

THE BEETLE COMMUNITY OF SMALL OAK TWIGS IN LOUISIANA, WITH A
LITERATURE REVIEW OF COLEOPTERA FROM FINE WOODY DEBRIS

MICHAEL L. FERRO, MATTHEW L. GIMMEL
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University AgCenter
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
spongymesophyll@gmail.com
phalacrid@gmail.com

KYLE E. HARMS
Department of Biological Sciences
Louisiana State University
202 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
kharms@lsu.edu

AND

CHRISTOPHER E. CARLTON
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University AgCenter
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
ccarlton@agcenter.lsu.edu

Abstract

We conducted a study to explore which beetles utilize dead twigs in a Louisiana secondary forest and the effect of debris position on the beetle community. Twigs averaging 14 mm in diameter from one tree of *Quercus falcata* Michaux (southern red oak) were placed randomly into bundles of ten. At each of three sites, three bundles were laid on the ground, three were propped at the base of a living tree, and three were tied tightly above the ground against the branch of a living woody plant. The bundles were collected 10 months later and each was placed into an emergence chamber. More than 400 adult Coleoptera specimens were collected, representing 35 species within 16 families. Cerambycidae (longhorn beetles) and Curculionidae (weevils) exhibited the highest species richness, with nine and five species, respectively. Species richness was significantly different among treatments. Bundles placed on the ground had the lowest richness, aboveground bundles had the highest, and propped bundles were intermediate. Twelve species (34%) were represented by singletons.

To our knowledge, no general survey of the saproxylic beetles associated with fine woody debris has been undertaken in the United States. However, several studies have shown considerable beetle richness in dead branches and twigs. The exemplary research on saproxylic beetle succession conducted by Blackman and Stage (1918, 1924) showed that beetle assemblages in limbs less than 6.35 cm in diameter were distinct from those in larger portions of the dead tree and at times had greater species richness (up to 32 species). Mecke *et al.* (2001) reared 34 beetle

species from dead 3–12 cm diameter *Araucaria* limbs in Brazil. Numerous beetle species have been associated with twigs girdled by adults of various species in the cerambycid genus *Oncideres* Lepeletier and Audinet-Serville in Lacordaire (Linsley 1940; Polk and Ueckert 1973).

Twigs are important reservoirs of beetle richness and students of Coleoptera know that twigs are an important habitat. Certain taxa are popularly characterized by their affinity to twigs. Many Scolytinae are reported from “unthrifty twigs and branches” (Wood 1982). Some Bostrichidae are commonly called “Twig and Wood Borers” (Stehr 1991). Species of *Oncideres* are commonly called “Twig Girdlers” (Linsley 1940). Species of the genus *Elaphidionoides* Linsley (= *Anelaphus* Linsley) are commonly called “Twig Pruners” (Solomon *et al.* 1999), and the curculionid *Pityophthorus opaculus* LeConte is commonly called the “Twig Beetle” (Stevens *et al.* 1979).

A review of the relevant literature (Table 1) shows that, aside from the economically important taxa mentioned above, little attention has been paid to the general insect community that inhabits dead twigs. Here the term community is meant to refer to the beetles inhabiting twigs *sensu* MacArthur (1971) (“... any set of organisms currently living near each other and about which it is interesting to talk”). Based on literature records and limited rearing, Hovore and Penrose (1982) listed 19 species of Cerambycidae and an additional 13 species within seven families of beetles associated with twigs girdled by *Oncideres pustulata* LeConte. Polk and Ueckert (1973) reported several families of Coleoptera, Hymenoptera, and Diptera (those of the latter not enumerated) reared from twigs girdled by *Oncideres rhodosticta* Bates. Rogers (1977) reported a bostrichid, a clerid, five species of cerambycids, and several parasitoids that were associated with twigs girdled by *Oncideres cingulata* (Say). Beer (1949) reported rearing three species of Buprestidae from limbs of various trees.

The dead twig habitat is a difficult medium from which to collect beetles. The most invasive method is direct dissection of the limb with removal of the (often immature) insects (Sanborn 1911; Polk and Ueckert 1973; Rogers 1977). While this may be the most expedient method of surveying twigs, the collector is biased toward species with large and easy-to-see adults and larvae, and against species with small adults and larvae (*e.g.*, Scolytinae with mature larvae 2–10 mm long [Stehr 1991]). Additionally, larvae are often difficult or impossible to identify to the species level using existing literature.

A second, and arguably more thorough, approach is to allow the emergence of specimens from the twig (Sanborn 1911; Linsley 1940; Beer 1949; Rogers 1977; Hovore 1980; Hovore and Penrose 1982). This has been accomplished using a variety of methods. Pollock (1988) reared subcortical larvae individually in 3-dram vials. Polk and Ueckert (1973) placed limbs into rearing chambers (the authors were unclear about whether single or multiple limbs were in each chamber) and collected positively phototactic specimens that accumulated in translucent jars beneath the chamber. We have tabulated all published U.S. records of Coleoptera emerging from twigs in community level surveys (Appendix A).

The purposes of our experiment were to: 1) record which beetles (if any) utilize dead twigs in a secondary forest in Louisiana; and 2) determine if Coleoptera species composition is affected by twig position. Previous studies used a wide size range of branches or twigs, did not standardize for time since death, failed to differentiate branch conditions (*e.g.*, hanging, on ground, etc.), and may have overlooked species with small body sizes. In this study, tree species, size of limb, date of death, treatment of limbs, inoculation time, and rearing time were known and held constant, and a full census of the emergent beetle community was undertaken.

Table 1. An annotated list of world literature about Coleoptera associated with fine woody debris. C = Community, SS = Single Species.

Author	Year	Country	Collection technique(s)	C / SS	Study system	Wood diameter	Plant vitality	Results (associated with emergence and twigs)
Sanborn	1911	United States	Dissection	SