 3, 19).—This species was reported from Michigan by Lattin (1999a) from fallen leaf clusters of black oak (*Quercus velutina* Lamarck). Another specimen, with the following label, corroborates the occurrence of this species in the state: MICHIGAN: Montmorency Co., ex: window pane trap, 18 July 1966, P. C. Kennedy, det. T. Lewis 2004 [1 male] (MSUC). In Canada, this species has been taken on Scotch pine (*Pinus sylvestris* L.) and jack pine (*Pinus banksiana* Lamb.), as well as from hickory (*Carya* sp.), spruce (*Picea* sp.), and bracket fungus on paper birch (*Betula papyrifera* Marsh.) (Kelton 1978). Lattin (1999a) did not explicitly mention the depository of his two specimens, although they are presumably located in the OSAC, the depository of the specimen of *Cardiastethus luridellus* collected from the same event. McPherson and Weber (1981) documented seasonal flight patterns of this species in North Carolina. 1 specimen examined. Collection dates from 18–21 July.

**Tribe XYLOCORINI Carayon, 1972**

**Genus XYLOCORIS Dufour, 1831**

**Subgenus XYLOCORIS Dufour, 1831**

*Xylocoris cursitans* (Fallén, 1807). (Figs. 3, 20).—This introduced, now Holarctic, species was reported tentatively from Michigan by Hussey (1922); Blatchley (1926) and Henry (1988) included the record. Hussey (1922) reported individuals “[c]ommon under the bark of dead trees in the Warren Woods, particularly on fallen beeches.” Members of the genus frequently are found among stored grains, where they prey upon pestiferous arthropods. Brachyptery is common among individuals of this species, which may help distinguish it from other “anthocoroids” in Michigan. Lattin and Stanton (1992) discussed this species in association with lodgepole pine (*Pinus contorta* Dougl. ex. Loud) in the western United States. Sands (1957) described the immature stages. Lattin (2000, 2007) discussed the positive impacts of several species of *Xylocoris* as a predator of pestiferous arthropods, as well as their global distribution. Schaefer (2000b) briefly mentioned other species of *Xylocoris* as an adventitious biter on humans. Carayon (1972b) revised the subgenera. 14 specimens examined. Collection dates from 27 March to 7 September.

**Family LASIOCHILIDAE Carayon, 1972**

A long time considered part of Anthocoridae, this group was removed and elevated to family status by Schuh and Štys (1991). Lasiochilidae is the most primitive of the three “anthocoroid” families, and its members lack many of the derived characters shared by the Anthocoridae and Lyctocoridae (Schuh and
Slater 1995). Carpintero (2014) proposed returning Lasiochilidae to a subfamily under Anthocoridae, although this suprageneric treatment, as previously discussed, is not followed here. Its members, however, do share a similar natural history, and bionomic information presented for Anthocoridae usually remains relevant for Lasiochilidae. In Michigan, this is the only “anthocoroid” genus in which the ostiolar canal curves conspicuously caudad; thus, it may be easily separated from other genera found in the state. The filamentous apical segments of the antennae, while not unique, are also distinctive to the group.

In the most current catalog for the U.S. and Canada (Henry 1988), the members of Lasiochilidae were included in Anthocoridae. After Carpintero’s (2014) revision, six species in five genera are known north of Mexico, of which only one is known to occur in Michigan:

Subfamily LASIOCHILINAE Carayon, 1972

Genus DILASIA Reuter, 1871

_Dilasia fuscula_ Reuter, 1871. (Figs. 3, 21).—Carpintero (2014) included label data for a single individual from Washternau [sic] County, Michigan in his revision, despite the fact that a second Michigian specimen from the central Lower Peninsula is evident on his map. Indeed, the recency of this new record from Michigan underscores the difficulties associated with “anthocoroid” identification, and specimens of _D. fuscula_ had been collected as early as 1919 in the state. During my study, I examined the following corroborative material: MICHIGAN: Barry Co., Otis Lake, T3N R9W Sec. 31, 30 August 1966, Toby Schuh, det. T. Lewis 2004 [1 female] (MSUC); Berrien Co., E. K. Warren Preserve, Warren Woods, 5 July 1919, R. F. Hussey, det. R. F. Hussey 1950, det. D. R. Swanson 2012 [1 male] (UMMZ); Cheboygan Co., under beech bark, 18 August 1919, E. P. Butler, det. D. R. Swanson 2012 [1 female] (UMMZ); Midland Co., 4 September 1943, R. R. Dreisbach, det. D. R. Swanson 2012 [1 female] (MSUC). As indicated above, this species has been taken under the bark of species of _Populus_ in Cheboygan County. It is unsurprising for this species to be present in Michigan, as it was known from Illinois, Indiana, New York, and Ontario,
among other states and provinces (Henry 1988). After Reuter (1884) relegated his genus to subgeneric status, this species was known under the combination Lasiochilus fusculus, until Carpintero (2002, 2014) restored Dilasia to generic rank. Very little is known about the natural history of this species or its congeners, although McPherson and Weber (1981) documented seasonal flight patterns of this species in North Carolina. 4 specimens examined. Collection dates from 5 July to 4 September.

Family LYCTOCORIDAE Reuter, 1884

Following the work of Schuh and Štys (1991), this group was removed simultaneously from the Anthocoridae with the previous family and restricted only to the nominate genus, Lyctocoris Hahn. Lyctocoridae is more closely related to Anthocoridae than Lasiochilidae (Schuh and Štys 1991, Schuh and Slater 1995), and its members also share similar natural histories.

As previously mentioned, Lyctocoridae may be difficult to separate from Anthocoridae, especially by the characters given in the key, and it may be more useful to compare the taxa on a case-by-case basis. In Michigan, the species of Lyctocoris most resemble members of Cardiastethini, Scolopini, and to a lesser extent, macropterous Xylocoris, all taxa previously contained in Lyctocorinae when the families were lumped. In fact, the third and fourth antennomeres of Lyctocoris are thinner than the second, a character associated with members of those tribes. The shape of the ostiolar canal and the attendant carina reaching the anterior metapleural margin probably most resembles Amphiareus in these groups; thus, the Xylocorini and Scolopini are segregated without difficulty, and specimens of Lyctocoris taken through the Anthocoridae key will arrive at couplet 4 with relative ease. Here, however, the ostiolar canal of Lyctocoris is neither directed posterolaterally (first lead) nor curves evenly cephalad (second lead); it is directed laterally but is distinctly bent at an approximate right angle. The coloration of Amphiareus obscuriceps (contrastingly dark head and pronotum), in addition to shape of the ostiolar canal, will help separate it from the mostly dark brown Lyctocoris. Additionally, Dufouriellus is easy to eliminate based on its small size, flattened habitus, midlongitudinal pronotal sulcus, and bicolored hemelytral membrane. The gentle, even curve of the ostiolar canal in Cardiastethus contrasts the distinct bend in that of Lyctocoris. Finally, several
characteristics of *Lyctocoris* will supplement its separation from Cardiastethini: fossula spongiosa present on pro- and metatibia, ovipositor of female well developed, somewhat explanate anterolateral margins of the pronotum, and size generally greater than 3.3 mm (Kelton and Anderson 1962, Kelton 1978).

Following the taxonomy of the time, Lyctocoridae, like Lasiochilidae, was included under the Anthocoridae in the most recent catalog for the United States and Canada (Henry 1988), and eight species are known north of Mexico. Only a single species has been found in Michigan:

**Subfamily LYCTOCORINAE Reuter, 1884**

**Genus LYCTOCORIS Hahn, 1836**

**Subgenus DOLICHOMERIUM Kirkaldy, 1900**

*Lyctocoris stalii* (Reuter, 1871). (Figs. 3, 22).—(NEW STATE RECORD). The examined material of *L. stalii* indicates that it has long been established in the state and simply remained undetected. Label data as follows: MICHIGAN: Ingham Co., East Lansing, 15 April 1966, Elwin D. Evans, det. T. Lewis 2004 [1 male, 1 female] (MSUC); Jackson Co., Sharonville State Wildlife Mngmt. Area, under bark of fallen tree trunk in woods, 19 August 2012, 42.1875°N 84.1443°W, 990 ft., D. R. Swanson, #79, det. D. R. Swanson 2012 [1 male] (DRS). Although this species was not anticipated for Michigan, its occurrence in Indiana and New York make it entirely plausible (Henry 1988). Kelton (1967) reviewed the genus, in which he reported this species found under the bark of dead *Quercus*, *Betula*, and *Pinus* species, as well as occasionally from bracket fungus (*Porphyrops* sp.). McPherson and Weber (1981) documented seasonal flight patterns of this species in North Carolina. 3 specimens examined. Collection dates from 15 April to 19 August.

**NOTES ON ADDITIONAL SPECIES**

The small size, inconspicuousness, and by extension, the difficulty in identification undoubtedly underestimates the biodiversity in the state and therefore warrants the mention of species that might eventually be found in Michigan. The following list is intended to make the avid collector or student of the Heteroptera aware of the levels of potential, rather than realized, biodiversity, as additions to the Michigan fauna will surely be found in the future. Characters which might aid in recognition are included, but as these species are not included in the key, broader treatments of the “anthocoroids” of North America (i.e., Herring 1976, Kelton 1978) should be consulted.

*Acompocoris pygmaeus* (Fallén, 1807).—This Palearctic conifer-associated species is known from New Brunswick, Nova Scotia, Ontario, and Prince Edward Island (Kelton 1977, 1978; Henry 1988; Scudder and Foottit 2006). In Canada, this species is known from Scotch pine (*Pinus sylvestris* L.), eastern white pine (*P. strobus* L.), and white spruce (*Picea glauca* (Moench) A. Voss) (Kelton 1977), all of which are found in Michigan (Barnes and Wagner 2004), and should it spread westward, this anthocorid may eventually be found in the state. Sands (1957) described the immature stages. The species will key to *Tetraphleps* in couplet 10 and may be separated from that genus by the metapleural ostiole being unelavated and curved slightly cephalad, whereas in *Tetraphleps* the metapleural ostiole is elevated toward the apex and directed nearly straight toward the lateral margin of the metapleuron (Herring 1976). Furthermore, the rostrum of *A. pygmaeus* surpasses the metacoxae, whereas the rostrum of *Tetraphleps* species found or potentially present in Michigan (see below) do not surpass the mesocoxae.
Anthocoris nemoralis (Fabricius, 1794).—This species is a Palearctic endemic intentionally introduced into the western United States for control of the pear psylla (Cacopsylla pyricola (Förster)) (Sternorrhyncha: Psyllidae) (McMullen 1971), although Horton et al. (2004) suggested the population in Ontario was introduced unintentionally. It has been reported from British Columbia, California, Ontario, Oregon, and Washington (Anderson and Kelton 1963, Kelton 1978, Henry 1988, Horton et al. 2004, Lattin 2007) and is known from a wide range of plant hosts (Horton et al. 2004). Horton et al. (2000) compared mating behavior between New and Old World populations of this species. Sands (1957) described the immature stages. Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. This species will key to couplet 11 in the key provided, and it shares pruinose hemelytra with the other introduced Palearctic species, A. confusus. However, A. nemoralis has an entirely shiny embolium (and an edentate paramere), whereas A. confusus has the embolium partly pruinose (Kelton 1978).

Elatophilus brimleyi Kelton, 1977 and Elatophilus minutus Kelton, 1976.—Two more members of this conifer-associated genus may be present in Michigan. The former species was described from Prince Edward County, Ontario (Henry 1988, Lattin and Stanton 1993) and probably preys on Matsucoccus macrocicatrices Richards (Coccoidea: Margarodidae) infesting eastern white pine (P. strobus L.) (Mendel et al. 1991). This species may be separated from all species of Elatophilus that might be found in Michigan by the incrassate second antennomere. The second species, E. minutus, is known from several territories across Canada (Alberta, Manitoba, Ontario, Quebec, and Saskatchewan) (Henry 1988) and also probably feeds on species of pityophagous Matsucoccus (Mendel et al. 1991). It may be separated from both E. inimicus and E. brimleyi by the completely white embolium (Kelton 1976b). Both species also possess a shorter rostrum than E. inimicus: in E. inimicus, the rostrum extends onto or beyond the metasternum, whereas the rostrum of E. brimleyi and E. minutus only extend to the middle or slightly beyond the middle of the mesosternum. Lattin and Stanton (1993) provided notes on both species, and Lattin (2000) discussed the positive impacts of both species as predators of pestiferous arthropods. Kelton (1976b, 1978) also provided useful information concerning this genus.

Tetraphleps latipennis Van Duzee, 1921 and Tetraphleps uniformis Parshley, 1920.—The former species is known from across Canada, as well as some western states in the U.S., and the latter species is known from across Canada, as well as Colorado, Maine, New Hampshire, and New York (Henry 1988). Lattin and Stanton (1992) discussed both species in association with lodgepole pine (Pinus contorta Dougl. ex. Loud) in the western United States. These species may be separated from T. canadensis by the length of the rostrum, which reaches to the mesocoxae in T. canadensis but barely surpasses the procoxae in T. latipennis and T. uniformis (Kelton 1966). It should be noted, however, that these rostral characters prevent T. latipennis and T. uniformis from keying to T. canadensis in couplet 10. The reddish basal half of the pronotum and short pubescence of the hemelytra of T. latipennis will separate it from the unicolorous black pronotum and long, dense pubescence of the hemelytra in T. uniformis (Kelton 1978).

Orius (Heterorius) majusculus (Reuter, 1879).—Henry (2008) first reported this Palearctic species from North America, where it was collected from several localities in southern Ontario. It has been known to prey on and control various pestiferous species in crop systems; for a brief summary, see Henry (2008). Sands (1957) described the immature stages. The large size (2.5 mm or greater) alone with separate this from the other Orius species found in Michigan (2.5 mm or less), although the almost uniformly pale and densely pubescent hemelytra (occasionally darkening toward the corial apex) also will aid in separating it from O. insidiosus and O. diespeter (Henry 2008).
Macrotracheliella nigra Parshley, 1917.—This easily recognized species is known from Manitoba, New York, and Ontario, among other states and territories and may occur in Michigan (Henry 1988). Large numbers of specimens have been collected from red osier dogwood (Cornus sericea L.) in Nova Scotia (Kelton 1978). Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. It will key to couplet 8 (Oriini) in the key provided, but may be separated most easily from Orius species found in Michigan by the smooth concave curve created by the lateral margins of the head, neck, and pronotum, as well as the apically straight or rounded metasternum, the long head produced in front of the eyes, the widely separated meso- and metacoxae, and the all black coloration (Herring 1976, Kelton 1978).

Xylocoris (Xylocoris) hirtus Kelton, 1976 and Xylocoris (Proxylocoris) galactinus (Fieber, 1837).—One member of the nominate genus, X. (X.) hirtus, is known from New York, Ontario, Quebec, and Saskatchewan (Henry 1988); thus, it may occur in Michigan. It may be recognized by the long dense pubescence and the yellow-brown body color (Kelton 1976a), and both macropterous and brachypterous forms are known. A member of the subgenus Proxylocoris Carayon, 1972, X. (P.) galactinus, is known from various northeastern and midwestern states and Canadian territories (Henry 1988, Lattin 2007) and thus, probably occurs in Michigan. It may be recognized by the deeply sickle-like male paramere, the grayish-white hemelytra, and the deep canaliculi of the evaporatorium; the latter feature characterizes the subgenus (Carayon 1972b). However, X. (P.) galactinus is only known from macropterous forms. As previously mentioned, members of this genus are mostly associated with subcorticular substrates or stored grains.

Ameroscolopa flavicornis (Reuter, 1871).—This species should be found in Michigan in the future, as it is known from Alberta, British Columbia, California, Florida, Indiana, Manitoba, Mississippi, New Brunswick, Nova Scotia, Ontario, Pennsylvania, Quebec, Saskatchewan, Texas, and the Yukon Territories (Henry 1988). This species is generally found under the bark of dead pines (Kelton 1976a, 1978). Lattin and Stanton (1992) discussed this species in association with lodgepole pine (Pinus contorta Dougl. ex. Loud) in the western United States. Lattin (2000) discussed the positive impacts of this species as a predator of pestiferous arthropods. This species was formerly included in Scoloposcelis Fieber, until Carpintero & Dellapé (2012) erected the new genus Ameroscolopa for the New World species. As a member of the Scolopini, it will key to couplet 3 and is easily separated from all genera (except perhaps Xylocoris) by the greatly incrassate profemora. In Ameroscolopa, the ventral face of the profemur also is armed with distinct teeth, whereas the profemora are unarmed in Xylocoris.

Lyctocoris campestris (Fabricius, 1794).—This Holarctic species will surely be found in Michigan as it is known from Illinois, Indiana, New York, Ontario, and Wisconsin, among other states and territories (Henry 1988). I have examined 1 male, 1 female, and 7 nymphs of L. campestris in MSUC; all specimens bear a label with “Ag. Coll. Mich.”. The following additional data is present on the indicated specimens: male: “2-1-'90/77/Van Duzee”; female: “5-7-'91/Ac. 130 sp.”; all nymphs: “4-18-'91/Ac. 55 sp.”. These specimens, however, are excluded because labels of this type typically denote ownership rather than a collecting locality (O’Brien 1998). This lyctocorid is known from a wide range of habitats, including compost piles and haystacks, nests and burrows, and under bark of decaying trees (Kelton 1978). It also is found in and readily transported with stored grain (Kelton 1978, Lattin 2007). This species is easily distinguished from all other Lyctocoris in North America by the short rostrum, which only reaches to the mesocoxae; the rostrum of L. stali surpasses the mesocoxae and reaches slightly beyond the apex of the metasternum (Kelton 1967, 1978). Sands (1957) described the egg and nymph, and Parajulee and Phillips (1992) detailed rearing the species in a laboratory setting. McPherson and Weber (1981) documented seasonal flight patterns of this species in North Carolina. Lattin (2000) discussed
the positive impacts of this species as a predator of pestiferous arthropods, and Schaefer (2000b) mentioned this species as an adventitious biter in Europe.

Acknowledgments

The majority of this study was carried out during my time in the University of Michigan Museum of Zoology, Ann Arbor, Michigan. To Mark O’Brien (UMMZ), I once again owe much gratitude for his support, loan sponsorship, access to the collection, and photographic expertise, the latter proving especially helpful with my minuscule subjects. Gary Parsons (MSUC) also continues to provide gracious assistance in my visits to the collection in East Lansing, and for those ever enjoyable visits, I am most grateful. I thank Abigail Alvarez for advice on obtaining swallow nests. I owe many thanks to Tamera M. Lewis (USDA-ARS, Yakima Agricultural Research Laboratory, Wapato, Washington) for correspondence regarding identified material and anthocorid state records. To two anonymous reviewers, I also express my thanks for their careful reading and helpful comments, which greatly improved the manuscript.

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Invertebrate Communities Associated with Three Early Phases of a Prairie Restoration Project

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Abstract

While specific invertebrate groups have been studied in prairie restorations, there are few studies that look at terrestrial invertebrate assemblages. We surveyed invertebrates in three phases of plant restoration that were part of a larger restoration project. This cross-sectional study of invertebrate recovery at two, four and five years post-restoration shows there was no overall difference in invertebrate taxa richness and diversity between restoration phases. Overall abundance was greatest in the most recently restored area. Richness, diversity and abundance of six functional groups did not differ. The conclusion is that all phases are still characterized by pioneer invertebrate assemblages, and development to more diverse and richer assemblages might take more than five years in prairie restoration projects. The new and unexpected finding was that the reestablishment of invertebrate assemblages was not closely tied to vegetation restoration.

The North American prairie has virtually disappeared due to human development and industrial agriculture (Taft et al. 1987). In Illinois, only a few thousand hectares of the remnant prairie exists—less than 0.1%, restricted to historical sites and rights-of-way (Johnson and Anderson 1986, Walk and Warner 1999). Historically the focus of prairie restoration projects has been to establish the prairie flora with little consideration given to the associated fauna (Taft et al. 1987). From an ecological point of view, the traditional focus on vegetation restoration makes sense because of the strong relationship between floral and faunal diversity. The habitat heterogeneity hypothesis predicts invertebrate species richness should be greater with greater structural and vegetation complexity (Nilsson et al. 1988). There are three general layers in the above ground vegetation structure of an established prairie. These include low growing forbs and grasses, a diverse intermediate layer, and tall perennials later in the season. Together these layers provide a diverse microhabitat for invertebrates.

Restorations are planned with careful selection of seeding mixes and use of specific management techniques, including prescribed fire and mowing (Schramm 1990, Kindtcher and Tieszen 1998, Dickson and Busby 2009). However, despite a successful prairie establishment, it does not indicate functionality of the ecosystem. Invertebrates have limited dispersal capabilities. since invertebrate succession is limited, the recovery of the complete prairie community may take time, if at all—particularly when soils are disturbed at

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the restoration site. Such a prairie could be unstable or have low resilience (Peterson et al. 1998, SER 2004).

Restoration success can often be subjective. However, a more rigorous scientific approach includes monitoring the restoration and comparison of native species during and after the restoration (Bradshaw 1993, Ruiz-Jaen and Mitchell Aide 2005). Post-restoration monitoring ranges from one or two years to a minimum of 15 years for some mine reclamation projects (Craft et al. 2002). Plant and invertebrate diversity and abundance are the most common measures of ecosystem recovery (Ruiz-Jaen and Mitchell Aide 2005). Invertebrate studies of restored prairie include soil arthropods (Lussenhop 1976), invertebrate herbivory (Gibson et al. 1990), and invertebrate response to management techniques (Benson et al. 2007). Most studies focus only on one group of organisms (Ruiz-Jaen and Mitchell Aide 2005, Picaud and Petit 2007, Wallner et al. 2012).

We took an opportunity to study invertebrate abundance, richness, and diversity at a project converting land use from agriculture to prairie within a new housing development. Conservation development is an alternative form of housing construction in which homes are located around a central area protected for conservation purposes. An approximately 33 ha prairie restoration followed an initial alteration of hydrology to add meanders, riffles and pools to the headwaters of a stream. Water quality was improved and fish abundance increased by 84.6% over the pre-restoration sample (Thomas 2012). Subsequent to the stream restoration, the area was seeded in three phases with prairie forbs and grasses to mimic pre-settlement vegetative conditions (Appendix A).

We were interested in the establishment of invertebrate assemblages after the earth-moving that occurred as part of the stream hydrology portion of the project. Our hypothesis was that invertebrate abundance, richness, and diversity would follow the establishment and maturation of prairie vegetation.

**Methods and Materials**

**Field-Site Description.** The study area is located in McLean County in the state of Illinois, USA (40°27'32.97"N, 88°52'36.59"W). This is part of the Grand Prairie Natural Division (Schwegman 1973). The Grand Prairie was once a vast plain of mostly tallgrass prairie with fertile soils developed from glacial outwash, lakebed sediments, and deposited loess. The topography is generally level to rolling. McLean County has a humid continental climate with hot summers and no dry period. The general environment within a 40 km radius is agriculture. Average temperatures range from 31° C in the summer to –9° C in the winter. Precipitation averages 1018 mm per annum (Midwestern Regional Climate Center 2009; Springfield, Illinois http://mcc.sws.uiuc.edu).

Construction of the restoration (Fig.1) and subsequent seeding (Appendix A) occurred in three phases over a four-year period (2008–2012). Phase I (Fig. 2) construction of approximately 10 ha, began in 2008 with the final seeding occurring in the spring of 2009. Phase II (Fig. 3) construction of approximately 19 ha began in 2009 with final seeding occurring in the spring of 2010. Phase III (Fig. 4) of approximately 4 ha was constructed in 2011 and had a fall dormant seeding, thus 2012 represented the first growing season of this phase. The construction of each phase involved total disturbance of the site within the phase area. The topsoil layer (A and B horizon) was removed and the new ground contours established in the parent material. Replacement of the A horizon topsoil layer (to provide substrate for seeding) occurred for each phase. B horizon soils were removed from the site. The earthwork resulted in removal of all invertebrate and small mammal populations within a given phase during construction.

Initial management was a mowing regime with the mower deck in the range of 25–35 cm off the ground conducted regularly in year one, reduced in year two and if necessary a single spring mow in year three. Management during
2012 included mowing with hay left in place in Phase II and mowing with hay removed in Phase III. A prescribed burn was conducted the first week of April, 2013 and covered approximately 90% of Phase I. Maintenance ‘high mows’ were used to control the annual weed population during the growing season were not required in Phase I or 2. Phase III was still early in establishment and had three maintenance mows: late June, early August and early September. Aggressive non-native species were either treated with herbicide or removed by hand.

**Sampling.** Invertebrates were sampled by pitfall trapping, sweep netting, and sticky boards May 7–14, June 30–July 7, and September 17–24, 2013 (de Snoo 1999). These methods were chosen to sample invertebrates with different modes of locomotion and structural occupation found in a prairie landscape. In each of the three construction phases, there were three transects of six sampling sites. Transects were placed parallel to the creek in the same soil type (Sawmill silty clay loam) as determined by NRCS (http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx: accessed June 20, 2013) and not in the floodplain at 15.8 m average distance (range 7.6-24.1 m) as measured with a GPS (Garmin Oregon 450t). Sticky boards and pitfall traps were placed ~10 m apart within each transect and transects were placed 20-40 m apart. Sweep net and pitfall
Figure 2. Phase I facing northeast taken July 3, 2013.

Figure 3. Phase II facing northwest taken July 3, 2013.
samples were placed in a separate clear bag containing 70% isopropyl alcohol (Eymann 2010).

Each sample site had a pitfall and sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm x 9 cm x 76 cm LimeGlo, Forestry Suppliers). Boards were placed with ~ ½ the board above the vegetation on to a maximum height of 75 cm. Sticky boards were retrieved two days later and placed in a clear plastic cover for future identification. Pitfall traps were 150 ml plastic cups each with an aperture of 70 mm that were placed in the ground with the rim flush with the surface. Each trap was filled with a solution of water and vinegar and a few drops of soap added to break the surface tension of the water. Contents of each pitfall trap were retrieved seven days after placement.

Sweep netting consisted of two 50 m linear transects (100 sweeps each) conducted 3 m on both sides of the sampling transects in each of the three construction phases. The sweep net was 38 cm in diameter with muslin netting (Forestry Suppliers). All samples were collected on sunny days between 10:00 and 14:00 with winds below 5.5 m/s as measured on the Beaufort scale. Invertebrates were placed in a “knockdown” jar (containing chloroform soaked cotton) for several minutes.

Invertebrates larger than 2 mm were identified to lowest operational taxonomic unit (OTU) possible which in most cases were to family using taxonomic keys (Triplehorn and Johnson 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC). Ten percent of the samples were re-examined as quality control. An expert was available

Figure 4. Phase III facing northwest taken July 3, 2013.
to assist with difficult identifications. Numbers of arthropods smaller than 2
mm were estimated. The method of locomotion for each OTU was classified as
mostly flying or mostly epigeic. The OTUs were categorized by functional guild
detritivores, herbivores, flower visitors, parasites or parasitoids, predators
or omnivores (Triplehorn and Johnson 2005).

**Data Analysis.** Our design was such that we sampled invertebrates re-
peatedly within each construction phase along three transects at fixed locations
using three sampling methods. Pseudoreplication issues were avoided with mod-
el-based remedies (Millar and Anderson 2004). Our nested design regarded the
locations as random locations within transects within phases. We regarded our
sampling methods as a random selection of all possible sampling methods and our
sampling date as randomly selected from all possible dates. As a result, in most
of our analyses, we used a mixed linear model with location, date, and method
as random effect variables and phase, our treatment, as the fixed effect variable.
By applying a mixed effects model, samples can be regarded as independent
across space and time (Millar and Anderson 2004, Lazic 2010, Winter 2013). In
one instance, we tested whether invertebrate dispersal affected the abundance
of the taxa. In that case, we regarded the taxa we found as a random selection
of all possible taxa and the phases as random selection of all possible phases.

All our models were maximum random effect models, i.e., including the
effects on both the intercept and the regression coefficient (Barr et al. 2013). Our
dependent variables were abundance, taxonomic richness (TR), i.e., the number
of OTUs, and taxonomic diversity (TD), the exponentially transformed Shannon
Weaver H', making it Hill numbers of order 1 (Hill 1973, Jost 2007). Residuals
were checked in all analyses. Normality was visually assessed. Abundance was
not normally distributed; therefore, we applied a log transformation. TD was
normally distributed. TR was checked with and without log transformation. Re-
sults were not significantly different so TR was treated as normally distributed.
Capture methods were not merged: abundance and diversity were per sample.
Data are reported as average ± standard deviation.

In all analyses we applied a Likelihood-Ratio Test (LRT). We performed
the statistical analyses using R software 3.1.1 (R Development Core Team 2013).
We used Linear Mixed-effects Models, lmer () of the package lme4 (Bates and
Maechler 2010), version 1.1-7. The likelihood ratio test is a comparison of the
fit of the GLMM that contains the variable of interest with the GLMM omitting
the variable of interest. This follows a chi-square distribution (Winter 2013).

**Results**

In total there were 105 OTUs sampled from the three restoration phases
(Appendix B). There were 26,263 individuals sampled over the three month
study period. Overall abundance averaged 76.8 ± 347.5 (Table 1). Abundance
was greatest in Phase III (142.55 ± 207.7), followed by Phase II (46.62 ± 50.0)
and Phase I (41.21 ± 49.8). The influence of phase on abundance was statistically
significant (LRT: Chi Sq = 820.78; df = 22; $P = 0.0454$; n = 342). The complete

<table>
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<th>Phase</th>
<th>TR</th>
<th>TD</th>
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<tr>
<td>P1</td>
<td>8.35 ± 4.43 (2-32)</td>
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<td>P2</td>
<td>9.04 ± 4.56 (2-34)</td>
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<td>P3</td>
<td>11.23 ± 4.74 (2-26)</td>
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<td>Overall</td>
<td>9.5 ± 4.97 (2-34)</td>
<td>5.1 ± 2.2 (1.2-11.7)</td>
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</tbody>
</table>
The effect of means of locomotion of the invertebrates on abundance was tested with the complete linear model: log (Abundance+1) ~ Locomotion + (1+Locomotion|Taxa) + (1+Locomotion|Phase). Airborne invertebrates had no difference in abundance compared to epigeic (LRT: Chi Sq = 0.0547; df = 1; \( P = 0.8151 \); n = 342).

Taxonomic richness (TR) in the complete study area averaged 9.5 ± 4.97 (2-34) per sample and was highest in Phase III (Table 1). The complete linear model is TR ~ Phase + (1+Phase|Date) + (1+Phase|Location) + (1+Phase|Method). Phase of restoration was not significant (LRT: Chi Sq = 3.956; df = 2; \( P = 0.1383 \); n = 342) (Table 2).

Taxonomic diversity (TD) in the complete study area averaged 5.1 ± 2.1 (1.2-10.50) per sample and was highest in Phase II (Table 1). The complete linear model is TD ~ Phase + (1+Phase|Date) + (1+Phase|Location) + (1+Phase|Method). Phase of restoration was not significant (LRT: Chi Sq = 0.3462; df = 2; \( P = 0.8411 \); n = 342) (Table 2). Both TR and TD were greatest in July (Table 3).

The effect of phase on invertebrate abundance within functional groups was tested with an LRT (Table 4). The complete linear model is Log (abundance per functional group+1) ~ Phase + (1+Phase|Date) + (1+Phase|Location) + (1+Phase|Method). There was no significant difference in abundance within functional groups between the three phases, but in all groups, abundance was highest in Phase III (Table 5). Detritivores were most abundant (54.38 ± 87.96) followed by omnivores (18.27 ± 70.07), herbivores (12.5 ± 32.44), parasites and parasitoids (6.01 ± 10.72), predators (5.87 ± 8.65) and flower visitors (2.11 ± 5.32). Most abundant taxa were Araneae: Lycosidae (1.5%); Colembola (13.0%); Orthoptera: Acrididae (2.3%) and Gryllidae (2.8%); Hymenoptera: Miridae (4.5%) and Cicadellidae (2.4%); Coleoptera: Carabidae (2.8%); Diptera: Chironomidae (8.2%), Culicidae (5.0%), Mycetophilidae (19.7%), Syrphidae (1.5%) and Muscidae (5.2%). The remaining taxa were either < 1% or unidentified Diptera species (Appendix B).

Benchmarks for vegetation success were a percentage of the species planted to be present each year during the sampling with a percentage of species observed increasing between years one and three. The majority of species planted

**Table 2.** Likelihood ratio test (LRT) of the effect of treatment on taxonomic richness (TR) and diversity (TD). The likelihood ratio test is a comparison of the fit of the GLMM that contains the variable of interest with the GLMM omitting the variable of interest. Differences are not significant.

<table>
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<th></th>
<th>Df</th>
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<th>BIC</th>
<th>logLik</th>
<th>Chisq</th>
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<td>Complete TR model</td>
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<td>1512.6</td>
<td>-697.96</td>
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<td>0.8411</td>
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</tbody>
</table>

**Table 3.** Average taxonomic richness (TR) and diversity (TD) ± sd (range) per sample in each of the sampling periods of May 7, July 7 and September 24.

<table>
<thead>
<tr>
<th>Phase</th>
<th>TR</th>
<th>TD</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>8.71 ± 3.6 (3-17)</td>
<td>4.69 ± 2.25 (1.28-10.2)</td>
</tr>
<tr>
<td>July</td>
<td>11.16 ± 5.93 (3-34)</td>
<td>5.91 ± 2.21 (1.25-11.68)</td>
</tr>
<tr>
<td>Sept</td>
<td>8.74 ± 4.74 (2-26)</td>
<td>4.83 ± 2.04 (1.21-10.7)</td>
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</table>
in both Phase I and 2 were observed in 2012. The FQI was used to measure the vegetative success. This is a ranking score which allows a comparison of native flora from different habitats. The FQI in the control area in 2012 was 9.3 with a total of 22 species observed. The total FQI for the in 2012 for the Phase I restoration was 28.1 and Phase II was 23.4 (Kaskaskia Engineering Group 2012). A Phase III report did not measure FQI. In general, FQI scores of less than 20 have severely degraded communities. Populations scoring between 20 and 34 are degraded, but have potential for recovery (Taft et al.1997).

### Discussion

We expected invertebrate diversity to increase along with plant diversity as the restoration became established with the greatest diversity and richness in Phase I—the oldest phase—and least in Phase III—the youngest phase (Young 2000). However, we found no significant difference in richness or diversity between phases, nor a difference in abundance of functional groups. Visually, Phase I seemed to meet the expected appearance of restored prairie (Fig. 2). As a direct result of vegetation management, Phases 2 and 3 (Figs. 3, 4) had less structure and fewer blooming forbs.

Picaud and Petit (2007) suggest a progressive gain of colonizing species over several years, then a plateau and possibly decline in species number. The first species to settle in a new area are likely to be those present in nearby ecosystems. Hendrychová (2008) reported spontaneous succession of plants and

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**Table 4.** Likelihood ratio test (LRT) of the effect of treatment on taxonomic richness (TR) within functional groups. The likelihood ratio test is a comparison of the fit of the GLMM that contains the variable of interest with the GLMM omitting the variable of interest. Differences were not significant.

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<th>BIC</th>
<th>logLik</th>
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**Table 5.** Average abundance ± sd within functional groups of each of the three project phases.

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<th>PI</th>
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<th>PIII</th>
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<td>38.85 ± 45.83</td>
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<td>1.04 ± 2.65</td>
<td>2.57 ± 5.6</td>
<td>2.71 ± 6.73</td>
<td>2.11 ± 5.32</td>
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<td>10.26 ± 26.79</td>
<td>9.7 ± 23.45</td>
<td>17.53 ± 43.25</td>
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<tr>
<td>Omnivores</td>
<td>8.04 ± 13.86</td>
<td>12.32 ± 15.13</td>
<td>34.44 ± 118.28</td>
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<td>Parasitoids</td>
<td>3.62 ± 5.55</td>
<td>5.18 ± 8.45</td>
<td>9.24 ± 15.09</td>
<td>6.01 ± 10.72</td>
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<tr>
<td>Predators</td>
<td>6.27 ± 9.31</td>
<td>4.28 ± 6.18</td>
<td>7.05 ± 9.83</td>
<td>5.87 ± 8.65</td>
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</table>

---
animals from neighboring high quality natural areas to often be more species rich and diverse than planned reclamation.

Our intent was to provide an overview of the invertebrates found in an early prairie restoration. The study area had the expected populations of highly mobile generalist species. The most abundant species were the Mycetophilidae. Fungus gnats occur around damp decaying vegetation, algae, and fungi. In general they serve a beneficial role as decomposers and convert dead vegetation into nutrients for plant growth (Whiles and Charlton 2006). They also serve as pollinators and as a food source for insect predators, reptiles and birds (Whiles and Charlton 2006). Chironomidae and Culicidae are also common in wet areas and serve as an important food source in the food chain (Triplehorn and Johnson 2005).

We observed numerous Collembola in each of the three phases. Collembola are wind dispersed in addition to actively migrating and available from the surrounding landscape (Warren et al. 1987). They reproduce several times year, which allows them to increase abundance in a short time period. Cicadellidae are part of a diverse group of Auchenorrhyncha closely associated with tallgrass prairie (DeLong 1948). With close to 700 species in Illinois (DeLong 1948), this taxonomic group has been proposed as an indicator of tallgrass prairie quality (Wallner et al. 2012). They comprised 2.4% of our study. Parmenter et al. (1991) showed early colonization of beetles and grasshoppers was similar in all stages of restoration. Our study had similar high numbers of carabid beetles and grasshoppers in each of the three phases.

Muscidae were plentiful and play an important role in breaking down dead organic material (Warren et al. 1987). There were numerous other Diptera that were not identified. Mostly these did not fit into the more common families that were identified or were smaller than 2 mm and could not be thoroughly examined on the sticky boards.

Invertebrates that inhabit the area below the surface generally move from undisturbed areas at the edges. Repopulation is generally slow due to limited mobility. Ants are a common example of epigeic species that would have to repopulate from neighboring areas. Our study showed the heaviest concentration of ants to be in Phase III. It is our belief that the ants were moving from the closest undisturbed area which was cultivated agricultural fields. Areas closest to Phase I were housing with newly seeded or sodded lawns (personal observation).

We also expected to find taxa such as Olicochaeta, Gastropoda, Isopoda, Coleoptera, and Lepidoptera. There were only six earthworms in all of the pitfall traps in contrast to other studies, in which there were often more than this number at each sampling location (personal observation). The same is true for isopods. Our results are consistent with those of Hutson (1980) who measured colonization of industrial reclamation sites. Other than carabid beetles there were few beetle individuals in our samples. Beetle larvae occupy the below ground strata and seemed not to be present. Adults of several species were present and the vegetation was appropriate so complete establishment of reproduction may take more time. Since butterflies are highly dependent on specific plants for reproductive success and they must come from non-agricultural habitats, they too may have been slow to establish reproduction. Our study area was surrounded by agriculture and quite distant from remnant prairies found elsewhere in the county.

It was noted that small mammals were frequently found in identical pitfall traps in other studies in central Illinois (personal observation). Associated with these samples were numerous carrion beetles. There were only 34 carrion beetles collected during this entire study and no traps had small mammals. Small mammals, earthworms, and carrion beetles all inhabit the soil, with beetles utilizing burrows created by earthworms and small mammals.
Lack of many of these organisms at the time of this study may indicate the invertebrate assemblage of the prairie is not yet restored. At least the functional group of soil inhabiting species or life stages (i.e. earthworms and larvae of Coleoptera, Lepidoptera and Diptera) seems reduced. This restoration project seems to follow a pattern more closely related to surface mine reclamation rather than to prairie restoration. Removal of soil and reconstruction of geological contours with partial replacement of topsoil provided a novel vegetative substrate. Recovery of soils after mining often requires more than 15 years to achieve values approximating those found in reference sites (Chambers and McComb 1994, Craft et al. 2002). Soil quality has been proposed as an indicator of sustainable land management (Herrick 2000). Soil formation is an ongoing process which requires ongoing measurements and increased costs which are seldom fit within the time-frames and budgets of most restoration projects.

Our data indicate that after the extreme disturbance created by topsoil removal and subsequent replacement, establishment of an invertebrate assemblage appropriate to the new vegetation may take time (Schramm 1990) or not occur at all. Restoration phases of our study (which were two, four and five years old) are apparently all characterized by early pioneer assemblages that do not differ significantly from each other. The restoration area was farmed for decades prior to the restoration. Species adapted to agricultural row crops can be supposed to have been available to repopulate the restoration. Mobile species are expected to populate the restoration eventually but for epigeic prairie specialist arthropods, this might take a very long time, or they may not reach the restoration site at all due to colonization problems. Our results indicate that a more long-term view is necessary with some prairie restoration projects and that achieving vegetative benchmarks may be inadequate to assess complete ecological restoration.

Plants are the basis of the ecological food web and thus the succeeding trophic levels are altered along with the vegetation. While we are able to physically restore prairie flora, there may be no source of invertebrate assemblages and soil microorganisms required for sustaining the vegetation and that may not arrive on their own (Palmer et al. 1997). Future research should include long-term monitoring to learn about the time-scale that is needed for prairie invertebrate restoration projects on former agricultural lands.

Acknowledgments

We thank D. Lamb and the City of Bloomington for background information and access to the prairie. We thank W. Hinsman for assistance with GIS layers.

Literature Cited


## Appendix A

Seed lists combined from Phase I, II, and III (Prairie Engineers of Illinois, 2013).

<table>
<thead>
<tr>
<th>Scientific name</th>
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</tr>
<tr>
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Appendix B

Abundance of Operational Taxonomic Units (OTU) in each of the three phases of restoration. Guild associations are detritivores (D), flower visitors (F), herbivores (H), not feeding as adults (NA), omnivores (O), parasites and parasitoids (PA), and predators (PR).

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1 Small Lepidoptera of the superfamilies Gelechioidea, Pyraloidea, Tineoidea, Gracillarioidea, Incurvarioidea, and families Tortricidae and Pterophoridae.
Attraction of Diabrotica barberi Smith and Lawrence (Coleoptera: Chrysomelidae) to Eugenol-Baited Traps in Soybean

Louis S. Hesler

Abstract

Diabrotica barberi Smith and Lawrence (the northern corn rootworm) is a native North American leaf beetle and a major pest of corn. However, adult D. barberi forage in various habitats outside of corn fields, including soybean, roadside vegetation, and prairie. Eugenol is a common floral volatile that has been shown to increase trap catch of D. barberi within corn and prairie habitat. This paper documents the first report of increased catch of D. barberi on eugenol-baited traps in soybean fields. In two successive tests, catch of D. barberi was increased eight-fold or more by baiting traps with eugenol compared to ethanol-baited control traps. The attraction of D. barberi to eugenol-baited traps in soybean expands the potential for using such traps in determining the landscape-wide spatial and temporal dynamics of this beetle.
Materials and Methods

Two successive tests were conducted in a 1.5-ha soybean plot at the Eastern South Dakota Soil and Water Research Farm (44°19' N, 96°46' W, 500-m elevation) in 2004 as part of a larger study to evaluate the response of insect natural enemies to volatile chemicals (Hesler 2016). The first test was conducted from 13–15 August, and the second was run from 24–26 August. Soybean plants were in the early (R3) and middle (R5) stages of bean and pod formation during each respective test, but indeterminate-type soybean continues to flower during these stages (McGuire 2014). Soybean was grown with common agronomic practices, and no insecticide was applied to the plot during the growing season.

Yellow sticky traps (Pherocon AM, Trecé, Adair, OK) were used to evaluate D. barberi response to the chemicals. Each trap was folded along its midline so that two faces of adhesive surface were exposed for capturing insects. The traps were baited with 100 mg of a volatile test chemical that was applied by pipette directly to a cotton roll (3.8 cm long; Patterson, St. Paul, MN). Treatments were eugenol, methyl salicylate and ethanol (control) in the first test, and eugenol and ethanol in the second test (all chemicals obtained from Sigma-Aldrich, Milwaukee, WI). The treated cotton rolls were kept cool until deployment in the field <24 hr later.

The traps were deployed individually on 1-m tall stakes and set just above the soybean canopy (= 0.7-m ht.) between rows. Treated cotton rolls were clipped onto the top center of a non-adhesive face of individual traps. Treatments were assigned according to a randomized complete block design, with five and 10 replicates in each respective test. The traps were spaced 15 m apart within replicate blocks, and blocks were 15 or 25 m apart depending on field configuration. Two days later, traps were retrieved and taken to the laboratory to count D. barberi on them. Counts for each trap period were subjected to separate analyses of variance using a generalized linear mixed model (PROC GLIMMIX; SAS Institute 2012). Treatment means were separated by the LSMEANS feature with Tukey-Kramer adjustment (Reeve and Strom 2004).

Results

In the first test, mean catch of D. barberi varied with volatile chemical (F = 349.6; d.f. = 2, 12; P < 0.0001), with ≥8 times greater response to eugenol than to methyl salicylate or the ethanol control (Fig. 1); catch did not differ between traps baited with methyl salicylate and ethanol. Similarly, in the second test (F = 11.41; d.f. = 1, 18; P < 0.0001), mean catch (± SE) of D. barberi on eugenol-baited traps (27.0 ± 2.5) was nine times greater than that on ethanol control traps (3.1 ± 0.5).

Discussion

After corn completes anthesis, D. barberi visit soybean fields (Hill and Mayo 1980, Campbell and Meinke 2006), with soybean often a co-dominant crop and typically situated adjacent to or near corn fields throughout much of D. barberi’s geographic range (Gardiner et al. 2009). However, results of the present study represent the first report of increased catch of D. barberi on eugenol-baited traps in soybean fields. Previous studies have shown an increased trap catch of D. barberi by baiting with various dosages of eugenol up to 100 mg within or at the perimeters of corn fields (Ladd et al. 1983, Yaro et al. 1987, Lance and Elliott 1991, Hesler et al. 1994) and within prairie (Lampmann and Metcalf 1988, Metcalf et al. 1998). Collectively, the results from various studies in corn, prairie and now soybean suggest that eugenol-based sampling of D. barberi may be useful across a diverse set of habitats, and that eugenol-baited
traps could potentially be used as a tool for determining the landscape-wide spatial and temporal dynamics of *D. barberi* populations (Metcalf and Lampmann 1997). Some have suggested that eugenol or other kairomonal attractants may be useful in pest management of corn rootworm beetles in corn fields (Quiring and Timmins 1990, Metcalf 1994, Hammack 2003). However, the results here also suggest that eugenol-baited traps might be useful for monitoring and managing *D. barberi* in soybean fields and other points in the landscape before this pest returns to oviposit in corn fields. Indeed, Campbell and Meinke (2006) suggested that a more holistic approach rather than a single-field view may be appropriate when managing corn rootworms.

Various factors influence the trap catch of *D. barberi*. Notably, catch of *D. barberi* on eugenol-baited traps varies with corn plant phenology, with attractancy lower during anthesis and relatively higher during later stages (Lance and Elliott 1991, Hesler et al. 1994). The influence of plant phenology on trap catch of *D. barberi* within other habitats has not been evaluated. In the present study, corn plants in nearby fields had completed anthesis; the indeterminate-type soybean plants (McGuire 2014) in the test plot had passed peak stages of flowering, but still had flowers remaining during both trapping periods.

Trap catch of *D. barberi* may also be influenced by differential responsiveness to attractants between the sexes at various phenological stages of corn. Typically, trap catch of females on attractant-baited traps increases more than that of males relative to non-baited traps during the later developmental stages of corn (Hesler et al. 1994, Hammack and Hesler 1995, Hammack 2003). Both sexes of *D. barberi* move out of corn into non-corn habitats later in the season (Campbell and Meinke 2006), and thus either sex or both sexes of *D. barberi* could respond to eugenol in soybean. However, the sex of *D. barberi* captured on traps in soybean in this study was not determined. Given the differential responses between sexes of *D. barberi* to attractants in corn but the presence of both sexes foraging outside of corn fields, future studies should determine the responsiveness of each sex of *D. barberi* to eugenol-baited traps in soybean.
at various phenological stages. Such studies would provide a more comprehensive understanding of the chemical ecology of *D. barberi* that might aid in its management (Campbell and Meinke 2006).

**Acknowledgments**

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**Literature cited**


**Gallery Characteristics and Life History of the Ambrosia Beetle Anisandrus obesus (Coleoptera: Curculionidae: Scolytinae) in Big Tooth Aspen**

Steven Cassar, Richard Roeper*, Robert Beck, Todd Pomeroy, and Mark Bunce

**Abstract**

*Anisandrus obesus* LeConte constructs entrance holes uniformly over the surface of Big Tooth Aspen (*Populus grandidenta* Michx.) in April each year. An individual female bores a single entrance tunnel about 7 mm into the sapwood and then two lateral tunnels parallel to the surface. After symbiotic fungal growth, eggs are laid along the gallery walls by May. Three larval instars consume the beetle’s symbiotic fungus and do not expand the gallery. Pupae develop through June with progeny adults appearing by mid-July. Progeny sex ratio of approximately 6 females to 1 male was observed. Progeny adults overwinter within the parental gallery; in the spring only females emerge through the parental entrance holes to fly and attack new woody hosts.

*Anisandrus obesus* LeConte (Coleoptera: Curculionidae: Scolytinae) was originally described and named in 1868 (Zimmerman and LeConte 1868, Atkinson 2015). The beetle has also been called and described as *Anisandrus populi* by Swaine (1917) and *Xyleborus obesus* by Bright (1968), Wood (1982), and Rabaglia et al. (2006). *A. obesus* is known to infest hardwood species, including *Acer, Betula, Fagus, Quercus, Liriodendron* and *Populus*, and its distribution is known from northeastern North America ranging from New Brunswick to Ontario, and Maine to Minnesota then south to Kentucky, West Virginia, and South Carolina (Bright 1968, Wood 1982, Rabaglia et al. 2006, Atkinson 2015). In Michigan the beetle has been collected from a variety of locations (Cognato et al. 2009).

Like all members of the tribe Xyleborini only the *A. obesus* female flies to attack a new host tree. The smaller males are flightless and have inseminated the females in the parental gallery (Bright 1968, Wood 1982). Ambrosia beetles are symbiotically associated with fungus which it transmits and propagates. Larvae consumes the fungus for its growth and development. The symbiotic fungus is transmitted in an organ that was described by Chu (1968) as a mesonotal mycangium. Despite knowledge of geographic and host range, little is known about its life history and gallery habits which are described in this study.

**Materials and Methods**

*Populus grandidenta* Michx. trees infested with *A. obesus* were collected from the Alma College Ecological Tract in Montcalm County, Michigan (43°23'N, 84°53'W). The host material consisted of 27 stressed, wind broken, or dead standing trees with wilted leaves or no leaves. Meter sections of the host trees were cut and ends covered with paraffin to prevent desiccation and stored outside in
a shaded area until studied. In 1993 four standing trees exclusively attacked by *A. obesus* were studied for density of attack and distributions of attack entrance holes on the surface of the bark. Patterns of entrance holes were recorded by counting the number of attack entrance holes per square meter and by measuring the nearest adjacent entrance hole in mm with a flexible ruler. The Clark and Evans (1954) test for nearest neighbor distribution characteristics was used to analyze for uniformity of distribution of entrance holes.

Weekly samples were made by cutting approximately six-inch discs from the tree sections; galleries were exposed using wood chisels. Gallery characteristics (n = 133) were made and measured and the life stages of progeny were recorded, collected, and preserved in 70% ethanol. Larval head capsules were measured in micrometers with an ocular micrometer.

**Observations and Discussion**

**Gallery Characteristics and Brood Development.** The breast height diameter of the standing Aspens used in this study averaged 19.5 cm (S.E. = 0.7 cm, n = 27; range 15 to 30 cm). The female landed and constructed an entrance hole generally at branch scars or fissures on the bark surface. The diameter of the entrance hole of *A. obesus* was 1.6 mm. Other ambrosia beetles observed attacking these host trees were *Monarthrum mali* (Fitch), *M. fasciatum* (Say), *Xyleborinus saxesenii* (Ratzeburg) and *X. attenuatus* (Blandford), all of which had smaller diameter entrance holes. Those beetles with similarly sized diameter entrance holes could be differentiated as *Xyloterinus politus* (Say) attacks which produce a cylinder of frass about 2 cm long and *Trypodendron retusum* (LeConte) attacks which produce a cone-like mass of frass around the entrance hole. The frass of *A. obesus* formed a loose pile around the entrance hole.

From four trees collected in 1993 with only *A. obesus* attacks, the average density of entrance holes was 23.1 entrance holes per square meter and ranged from 7 to 60.7; n = 11 sections. The measurement of nearest neighbor entrance hole distance averaged 14.2 cm (S.E. = 0.8; n = 234 holes). When the Clark and Evans test was applied to these data, an R value of 1.79 (P > 0.0001) was calculated. Thus *A. obesus* was significantly spacing its entrance holes uniformly over the surface of bark of these Aspen trees. This spacing of entrance holes on the surface of the host minimizes competition between gallery systems. We never found two gallery systems fusing within the sapwood in all the tree sections we studied.

The entrance tunnel was bored through the bark and directly into the sapwood. The mean length of this entrance tunnel into the sapwood was 7.2 mm (S.E. = 0.3 mm; n = 103) and ranged from 4.0 mm to 10.0 mm. All tunnels had a diameter of 1.6 mm.

By mid-April a lateral tunnel was initiated from the end of the entrance tunnel generally following a ring of xylem in one direction. At this time fungal growth became evident in the tunnel system because the fungus had been released from the female’s mycangium. Frass pushed out the entrance hole changed from a white color to a fungal-stained, brownish shade. By mid-May, the first lateral tunnel had been fully extended to about 30.0 mm. Then the female bored a second lateral tunnel from the entrance tunnel in the opposite direction from the first lateral tunnel. Usually two lateral tunnels per gallery system were observed with a mean length of 29.8 mm (S.E. = 0.9 mm) and ranged from 3 to 86 mm (n = 195) for each lateral tunnel. Eleven of 103 mature gallery systems (10.7%) had only a single lateral tunnel, and these single laterals were longer with a mean of 46.6 mm (S.E. = ± 3.99 mm; n = 11) and ranged from 19-68 mm. The entrance tunnel or lateral tunnels did not extend into the heartwood of the tree and did not vary up or down in the long axis of the tree’s bole.
In 11 galleries a short side tunnel was observed. The side tunnel was bored at a right angle deeper into the sapwood from an existing lateral tunnel. It had a length averaging 4.7 mm (S.E. = ± 0.3). Fungal growth occurred in these short tunnels, but only twice were eggs and larvae observed.

By mid-May eggs were deposited in the first lateral tunnel where the symbiotic fungal growth had developed and the female had ceased boring activity. Then the same sequence of events occurred in the second lateral tunnel. Larvae were observed from early June to mid July in both laterals, but never in the entrance tunnel. The larvae did not enlarge the gallery system, consuming only the symbiotic fungus lining the tunnels walls; thus larvae should be considered to be strictly mycetophagous. Three larval instars were observed. The first instar had a mean head-capsule measurement of 252 um and a range from 234-263 um (n = 25 larvae); the second instar, a mean of 320 um and range of 301-330 um (n =142 larvae); and the third instar, a mean of 573 um and a range from 551-600 um (n = 92 larvae). These instars probably represent the female larvae. A minor grouping with a mean of 446 um and a range from 426-455 um (n = 20) probably represent the final instar of the smaller male larvae.

Progeny eggs, larvae and pupae were observed only in the lateral tunnels. Larvae were observed with eggs stuck to them. The single maternal female was seen moving eggs and larvae out of her way as she moved through the gallery system. The female tended to be found at the entrance to the gallery system with her head facing inwards.

Six of 62 completed galleries were found abandoned and/or lacked progeny in late July. Abundant fungal growth (perhaps a fungal contaminant), two undetermined predatory beetles, mites, and nematodes were observed in various galleries and could be responsible for these failed brood galleries.

The first pupae were generally found between late June and late July (n = 108). Ninety-one were female pupae with a length about 3.5 mm and 17 were male pupae with a length of about 1.8 mm. The sex ratio was 5.4 females to 1 male. The first progeny adults were found in early July. At this time fungal growth on the walls of the tunnels was greatly reduced or almost absent, and the walls were stained a dark brown about one centimeter into the surrounding sapwood by pigments produced by the symbiotic fungus.

By the first week of August only adults were found. From 18 galleries observed in August the average number of adult progeny was 12.5 adults per gallery and ranged from 4 to 18 adults. With 192 females to 33 males observed, we calculated a sex ratio of 5.8 females to 1 male. In winter these adults appeared relatively inactive within the parental gallery system. The progeny males apparently mate with their sibling females at some unknown time within the parental gallery. The following spring the females will emerge through the parental entrance hole for flight and attacking new woody hosts.

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Literature Cited


Sirex nigricornis (Hymenoptera: Siricidae) Oviposition Preference and Development in Relation to Host Age, and a Novel Live-Trapping System for Wood-Borers

Jessica A. Hartshorn1,2,*, Larry D. Galligan1, Ace J.W. Lynn-Miller1 and Fred M. Stephen1

Abstract

Sirex nigricornis F. (Hymenoptera: Siricidae) is a pine-inhabiting wood-wasp native to eastern North America. A non-native congener, S. noctilio F., was discovered along the southeastern shore of Lake Ontario in New York in 2004 and its current distribution now includes seven northeastern states, Ontario, and Quebec. Its discovery led to a sharp increase in research focusing on S. noctilio as well as S. nigricornis. Research on these two species, and their associates, requires efficient methods for field collection and laboratory rearing. Success of these programs relies on successful collection of, and oviposition by, live females in artificial conditions. Moisture content has been implicated as a key factor in determining host suitability for oviposition and development of Sirex, but an optimum moisture level for rearing has not been determined. We measured changes in moisture content along the length of shortleaf pine bolts over time. We exposed S. nigricornis mating pairs to ten replicates of three shortleaf pine bolts, each of which was cut and field-seasoned for 0, 15, and 30 days. Laboratory emergence was monitored and, after emergence ceased, oviposition preference was quantified among bolt ages and their associated moisture contents. Moisture content decreased over time, with the majority of moisture loss occurring at the ends of bolts. Females significantly preferred drilling in freshly cut bolts, however, successful development and emergence occurred only in 15-day-old bolts. Future studies incorporating laboratory rearing should keep bolts protected from wood-borers either outdoors, or in a humidity and temperature controlled room to mimic environmental conditions, for approximately 15 days prior to laboratory oviposition. These conditions will enable successful laboratory oviposition and development. A description of a novel live trapping method for collection of adult female S. nigricornis is provided.

Keywords: Forest entomology, monitoring, sampling & detection, wood-wasp rearing

Sirex nigricornis F. (Hymenoptera: Siricidae) is a pine-inhabiting wood-wasp native to eastern North America (Schiff et al. 2012). A congener, S. noctilio F., is native to Eurasia and North Africa but was discovered in New York in 2004 (Hoebeke et al. 2005). Since its initial discovery, S. noctilio has been found in seven states and two eastern Canadian provinces (Dodds et al. 2010), and poses a threat to the multi-billion dollar timber industry of the southeastern United States (Borchert et al. 2006). While similar in morphology and biology, these two species also have some significant differences. The most prominent difference

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is that *S. nigricornis* attacks trees that are dead or dying, while introduced *S. noctilio*, attacks stressed (e.g. drought) or overstocked but otherwise healthy standing pines. Additionally, *S. nigricornis* is commonly found in all eastern North American pine species, and has been occasionally reported from spruce, while *S. noctilio* attacks mainly Scots pine in North America, even though its recorded host range is much wider (Dodds et al. 2010, Schiff et al. 2012). However, host suitability studies have shown that *S. noctilio* can oviposit and develop in native pines of the southeastern United States (Dinkins 2011).

*Sirex noctilio* and *S. nigricornis* oviposition behaviors are very similar (Madden 1974, Lynn-Miller 2012). A female inserts her ovipositor into a pine host, presumably checking for suitability with the first drill. If the host is not suitable, the female removes her ovipositor completely and moves to another area on the same host, or to a new tree. If the host is suitable, the female partially removes her ovipositor after the first drill, changing directions at the cambium, and inserting it one to five more times into the xylem. This results in the appearance of a single drill hole on the surface of the bark and multiple tunnels beneath the cambium (Fig. 1). If a female drills multiple times, all but the last drill tunnel contain one or two eggs. The final tunnel contains a symbiotic fungus, *Amylostereum* Boidin (Russulales: Amylostereaceae) (Boros 1968), and in the case of *S. noctilio*, a phytotoxic venom (noctilisin) that conditions the tree for larval development (Bordeaux et al. 2014). While *S. nigricornis* females have venom glands, their venom has not been characterized for its toxicity. Given that a single drill hole could contain anywhere from zero to ten eggs, destructive sampling is required to measure successful oviposition and inevitably results in death of any eggs or larvae within the tree.

Recent studies have largely focused on the efficacy of monitoring methods used to collect adult *Sirex* females, which are killed upon collection, (e.g. Barnes et al. 2014, Haavik et al. 2014, Sarvary et al. 2015) and to examine interactions among *Sirex* and their associated parasites and parasitoids (e.g. Kroll et al. 2013, Morris et al. 2013, Foelker et al. 2016). However, extending these studies to further examine host preference and host defenses, improve life tables, and to quantitatively examine effects of parasites in the presence and absence of other parasites and competitors requires consistent artificial laboratory rearing.

Individual *Sirex* collected for laboratory colonies have largely been obtained using trap trees (Dodds 2007) which require a year of development before adults can be collected for oviposition. Live trapping of adult female *Sirex* provides another method for colony establishment in the laboratory and could facilitate controlled oviposition for laboratory experiments. Moisture content (MC) of host trees is considered important in oviposition success of *S. noctilio* and, presumably, *S. nigricornis* (Bedding and Akhurst 1974, Madden 1974), and significant moisture loss is known to occur quickly when trees and logs (bolts) are held in field conditions (Stokes et al. 1987). Determining the host moisture range

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**Fig. 1.** Diagram showing oviposition behavior of *Sirex* females [adapted from Coutts (1965)].
necessary for successful oviposition and development of *Sirex* in a laboratory setting, and therefore the length of time bolts are allowed to dry in the field, is a necessary component to establishing consistent rearing.

Our overall objective was to develop an effective method for establishing and rearing laboratory colonies of *S. nigricornis*. We set out to complete this objective by 1) creating an effective live trap for collecting adult female *S. nigricornis* from the field, and 2) examining oviposition preferences, and subsequent *S. nigricornis* development, in relation to bolt moisture content.

**Materials and Methods**

**Live Trap.** Live traps were developed from methods used to introduce *Sirex* and associated wood-borers into bolts in field conditions (Lynn-Miller 2012). To collect live adult female *S. nigricornis*, a 125 L (33 gallon) Rubbermaid® trashcan was attached to an APTIV Intercept™ (Portland, OR) panel trap (Figs. 2a, 3). A square hole (~15 x 15 cm) was cut into the center of the trashcan lid and the bottom funnel of the panel trap was inserted through the top of the hole. To use an alternate trap type (e.g. Lindgren funnel trap), a circular hole would be cut instead of a square hole. To allow airflow, fourteen holes (6.25 cm dia) were cut from the sides of the trashcan in three rows (6 cm, 30 cm, and 56 cm from the top), covered with Lumite® mesh, and secured with hot glue. The plastic circles which were removed to create these ventilation holes were then folded in half and riveted to both the trashcan lid and the bottom funnel of the panel trap, forming a flexible ‘L’ shaped bracket to secure both trap sections in place (Fig. 2b). Silicone caulk was used to seal any gaps where the panel trap connected to the trashcan lid that were visible from the outside. Duct tape was used to secure the panel trap to the inside of the trashcan lid. Four 8 mm holes were drilled into the bottom of the trashcan to allow water to drain. Weather stripping was placed around the outside of the trashcan rim to tighten the seal between the trashcan rim and lid. The lid was also secured to the base handles with zip ties. Using a foam paintbrush, a polytetrafluoroethylene (PTFE) suspension (Withford Corp., Frazer, PA) was applied to the inside of the bottom funnel, trashcan lid, and around the rim of the can to create a slippery surface which prevented insects from escaping. The outer surface of the trashcan was painted white to reduce heat absorption. Using metal tie wire, the panel trap was suspended from 19 mm (3/4 inch) conduit which was bent to an inverted L-shape using a conduit bender. Traps were baited with *Sirex* lure (70/30, α-/β-pinene) and Ultra High Release (UHR) ethanol (Synergy Semiochemicals, Burnaby, CA). Fresh pine bolts, branches, and foliage were placed inside each live trap to provide refuge and minimize interactions among captured insects and to serve as an additional source of host volatiles (Barnes et al. 2014) (Fig. 2c).

Very small or active insects, such as cerambycids and scolytines, were removed using a large funnel constructed from a trashcan lid and sheet of polyethylene (Fig. 2d). The ends of the polyethylene sheet were riveted together to form a cone with a basal opening that was 38 cm in diameter and a distal opening that was 8 cm in diameter. Flanges were created around the basal edge of the funnel by making cuts 2 cm deep and 10–15 cm apart. A 38 cm hole was cut in the outside of a separate trashcan lid and the funnel was attached by riveting funnel flanges to the inside of the lid. Silicone caulk was used to seal the lid to the funnel. This meant that the modified lid could be snapped onto the trashcan for collections. The entire unit, after bolts and foliage were removed, was then inverted to funnel insects into a collection bag.

**Moisture Content.** Measuring MC is a destructive process and, therefore, cannot be done on oviposition-preference bolts containing *S. nigricornis* eggs and larvae. We thus completed preliminary MC measurements on five shortleaf pine trees (7-10 cm DBH) that were felled in August 2011 at the University of Arkansas Agricultural Research Station, Fayetteville, AR. Trees were selected
Fig. 2. Live trapping system created to collect adult female *S. nigricornis* for laboratory studies: a) whole trap assembled, b) circles removed from trashcan for airflow folded and riveted to the trap and lid c) trap with lid removed showing enclosed foliage which acts as refuge and attractant, d) modified lid with funnel to collect insects.
based on shared characteristics (i.e. crown condition, DBH, height) and were cut into four bolts, each 75 cm in length to fit in rearing cages (76 cm H x 25 cm W x 30 cm D). Four groups of randomly selected treatment bolts (five bolts per treatment, 20 bolts total) were wrapped in course fiberglass window screen mesh (mesh size can vary based on species to be excluded), closed at each end with zip ties. Bolts were laid flat on their sides, elevated from the ground by a slab of oriented strand board and left under the forest canopy for 15 day-intervals (i.e. 0, 15, 30, 45 days). At the end of each treatment group interval, bolts were destructively sampled to measure wet and dry weights (g) of three-cm-thick, cross-sectional-cuts at the top, bottom, and center of each bolt. MC was calculated based on de Groot et al. (2006):

\[
MC\% = \frac{\text{Wet Weight (g)} - \text{Dry Weight (g)}}{\text{Dry Weight (g)}} \times 100
\]

**Oviposition Choice Tests.** Shortleaf pine “trap trees” were felled in the Ozark-St. Francis and Ouachita National Forests in September and October 2010 to attract dispersing *S. nigricornis* for oviposition preference studies. Trees were left intact, lying flat on the ground, and cut into 75 cm long bolts in July and August 2011, at which time they were collected, brought back to the laboratory, and placed in plastic rearing containers, which were connected to hoses that provided airflow, in an unheated storage building. Rearing containers were checked daily throughout September and October and emerged *S. nigricornis* adults were collected and sorted as mating pairs for use in oviposition choice tests.

Preliminary measurements from August-felled trees suggested that 30 and 45-day-old bolts were virtually identical in terms of MC, so the 45-day treatment was eliminated from oviposition choice experiments. Thus, trees were felled and cut into 75-cm-long bolts at 15-day intervals, beginning in mid-September (30 days prior to expected *S. nigricornis* emergence) and ending in mid-October (peak of *S. nigricornis* emergence), until there were at least 10 bolts cut on each date. While temperatures are lower in September and October compared to August, humidity is similar and all bolts were kept in the same environment (under the forest canopy) likely buffering them from temperature extremes. In mid-October,
a randomly selected *S. nigricornis* mating pair was obtained from outdoor rearing sheds and placed in each laboratory-housed rearing cage containing three randomly selected bolts representing each treatment age, totaling 10 mating pairs (cages) per treatment (i.e. choice of 0, 15, 30-day-old bolts) and 30 bolts total. Bolts were kept at a constant temperature of 29°C (Madden 1981) with a 16:8 D:L photoperiod during oviposition. Bolts in previous studies were waxed on each end to reduce moisture loss. However, this often resulted in mold and no successful *S. nigricornis* development, therefore, for MC and oviposition experiments, bolts were allowed to dry from both ends without wax. Females were allowed to oviposit until death, at which point both *S. nigricornis* were removed and were not replaced with additional mating pairs.

After oviposition by *S. nigricornis* females, bolts were maintained at a constant temperature and relative humidity (26°C, 50% RH) until progeny emerged approximately four months later (February). Adult emergence was monitored and, after no adult emergence had been detected for a week, bolts were destructively sampled (mid-April). Drill holes on the outer bark were marked before bolts were debarked to help locate oviposition tunnels in the sapwood. To account for the large variance in individual female drilling activity, the mean number of drill holes per bolt was calculated for each of the three treatments by dividing the number of drills per bolt by the total number of total drills for all three bolts. Each oviposition tunnel was individually excavated using gouges and knives from a wood carving kit. Tunnels were followed until either a developing larva was found or the tunnel stopped. Specific mortality factors were not identified.

**Data Analyses.** Data were analyzed using R 3.2.3 (R Core Team 2015). A Kruskal-Wallis rank sum test was used to evaluate significance among MC because data could not be transformed to fit a normal distribution with equal variances. Comparison of means within a significant Kruskal-Wallis test was performed using the ‘pgirmess’ package in R (Giraudoux 2014). A one-way ANOVA was used to compare mean MC of cross-sectional cuts taken from bolt ends (top and bottom) to those from the bolt centers.

Proportion of drills per treatment bolt were not normally distributed and did not have equal variances, so a Kruskal-Wallis rank sum test was used to examine significance among treatment levels. Comparison of means within a significant Kruskal-Wallis test was performed using the ‘pgirmess’ package in R (Giraudoux 2014).

**Results**

The modified trap successfully collected live adult female *S. nigricornis* \((n=156)\) as well as several families of beetles \(\text{[e.g. Buprestidae (n=88), Cerambycidae (n=7481)], Sirex parasitoids (Ibalia leucospoides Hochenwarth; Hymenoptera: Ibalidae), and other siricid species (Urocerus cressoni Norton, Tremex columba L.].}\) These numbers are comparable to previous years of siricid trapping in Arkansas (Keeler 2012, Hartshorn et al. 2015). When checked at short intervals (2–3 days), insects can easily be placed into sealed containers and stored in a cooler with ice packs or a refrigerator, to be later used in laboratory experiments. *Sirex* were often docile when captured and preferred to cling to bolts or foliage while inside the trapping containers. These were removed from the foliage by hand and placed in individual containers.

**Moisture Content.** MC was significantly different among treatments \((\chi^2 = 10.03; \text{d.f.} = 3; P = 0.0183)\), averaging \((\pm \text{SE}) 73.4 \pm 4.4, 68.3 \pm 5.5, 50.6 \pm 6.0, \text{and } 52.7 \pm 6.2 \% \text{MC for } 0, 15, 30, \text{and } 45\text{-day treatments respectively. MC was significantly different among cross-sectional position (\chi^2 = 30.993; \text{d.f.} = 2; P < 0.0001) with the center (84.8\% \pm 2.4 \text{ SE) being higher in MC compared to the bottom (52.0\% \pm 3.9 \text{ SE) and top (47.0\% \pm 4.3 \text{ SE) cuts (Table 1). Center}}\)
cross-sectional MC did not change significantly over time ($F = 0.057$; d.f. = 1; $P = 0.813$), averaging ($±$ SE) 81.1 ± 9.7, 94.4 ± 13.2, 79.4 ± 7.5, and 84.4% ± 5.7 at 0, 15, 30, and 45-days old respectively. A summary of these results can be found in Figure 4.

**Oviposition Choice Tests.** Female *S. nigricornis* drilled significantly more often in freshly cut bolts compared to both 15-day and 30-day old bolts ($\chi^2 = 10.78$; d.f. = 2; $P = 0.0046$). Proportions of drills in 0, 15, and 30-day-old bolts averaged ($±$ SE) 0.61 ± 0.09, 0.26 ± 0.09, and 0.12 ± 0.03 (Table 1). Drill hole dissections revealed no successful development of siricid larvae either in 0 or 30-day-old bolts. A total of 33 eggs was found in tunnels of 0-day-old bolts, however, all eggs were dead. Five adults total emerged from three of ten 15-day-old bolts prior to destructive sampling. Both sexes emerged from 15-day-old bolts indicating successful mating within laboratory cages. A total of four dead eggs, 32 dead larvae, four live larvae, 2 dead pupae, and a teneral adult was found in 15-day old bolts. No obvious cause of mortality was evident for the dead life stages found within bolts. Adult female *S. nigricornis* size is highly variable (Hartshorn et al. 2016a) and numbers of laboratory-emerged adults were relatively low, not allowing us to statistically analyze size differences of lab-reared and field-caught specimens.

**Discussion**

Intercept panel traps fitted with the modified trashcans successfully captured *S. nigricornis* and other Siricidae. These modified traps were also effective for capturing and holding live adult *Monochamus titillator* (F.) (Coleoptera: Cerambycidae) and other longhorned beetles in separate studies as well (Ethington 2015, Rastok 2015). While panel traps were adapted for this study, there are no significant differences in *Sirex* trap collections when using other trap types and various traps could be effectively modified in this way (Haavik et al. 2014).

Table 1. Moisture content averages ($±$ SE) by treatment level and position along the length of the bolt; average proportion of drill holes ($±$ SE) made by of female *S. nigricornis* per bolt age class in relation to bolt age and MC.

<table>
<thead>
<tr>
<th></th>
<th>0-day</th>
<th>15-day</th>
<th>30-day</th>
<th>45-day</th>
</tr>
</thead>
<tbody>
<tr>
<td>Top MC ± SE (%)</td>
<td>69 ± 9.5 (a)</td>
<td>52 ± 2.2 (ab)</td>
<td>33 ± 3.2 (b)</td>
<td>34 ± 1.5 (b)</td>
</tr>
<tr>
<td>Center MC ± SE (%)</td>
<td>81 ± 3.9 (a)</td>
<td>94 ± 5.3 (a)</td>
<td>79 ± 3.0 (a)</td>
<td>84 ± 2.3 (a)</td>
</tr>
<tr>
<td>Bottom MC ± SE (%)</td>
<td>70 ± 6.3 (a)</td>
<td>58 ± 4.1 (ab)</td>
<td>39 ± 5.2 (b)</td>
<td>40 ± 3.7 (b)</td>
</tr>
<tr>
<td>Drilling activity ± SE</td>
<td>0.61 ± 0.09 (a)</td>
<td>0.26 ± 0.09 (b)</td>
<td>0.12 ± 0.03 (c)</td>
<td>N/A</td>
</tr>
</tbody>
</table>

*letters denote significance level at $\alpha = 0.05$. 

**Fig. 4.** Average moisture content decline over time in shortleaf pine bolts declines ($\chi^2 = 10.03$; d.f. = 3; $P = 0.0183$) with most moisture loss occurring at the ends of bolts ($\chi^2 = 30.993$; d.f. = 2; $P < 0.0001$).
Trap trees in the northeastern United States are herbicidally girdled in early to mid-June to be most attractive to *S. noctilio* (Dodds 2007, Zylstra et al. 2010). These recommendations are specific to the northeastern United States and only cover girdling techniques for field rearing *Sirex* adults. *Sirex* populations can vary between years, and trap trees are not always reliable or consistent for collecting *S. nigricornis* (Hartshorn et al. 2016b). Live trapping can provide a reliable source of live adult female *S. nigricornis* for laboratory research without requiring that the collector be present to field-collect females attempting to oviposit in host material (Zieman et al. 2015). Many options exist for the use of this live trapping system alone and in combination with trap trees. Females collected in live traps can be used for laboratory studies immediately or kept in rearing cages for oviposition. Furthermore, *Sirex* may be collected from a wider geographical range without requiring a proportional increase in labor; two people can collect trapped insects from multiple locations in one day. Rearing insects in artificial situations is often necessary for entomological research, especially experiments which investigate developmental thresholds and biological control (Cohen 2001). Recent studies have called for examination of *Sirex* mortality factors such as a non-native, *S. noctilio*-associated nematode able to infest native woodwasps (Haavik et al. 2016, Zieman et al. 2015) and to associate larval morphology of *S. noctilio* parasitoids with emerging adults (Foelker et al. 2016). These studies necessitate laboratory-based rearing techniques for *Sirex*.

Shortleaf pine bolts exhibited the most moisture loss at the ends of bolts while the center retained high moisture (>79%) even after 45 days of exposure to hot field conditions, regularly reaching 35°C or higher, and extremely variable relative humidity that often ranged from 45 to 90% in a day with average RH changing just as dramatically. Insect oviposition and feeding that removes bark and destroys phloem, exposes the tree to additional moisture loss and expedites the degradation process, increasing the rate of moisture loss. Therefore, the exclusion of other wood-boring insects probably allowed bolts to maintain higher moisture content for a longer time than if additional insects had been allowed to oviposit and feed on phloem. Additional moisture loss due to the presence of other wood-borers, as well as the introduction of antagonistic fungi, should be thoroughly considered if insect exclusion is not possible.

Due to the low number of oviposition holes relative to the surface area of logs we did not statistically examine drilling activity spatially. However, drilling patterns appeared to be distributed along the entire length of bolts and were not confined to the ends of bolts, which declined significantly in MC compared to bolt centers (<40% after 45 days in the field). Thus, MC may not be the major determinant of host tree suitability for *S. nigricornis*. While field methods (i.e. tree felling) described herein are appropriate to obtain female *Sirex* for laboratory rearing, timing may be difficult as these trees must be felled a year in advance of *Sirex* emergence. Therefore, live trapping with fresh (0-day) pine twigs and foliage and introducing them to 15-day-old bolts in the laboratory is more convenient because it does not require planning a year or more in advance as is required when using trap trees.

Resin is known to be fatal to many woodboring insects, including *S. noctilio*, and presumably *S. nigricornis* (Coutts and Dolezal 1966). Resin production is also tied closely to high osmotic pressure (Gershenzon 1984) and high osmotic pressure tends to result in *S. noctilio* rejecting a tree for oviposition, possibly because of a higher potential for her eggs to be killed by resin (Madden 1974). Thus, the lack of development within 0-day-old bolts is most likely due to high resin pressure. The fact that fresh bolts had significantly more drill holes than any other age class, may indicate that host volatiles are more important than...
resin or osmotic pressure in terms of host attractiveness while resin pressure is more important in terms of survival and development. These differences may also be due to differing host responses of phytotoxic venom. Only *S. noctilio* venom has been fully characterized (Bordeaux et al. 2014) and a previous study that evaluated venom toxicity of several siricid species did not include *S. nigricornis* (Spradbery 1973). Since their venom is known to condition the tree for *Sirex* development, the results of the current study may suggest that *S. nigricornis* venom is less toxic to short leaf pine compared to that of *S. noctilio*. This may help explain why native Siricidae attack weaker trees with lower resin pressure.

The required seasoning period of pine bolts may differ depending on the objective of the study. Freshly cut bolts and foliage are recommended if the goal is simply to attract and collect live female *Sirex*. Materials can be placed in or suspended on modified traps containing no preservative which is collected daily or every other day. However, the use of freshly cut bolts in laboratory rearing will likely result in eggs being killed by resin exudation. Thus, bolts that have been held in natural conditions for 15 days, but protected from other wood-borers, are more suitable for successful rearing.

Overall, live trapping using the methods described was an effective way to collect adult female *S. nigricornis*. Additionally, we successfully reared adult *S. nigricornis* in the lab, using protected bolts that were field-seasoned for 15 days prior to *S. nigricornis* mating and oviposition. Both sexes of adults were reared from bolts, indicating successful mating in the lab. Adult *Sirex* may be obtained through use of trap trees, live trapping, laboratory rearing, or a combination of these methods.

**Acknowledgments**

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Assessing the contribution of geography and host use to genetic structure in New York populations of the parasitoid wasp, *Aphidius ervi*

Haley J. Plasman and David M. Althoff*

**Abstract**

Host-associated differentiation (HAD) has been proposed as a general mechanism for differentiation of many groups of parasitic organisms including plant-feeding insects and their natural enemies. In particular, parasitoid wasps that attack herbivorous insects have many life habits similar to other parasitic taxa, suggesting that HAD also may be important in differentiation. We tested for the population genetic signature of HAD in a parasitoid wasp, *Aphidius ervi* (Haliday), a biocontrol agent that uses many species of aphids throughout Europe, but is mainly limited to the clover and alfalfa host-races of the pea aphid *Acyrthosiphon pisum* (Harris) in North America. We assessed allelic variation from 6 microsatellite loci across 16 localities along a 200 km transect in New York State to examine genetic structure in relation to pea aphid host race use and geography. Results from AMOVA and pairwise $F_{ST}$ values indicate that there is no genetic structure in *A. ervi* due to HAD, and there was a general lack of genetic structure across the geographic range. These findings suggest that *A. ervi* localities are connected by high levels of gene flow that likely swamp out selection for specialization on the pea aphid host races that differ in defenses and resource quality as hosts for *A. ervi*. The spatiotemporal distribution of hosts as well as dispersal characteristics of parasitoids in general need to be integrated into consideration of the potential role of HAD in parasitoid taxa.

Central in the ecology of every organism are the interactions with other species (Thompson 1982, 1994). Direct and indirect interactions among species have the potential to influence both local adaptation as well as determine the distribution of a species in time and space (Sexton et al. 2009, Freeman and Mason 2015). This is especially true for parasitic organisms that are completely reliant on their host species (Price 1980, Stewart et al. 2015). Almost every aspect of life history from dispersal, mating, and development is tied to the hosts. Not surprisingly, adaptation of parasites to different host species is considered to be instrumental in determining population differentiation within species as well as patterns of speciation within parasitic lineages (Clayton et al. 2015).

The mechanism by which adaptation to different hosts can lead to population divergence and potentially speciation has been termed ‘host associated differentiation’ (HAD) (Bush 1969, Abrahamson et al. 2001, Stireman et al. 2005). HAD has been widely studied in plant-feeding insects that are in most cases parasites on their plant hosts—larvae complete their development on a single host individual (Funk et al. 2002, Abrahamson and Blair 2008) speciation, and radiation: the evolutionary biology of herbivorous insects. The premise of HAD is that host plant species have different physical and chemical defenses that

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cause their associated plant-feeding insects to adapt to distinct feeding challenges (Ehrlich and Raven 1964, Bush 1969, Funk et al. 2002, Gatehouse 2002, Poelman et al. 2008, Furstenberg-Hagg et al. 2013). As adaptations accumulate in insect sub-populations to increase feeding efficiency, these sub-populations become specialized to a particular host plant (e.g., Zangerl and Berenbaum 2003). Specialization then may be reinforced by the increased reproductive success of efficient feeders, proximity of mates on similar plants, and diverging sexual communication signals that lead to genetic structuring based on host use (Funk 2010, Mullen and Shaw 2014). HAD is viewed as a critical mechanism driving population divergence as well as the incredible species diversity within herbivorous insects (e.g., Ehrlich and Raven 1964, Bush 1969, Wood and Keese 1990, Funk 1998, Berlocher and Feder 2002, Dickey and Medina 2010, Mullen and Shaw 2014).

In recent years, HAD has also been proposed as a potential mechanism of differentiation in natural enemies of plant-feeding insects, particularly for insect parasitoids (Kankare et al. 2005, Stireman et al. 2006, Forbes et al. 2009, Feder and Forbes 2010). Parasitoids are similar to parasites in that offspring complete development in or on a single host individual. The major difference is that the developing parasitoid kills the host. Not unlike the selection pressures placed on plant-feeding insects by their plant hosts, parasitoids must adapt to a specific set of feeding challenges posed by their host insects (Vinson 1990, Kraaijeveld and Vanalphen 1994, Fellowes and Godfray 2000, Vorburger et al. 2009). Thus, there are many parallels among parasites, plant-feeding insects, and parasitoids that would suggest HAD may be an important mechanism in parasitoids as well.

Results from studies in the last 15 years offer some support that this process contributes to differentiation in parasitoids, but the extent of its importance is still unclear. There are a suite of papers demonstrating that HAD can occur within parasitoids (e.g., Pungerl 1984, Kankare et al. 2005, Antolin et al. 2006, Henry et al. 2008, Forbes et al. 2009, Kolaczan et al. 2009, Sandrock et al. 2011, Desneux et al. 2012, Schar and Vorburger 2013). For example, Schar and Vorburger (2013) demonstrate significant HAD in Lysiphlebus parasitoids attacking two syntopic thistle aphid species. They find clear evidence for genetic differentiation between parasitoids attacking different thistle aphid species. Moreover, there was also evidence for cascading HAD in the hyperparasitoids attacking the parasitoids. Conversely, several other recent papers have found host-related factors contribute little to parasitoid genetic structure, and instead suggest geography or local adaptation to abiotic factors as the primary reason for divergence (e.g., Baer et al. 2004, Althoff 2008, Lozier et al. 2009, Dickey and Medina 2011, Simonato et al. 2012, Bilodeau et al. 2013, Mitrović et al. 2013). Determining the general importance of HAD versus other factors in parasitoid population differentiation requires additional tests in many different parasitoid species.

Here, we test the potential role of HAD in parasitoid population differentiation by examining the genetic structure of the braconid parasitoid Aphidius ervi (Haliday), associated with two different host-races of pea aphid (Acyrthosiphon pisum (Harris)) in New York state. Aphidius ervi is an agriculturally important biological control agent of aphids. In 1959, a population of 1,000 individuals was introduced from France to New Jersey in an effort to control the accidentally introduced pea aphid, and periodic re-introductions over the next decade included 11,000 individuals released into aphid-infested fields in California, Arizona, Idaho, Maine, Oregon, Washington, and Delaware (Halfhill et al. 1972, Mackauer 1972, Angalet and Fuester 1977). Since its introduction, A. ervi has spread across North America primarily by its use of the pea aphid.

Adult A. ervi wasps follow plant volatiles to locate aphid hosts and mates (He et al. 2004, Sasso et al. 2007, He and Wang 2008). When the female wasp
locates an aphid on a plant, she assesses cuticular hydrocarbons found on the aphid body with her antennae (Battaglia et al. 1995, 2000). If the aphid is a suitable host, a female injects venom and a single egg using her ovipositor. *Aphidius ervi* is a koinobiont, so the wasp larva develops internally for several days while the aphid is still alive and feeding. After 5-6 days, the wasp induces behavioral changes in the aphid to cause it to climb to the top of the plant and the upper center of a leaf, where it perishes. The aphid's body is then transformed into a puparium, or “mummy” spun from the wasp larva’s silk and adhered to the plant through a small ventral hole. The wasp will continue to develop within the mummy for about two weeks, at which point the fully formed adult wasp will chew a dorsal escape hole and eclose (Sequeira and Mackauer 1992, Malina et al. 2010). Successful reproduction by the wasp involves several stages on which selection can act to generate HAD: locating an aphid host, acceptance of the host, oviposition, and larval development (Godfray 1994). Aphids are soft bodied, and thus highly vulnerable to wasp attack; however, they have evolved defenses against attack. Behavioral defenses such as kicking with the hind limbs or simply falling off the plant can prevent oviposition (Dixon 1998). Furthermore, aphid populations have integrated a bacterial symbiont, *Hamiltonella defensa*, which acts as a post-oviposition defense by halting the development of the wasp at the egg stage (Oliver et al. 2003). Thus, as with many parasitoid species, there are multiple avenues by which selection via hosts could potentially drive host-associated differentiation.

Though *A. ervi* has been documented to use 10 aphid hosts (Stary 1970), the most widely used host in North America is the pea aphid (*Ac. pisum*). *Acyrrthosiphon pisum* is divided into at least seven host-races based on plant host species used, two of which occur on alfalfa (*Medicago sativa* L.) and clover (*Trifolium repens* L. and *T. pratense* L.) (Peccoud et al. 2009). The alfalfa and clover host-races of *Ac. pisum* exhibit HAD (Bilodeau et al. 2013) and perform extremely poorly when reciprocally transplanted to each other’s host (Via 1991, Via 1999, Via et al. 2000). Host resource quality and the magnitude and prevalence of aphid defenses differ between the alfalfa and clover host-races, suggesting selection pressures on *A. ervi* to specialize on either host (Henter and Via 1995, Hufbauer and Via 1999). Moreover, *A. ervi* has significant genetic variation and is capable of adapting to these aphid defenses in the lab (Henter 1995, Dion et al. 2011). If strong enough, these divergent selection pressures could lead to genetic structure among populations using different pea aphid host races.

Previous research on the genetic structure of *A. ervi* at the global scale found significant population genetic structure between European and North American populations, indicating an important role of geography in population structure (Hufbauer et al. 2004). Because all the parasitoids were collected from alfalfa pea aphids, what remains to be tested is if there is HAD between host-races of pea aphids. Bilodeau et al. (2013) made the first comparison and showed no host-associated genetic structure at a very local scale. In the present study, we expand on previous analyses of population structure based on host use of pea aphid host races. Specifically, we address the following questions: i) What is the genetic structure of *A. ervi* populations along an 200 km transect in New York, and ii) what are the relative roles of host use and geography in determining genetic structure? Answering these questions will bridge the gap between local and global population studies and provide further information on the population structure of this important biological control agent at intermediate geographic scales.

**Materials and Methods**

**Sampling Design.** From May-July 2015, we surveyed a 200 km longitudinal transect in New York State spanning from Pompey, NY near the center of the state to Alexander, NY near the western border (Fig. 1). At all localities
alfalfa was the dominant plant species in agricultural fields and clover was interspersed within the fields or was found in the surrounding edges of the fields. Mummies were collected haphazardly with at least a distance of 2 meters between mummy collections. Mummies collected from each host species were assumed to be from the aphid host race based on the plant from which they were collected. Because aphids feed for several days before succumbing to the parasitoid, finding a mummy on a non-host is unlikely. We surveyed 10 agricultural fields, six of which also had clover present, and collected a total of 356 aphid mummies containing female *A. ervi* larvae (Table 1). 114 of these mummies were from the clover host race of *Ac. pisum*.

After removal from a leaf, each mummy was placed into a gelatin capsule (Capsuline Clear Gelatin Capsules, Size #2), and stored at room temperature until eclosion. We monitored capsules for eclosed wasps for three weeks after collection. Upon emergence, females were immediately placed into a -10°C freezer, and then identified to species using the dichotomous key by Pike et al. (1997). After confirmation of species identity, *A. ervi* specimens were stored in a -80°C freezer until genetic analysis. Only female wasps were used in the analysis of heterozygosity because hymenopteran males are haploid. The use of F-statistics is predicated on the assumption that individuals are diploids.

**Microsatellite Analyses.** DNA from individual female wasps was extracted using a method modified from Bender et al. (1983) (courtesy of Dr. Daniel Funk, Vanderbilt University). We used the entire individual for each extraction.

Table 1: Site locations for *Aphidius ervi* in central New York. Site numbers correspond to those in Figure 1.

<table>
<thead>
<tr>
<th>Site #</th>
<th>Site Locations</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Number of <em>A. ervi</em> mummies from alfalfa</th>
<th>Number of <em>A. ervi</em> mummies from clover</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Jamesville</td>
<td>42°58'38.42&quot;N</td>
<td>76°3'52.15&quot;W</td>
<td>23</td>
<td>13</td>
</tr>
<tr>
<td>2</td>
<td>Lafayette</td>
<td>42°53'39.23&quot;N</td>
<td>76°7'13.34&quot;W</td>
<td>23</td>
<td>47</td>
</tr>
<tr>
<td>3</td>
<td>Otisco Lake</td>
<td>42°54'43.35&quot;N</td>
<td>76°13'45.99&quot;W</td>
<td>21</td>
<td>8</td>
</tr>
<tr>
<td>4</td>
<td>Skaneateles</td>
<td>42°56'8.5&quot;N</td>
<td>76°21'57.65&quot;W</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>Auburn</td>
<td>42°55'31.9&quot;N</td>
<td>77°38'1.20&quot;W</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>Geneva</td>
<td>42°51'40.50&quot;N</td>
<td>77°4'38.68&quot;W</td>
<td>24</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>Canandaigua</td>
<td>42°52'50.27&quot;N</td>
<td>77°19'16.32&quot;W</td>
<td>22</td>
<td>2</td>
</tr>
<tr>
<td>8</td>
<td>Lima</td>
<td>42°54'7.25&quot;N</td>
<td>77°37'39.21&quot;W</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>Bethany</td>
<td>42°54'15.08&quot;N</td>
<td>78°6'31.17&quot;W</td>
<td>23</td>
<td>38</td>
</tr>
<tr>
<td>10</td>
<td>Alexander</td>
<td>42°54'10.68&quot;N</td>
<td>78°17'38.31&quot;W</td>
<td>22</td>
<td>6</td>
</tr>
</tbody>
</table>
A combination of seven previously developed microsatellite loci from both *A. ervi* (Hufbauer et al. 2001) and *A. transcaspicus* Telenga (Lozier et al. 2006) were used to assess the genetic structure of *A. ervi* (Table 2). The forward PCR primer for each microsatellite locus was labeled with a fluorescent dye (either 6-FAM, VIC, NED, PET; Life Technologies, Carlsbad, CA, USA). One µL of template DNA was combined with 4.01 µL of PCR water, 2 µL of 5x PCR buffer, 1 µL of 1 µM BSA, 1 µL of 25 mM MgCl₂, 0.21 µL of 10mM dNTPs, 0.35 µL each of 10 µM forward and reverse primers and 0.08 µL (4 units) of Promega GoTaq to yield a 10 µL reaction volume. Reactions were cycled in a BioRad PTC 100 Thermal cycler programmed for 95°C for 1 min, 35 cycles of 95°C for 30 s, the optimized annealing temperature for 1 min, 72°C for 1 min, followed by 72°C for 10 min. A separate reaction was performed for each individual at each locus.

The resulting PCR products tagged with different fluorophores were combined with either three or four differently labeled PCR products in a single well with 1µL LIZ-500 bp DNA size standard and 7 µL of deionized water. Because the fluorophores differ in intensity, we used the following ratios when combining products labeled with different fluorophores--1 µL for FAM labeled, 1 µL for VIC labeled, 3 µL for PET labeled, 3 µL for NED. Multiplexed samples were analyzed by the Cornell University Biotechnology Resource Center (Ithaca, NY, USA) on an ABI 3730xl capillary electrophoresis DNA Analyzer. We scored all alleles manually in GENEMARKER 2.4.2 (SoftGenetics, State College, PA, USA).

We used FSTAT (Goudet 1995) to test whether each of the microsatellite loci were in Hardy-Weinberg equilibrium and to test for linkage disequilibrium among the loci. MICROCHECKER (Van Oosterhout et al. 2004) was used to test for null alleles, and none were found. We analyzed genetic structure in several ways. First, AMOVA (Excoffier et al. 1992) was used to test for genetic structure based on pea aphid host race. Second, pairwise FST values were generated for all site comparisons to examine levels of genetic structure among sites. Finally, an isolation by distance analysis was used to examine the role of geographic distance in FST estimates. Analyses of genetic structure were conducted in GenAlEx 6.0 (Peakall and Smouse 2012).

**Results**

We collected a total of 1332 parasitoid mummies—1072 from alfalfa plants and 260 from clover plants. From these mummies, we reared 897 *A. ervi*, 28 *A. rhopalosiphi* De Stefani-Perez, and 407 hyperparasitoids. Approximately 66% of *A. ervi* mummies produced female wasps (alfalfa- 474 females out of 723 mummies, clover—119 females out of 174 mummies). Of the 395 *A. ervi* females that were collected and suitable for DNA extraction, we were able to genotype 348 (DNA extractions failed for eight individuals and 39 individuals failed to amplify during PCR). The surveyed microsatellite loci provided adequate allelic variation to survey population structure in *A. ervi* (Table 2). A total of 57 alleles were observed at six loci that had been genotyped in 348 individuals from 10 sites across the 200 km transect. The six microsatellite markers ranged from 4-23 alleles per locus, with an average of 2.7–13 different alleles per population (Table 2). Locus Ae4 had the highest number of alleles, much more so than the other five. An additional locus (At14) was genotyped, but was removed from analysis due to fixation within all individuals. Tests for linkage disequilibrium between all pairwise loci combinations were not significant, as were tests for null alleles. Tests for divergence from Hardy-Weinberg equilibrium among alleles were also not significant.

Results from AMOVA (Table 3) in which wasps were grouped by pea aphid host race indicated that host use did not contribute to population structure: there was no genetic variance attributed to aphid host races. Furthermore, there was little evidence of population structure among geographic locations. Only 1% of the observed variance was partitioned among populations. Due to lack
of evidence for the influence of aphid host race use on population structure, we combined individuals that were collected from sympatric aphid host races at each site into a single geographic location for the remaining analyses, resulting in 10 non-host specific populations.

The overall $F_{ST}$ among all 10 non-host specific localities was 0.011**, indicating significant but quite low genetic structuring. Pairwise $F_{ST}$ values between some localities were significant, but values ranged from 0.00 to 0.024 again indicating a very low level of genetic differentiation among *A. ervi* localities (Table 4). The pairwise $F_{ST}$ values were used in a Mantel test to examine the relationship between population structure and geographic distance (Fig. 2). A slightly negative but non-significant correlation ($r = -0.03; P = 0.45$) was observed between genetic ($F_{ST}$) and geographic distance (km), indicating that geography does not contribute to the genetic structure of *A. ervi* at this scale. Thus, in New York, there does not appear to be any significant population structure among *A. ervi* sampled along a 200km transect.

### Discussion

HAD has been proposed as a major mechanism of differentiation for many diverse taxa (Janz et al. 2006, Hoberg and Brooks 2008, Hardy and Otto 2014, Clayton et al. 2015). In plant-feeding insects, there are myriad examples of host adaptation resulting in genetic differentiation and in many cases, speciation (Funk et al. 2002, Funk 2010). Indeed, herbivorous insects have been shown to undergo greater rates of speciation than their predatory or saprophagic counterparts (Mitter et al. 1988), and this phenomenon has been attributed to adaptation to different host plant defenses against herbivory that result in subsequent specialization. What has been less frequently tested is whether the large diversification of plant feeding insects has led to comparable adaptation and specialization in their parasitic natural enemies (Abrahamson and Blair

### Table 2. Allelic diversity for the six microsatellite markers used to assess population structure of *Aphidius ervi* in central New York (bp is base pairs).

<table>
<thead>
<tr>
<th>Locus name</th>
<th>Number of alleles</th>
<th>Range of allele sizes (bp)</th>
<th>Average number of alleles per population</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ae4</td>
<td>23</td>
<td>216–306</td>
<td>13</td>
</tr>
<tr>
<td>Ae47</td>
<td>6</td>
<td>290–293</td>
<td>4.6</td>
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<tr>
<td>Ae51</td>
<td>8</td>
<td>289–310</td>
<td>5.2</td>
</tr>
<tr>
<td>Ae74</td>
<td>5</td>
<td>123–138</td>
<td>2.7</td>
</tr>
<tr>
<td>Ae78</td>
<td>4</td>
<td>122–131</td>
<td>3.5</td>
</tr>
<tr>
<td>At17</td>
<td>8</td>
<td>165–179</td>
<td>5.3</td>
</tr>
</tbody>
</table>

### Table 3. Results of AMOVA to test for population subdivision of *Aphidius ervi* based on pea aphid host race (**= P < 0.01). 

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Estimated variance</th>
<th>Percent variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Among aphid host races</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Among populations within races</td>
<td>14</td>
<td>0.026**</td>
<td>1</td>
</tr>
<tr>
<td>Within populations</td>
<td>340</td>
<td>1.89**</td>
<td>99</td>
</tr>
</tbody>
</table>

| Overall $F_{ST} = 0.011**     |
Table 4: Pairwise $F_{ST}$ values for the 10 sampled geographic locations of *Aphidius ervi* in central New York. (Bolded values indicate statistically significant values at $P < 0.05$).

<table>
<thead>
<tr>
<th></th>
<th>Alexander</th>
<th>Auburn</th>
<th>Bethany</th>
<th>Canandaigua</th>
<th>Geneva</th>
<th>Jamesville</th>
<th>LaFayette</th>
<th>Lima</th>
<th>Ostico Lake</th>
<th>Skaneateles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alexander</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Auburn</td>
<td>0.004</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bethany</td>
<td><strong>0.003</strong></td>
<td>0.019</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Canandaigua</td>
<td>0.016</td>
<td>0.016</td>
<td>0.010</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Geneva</td>
<td><strong>0.024</strong></td>
<td>0.024</td>
<td>0.011</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jamesville</td>
<td>0.006</td>
<td>0.017</td>
<td>0.000</td>
<td>0.006</td>
<td>0.011</td>
<td>—</td>
<td></td>
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<tr>
<td>LaFayette</td>
<td>0.015</td>
<td>0.021</td>
<td>0.010</td>
<td>0.000</td>
<td>0.000</td>
<td>0.009</td>
<td></td>
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In essence, is HAD a process that is applicable to natural enemies, particularly parasitoids of phytophagous insects? Parasitoids exhibit some of the same characteristics as other parasitic taxa like plant-feeding insects. Females search for and lay eggs on or within hosts and the developing larvae feed on a single host individual to complete development. The major difference is that parasitoids kill the host individual in almost all cases (Godfray 1994). Parasitoids employ two different development strategies, idiobiont and koinobiont that may also influence the likelihood of HAD (Askew and Shaw 1986). Idiobiont parasitoids stop host development and usually feed externally on the host whereas koinobiont parasitoids allow hosts to continue to develop and usually feed internally (Godfray 1994). This difference sets up the conditions for which koinobiont parasitoid taxa such as A. ervi may specialize on a particular host species or set of host species (Althoff 2003). Several studies have supported HAD in parasitoids through genetic, morphological and life history trait evidence. For example, Stireman et al. (2006) found that two species of koinobiont parasitoids, Copidosoma gelechiae Howard and Platygaster variabilis Fouts using host races of two goldenrod gall-making insect species each showed degrees of genetic differentiation based on gall-maker host-races. For P. variabilis parasitoid populations, genetic differences among populations using host races of the gall midge Rhopalomyia solidaginis Loew were large enough to suggest host-associated cryptic sibling species. In contrast, others have found no evidence (e.g. Cronin and Abrahamson 2001, Baer et al. 2004, Althoff 2008, Dickey and Medina 2011). Given the limited number of studies testing the role of HAD in parasitoids, further studies are needed in order to determine whether HAD is a ubiquitous process for parasitoids and whether HAD has influenced large scale patterns of speciation.

We examined the potential role of HAD in population differentiation of the biocontrol agent A. ervi. Though it is widely considered a generalist that uses many aphid species (Stary 1970), it is a putative candidate for HAD based on evidence from a number of studies. Henter and Via (1995) and Henter 1995 documented genetic variation in pea aphid clones to vulnerability to parasitoid attack and genetic variation among A. ervi families in the ability to attack pea aphids. This is partly due to immune defenses in the pea aphids as well as bacterial symbionts (Oliver et al. 2003). Hufbauer (2001, 2002) further demonstrated that the pea aphid host races on clover an alfalfa differed in susceptibility to attack by A. ervi. Others studies have confirmed the propensity for A. ervi to exhibit fitness costs when using alternate host species (i.e. hosts in which they did not develop) and selection experiments demonstrate that A. ervi can adapt to different host species under laboratory conditions (Daza-Bustamante et al. 2003, Henry et al. 2010, Zepeda-Paulo et al. 2013).

Contrary to the evidence of the ability of A. ervi to specialize to different hosts in laboratory experiments, the survey of population genetic variation of A. ervi in central New York state suggests that adaptation to different host races of pea aphids does not appear to be influencing long term genetic structure. Results from the AMOVA when populations were grouped by pea aphid host race showed no evidence for population structure. Furthermore, there was no evidence for the influence of geographic distance on genetic structure. An analysis of pairwise $F_{st}$ scores among sites were all quite low, and there was no correlation between genetic and geographic distance (Fig. 2). The lack of genetic structure in A. ervi in central New York is similar to other surveys of population structure for this species at varying geographic scales. Bilodeau et al. (2013) found that geographically proximal populations A. ervi using different host races of aphids were not differentiated, although the host-races of aphid showed clear population structure based on host plant species. Zepeda-Paulo et al. (2013) also examined the effects of intra- and inter-species host use on the population structure of introduced A. ervi across Chile. They detected no
evidence for HAD at the host-race level or the host-species level, nor, did they find any evidence for geographic influence on population structure.

The population genetic results for *A. ervi* from the current and previous studies suggest that the dynamic between local adaptation and gene flow that can generate HAD may be heavily biased by high rates of gene flow among populations. Selection at the host level due to differences in aphid defense mechanisms, aphid symbiont communities, aphid host quality, and population origin of *A. ervi* is very likely (Hufbauer and Via 1999), and it has been suggested that successful biocontrol agents are those that evolve to become locally adapted (Debach and Rosen 1991, Hopper et al. 1993). For this pattern of local adaptation to occur, however, gene flow must be limited enough so that it does not counter selection within populations that use different hosts. Selection driven by differences in host use among populations of *A. ervi* could be occurring, but is likely undone due to high gene flow. Gene flow often correlates with mobility, and *A. ervi* is a highly mobile parasitoid wasp, capable of migrating across agricultural landscapes to find hosts or mates. In the last 40-50 years, *A. ervi* has spread across all of North America. Populations are essentially contiguous throughout North America, making it almost impossible to define or maintain distinct population boundaries.

Another possible explanation for the absence of *A. ervi* genetic structure in New York is that small populations sizes used in the initial introduction to North America may have caused a bottle neck in the population, resulting in a lack of sufficient genetic variation to facilitate adaptation to host populations (Hufbauer et al. 2004). The initial introduction was only of 1,000 individuals, and it is unknown from where in France these individuals where collected, i.e. if they represent a diverse group from multiple localities or if they were all from the same field (Hufbauer et al. 2004) However, subsequent introductions over the next several decades from several other source countries make this explanation less likely. Additionally, selection experiments in laboratory stocks have shown that adaptations to a new host species can occur in as little as three to four generations (Henry et al. 2008). Thus, it seems unlikely that lack of genetic variation is a strong impediment to local adaptation by *A. ervi* populations.
The assumption of HAD is that differences in host use among populations sets up the condition under which local specialization will be favored. This will in part be determined by the stability of host populations in both space and time (Loxdale et al. 2011, Poisot et al. 2011). For A. ervi, however, there may be large variability in host availability. For example, aphid host races and aphid species are available in different agricultural fields and at different times throughout the growing season (Gagic et al. 2012, Raymond et al. 2015). Additionally, agricultural areas are typically variable patchwork landscapes with many fields of different crops adjacent to each other and to natural and developed areas, resulting in discrete habitat types (Bianchi et al. 2006). This variability in host availability coupled with how quickly A. ervi colonized and migrated across North America suggests that there are many constraints on the evolution of specialization for this parasitoid, and there is likely selection for being a generalist. Thus, even though some species of aphid host are of higher resource quality and less defended, we did not detect HAD in A. ervi.

Acknowledgments. The authors thank Thomas Anneberg, Laura Porturas, Kari Segraves, and Shengpei Wang for comments on the manuscript. Alice Fox provided much support and expertise for the microsatellite analyses. Jesse Lehnert and Charlie LaNoue helped with the field collections and Nick Palladino kindly provided access to his farms. Partial funding for this work was provided by National Science Foundation grant DEB-1556568.

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Adults of the Eurasian sawfly, *Xiphydria prolongata* (Geoffroy) (Hymenoptera: Xiphydriidae), were reared from *Salix nigra* Marshall in Connecticut and from *Salix alba* L. in New York. These are the first reported hosts for North America, and the collecting localities represent the first state records.

The Eurasian xiphydriid, *Xiphydria prolongata* (Geoffroy), was first discovered in North America in Michigan in 1980 (Smith 1983). Subsequently, it was found in New Jersey (Smith 1983), Oregon (Mudge et al. 2001), and Washington (Looney et al. 2016). It apparently is the lone exotic species among the 10 species of *Xiphydria* Latreille known from North America (Smith 1976, 1983; Smith and Schiff 2001). Based on recorded hosts in its native range (summarized in Smith 1978, 1983), *X. prolongata* has a relatively wide host range compared to native species in North America (Deyrup 1984, Smith 1976, Smith and Schiff 2001), with the exception of *Xiphydria tibialis* Say. Larval hosts of *X. prolongata* and *X. tibialis* probably should be reexamined because we suspect that some were recorded erroneously.

Here we identify hosts for the first specimens of *X. prolongata* collected in Connecticut and New York. Adult specimens from Connecticut were reared from dead branches of field-collected black willow, *Salix nigra* Marshall (Salicaceae), which provides the first definitive proof of its establishment. The method of rearing adults from dead wood of willow is given by Maier (2009). Adult specimens from New York also apparently emerged from the dead wood of a willow, *Salix alba* L. var. *vitellina* (L.) Stokes (now considered a junior synonym of *S. alba*), that was brought into a house to be used for firewood, but the origin of the firewood was not specified on the labels. Also, no information was given about rearing or how the host association was made.

In its native range, *X. prolongata* has been reported to develop not only in species of *Salix* L., but also in one or more species of *Acer* L. (Sapindaceae), *Alnus* Miller, *Betula* L. (Betulaceae), *Quercus* L. (Fagaceae), *Platanus* L. (Platanaceae), *Populus* L. (Salicaceae), and *Ulmus* L. (Ulmaceae) (see Smith 1978). Based on the number of host records, *Salix*, *Populus*, and *Ulmus* seem to be the preferred hosts. In a project to determine larval hosts of cerambycids in New England, the senior author has collected dead branches (1.0–7.5 cm in diameter; dead 1–2 years) from all of the reported host genera of *X. prolongata*.

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Rearing with the methods of Maier (2009) did not yield any additional adults of *X. prolongata* from this dead wood of mostly native species of *Acer* (22 samples), *Alnus* (10), *Betula* (23), *Quercus* (38), *Platanus* (2), *Populus* (40), *Salix* (27), and *Ulmus* (6). Samples of *Salix* without *X. prolongata* included *S. alba* (2 samples), *S. bebbiana* Sargent (5), *S. discolor* Muhlenberg (4), *S. nigra* (6), *Salix x sepulcralis* Simonkai (formerly considered *S. babylonica* L. in northeastern states) (5), and unidentified *Salix* spp. (5).

Now that *X. prolongata* has been found in several states in the northern half of the United States (Smith 1983, Mudge et al. 2001, Looney et al. 2016, this paper), it likely will be found in additional northern states and southern Canada.

**New Records:** CONNECTICUT, Litchfield Co., Canaan, 0.19 km W jct. U.S. Highway 7 and Barnes Road, Hollenbeck Preserve, 41.95275° N, 73.20066° W, reared from dead branches of *Salix nigra* confined in cardboard drum in passively heated greenhouse on 21 May 2014, adults emerged on 1 (2♂♂), 3 (2♂♂), 6 (1♂), 8 (1♀), 19 (2♂♂, 1♀), and 20 June 2014 (2♂♂), Chris T. Maier. NEW YORK, Tompkins Co., Ludlowville, 14 (1, sex unknown), 27 (1, sex unknown), and 31 January (1, sex unknown), 1 (1♀, 1 sex unknown) and 15 February 1988 (1♂), in house from firewood, *Salix alba* var. *vitellina*, L.L. Pechuman. One male (20 June) and one female (19 June) from Connecticut and both sexed specimens from New York are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining specimens from Connecticut and New York are deposited at the institution of the senior author and at Cornell University, Ithaca, New York, respectively.

**Acknowledgments**

We thank Jason Dombroskie for providing label data on specimens deposited at Cornell University. The Connecticut Chapter of The Nature Conservancy, New Haven, kindly allowed us to sample at the Hollenbeck Preserve. This study was supported, in part, by McIntire Stennis Cooperative Forestry (CONH00397).

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Phyllopalpus pulchellus Uhler, the Handsome Trig (Orthoptera: Gryllidae), A Confirmed Michigan Resident

Mark F. O’Brien¹ and Julie A. Craves²

Phyllopalpus pulchellus Uhler is a member of the Trigonidiinae, also called trigs, sword-tail crickets (Capinera et al. 2004), or more informally, bush crickets; the common name is the Handsome Trig or Red-headed Bush Cricket. The distinctive features of this small cricket (less than 15 mm)—the large black palps, light yellow legs, shiny black wings, and red pronotum and head—are not seen in any other crickets within its range. The Handsome Trig can be found throughout much of the U.S. east of extreme east Texas and south of approximately 41.5° latitude, just south of the Michigan state border (Walker 2003).

In the early 20th century, P. pulchellus was not recorded north of southern Indiana (Blatchley 1903, Blatchley 1920) and southern and central Illinois (Hebard 1934). This species has apparently been expanding north in Ohio (Rainsong 2012, Rainsong 2014), but despite thorough local studies and broader compilations of Michigan Orthoptera, no Michigan records of P. pulchellus have been previously published (Hubbell 1922, Cantrall 1943, Cantrall 1968, Alexander et al. 1972, Bland 2003).

On 9 September 2016, MFO captured a female P. pulchellus in his backyard, at around 1900 hr. The specimen was placed into ethanol and bears the following locality data: MICHIGAN: Washtenaw Co., Ann Arbor, 42.25694°, -83.71502°, 09 Sept. 2016, Mark & Adrienne O’Brien, coll. The voucher has been deposited into the University of Michigan Museum of Zoology (UMMZI-00266003).

On 15 September 2016, JAC collected a female P. pulchellus on the campus of the University of Michigan-Dearborn, Dearborn, Wayne County, 42.31963°, -83.23808. It was on the leaves of Common Buckthorn, Rhamnus cathartica Linnaeus, at just over 1 m above the ground. The voucher has been deposited into the University of Michigan Museum of Zoology (UMMZI-00266047). These are the first specimen vouchers for Michigan.

On 5 October 2016, JAC found several singing male P. pulchellus and heard several dozen more along a 500 m trail near the collection site on the University of Michigan-Dearborn and Henry Ford College campuses.

Taken together, these records, along with a single photographic record from 2009 (Franklin, Oakland County [approximately 42.51° latitude] 27 September 2009, Hilma Anderson; http://bugguide.net/node/view/337912) indicate that P. pulchellus is established in southeast Michigan.

Northward distribution shifts in insects in response to climate change have been increasingly well-documented (reviewed in Menéndez 2007, Guo et al. 2011, Hill et al. 2011), and include a number of Orthoptera (Hickling et al. 2006). Another cricket that was only recently found in Michigan, Orocharis saltator Uhler, also was shown to have a similar range as that of P. pulchellus outside of Michigan (O’Brien and O’Brien 2015), and is now found at least as far north as Calhoun County, Michigan (http://bugguide.net/node/view/1162371). Phyllopalpus pulchellus has not yet been documented for Canada, but Paiero and Marshall (2014) speculate it is a likely candidate in response to a warming

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climate. Observers should be on the lookout for this unobtrusive but distinctive little cricket at the northern edge of its range.

**Literature Cited**


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Correction to the Key (page 92) of Description of the Nymph of Ophiogomphus smithi (Odonata: Gomphidae), With a Key to the Species of Ophiogomphus in the Western Great Lakes Region TGLE 49(1 & 2): 78–97

William A. Smith¹ and Kenneth J. Tennessen²

In our paper describing the nymph of Ophiogomphus smithi (TGLE, vol. 49, pages 78–97), we characterized Ophiogomphus howei in couplet 1 of the Primary Key (p. 92) as “Head W [width] greater than maximum abdomen W”. The statement was based on our misinterpretation of data reported online. We have since measured head width and abdomen width in 10 specimens of O. howei (from GA, NC, TN, WI) and found that the correct ratio of head W:max abdomen W in this species varies from 0.79 to 0.84. Therefore, we amend the first character in couplet 1 of the Primary Key on p. 92 as follows:

1. Head W 0.79–0.84 times maximum abdomen W; lateral spines absent or greatly reduced on S7; antm4 small, width < 0.3 times maximum width of antm3 (Fig. 16a); F-0 nymph < 22 mm long; DH absent or vestigial (if vestigial hooks, not projecting posteriorly over intersegmental membranes) ................................................................. howei

1’. Head W 0.65–0.75 times maximum abdomen W; lateral spines developed on S7; antm4 usually larger, width at least 0.3 times width of antm3 (Figs. 16b and 16c); F-0 nymph > 21 mm in length; DH usually distinct, projecting posteriorly over intersegmental membrane, sometimes vestigial ................................................................. 2

The other characters in couplet 1 are correct. For exuviae, abdomen W was determined in ventral view by flattening the venter of the abdomen with tips of forceps and measuring width at S6.

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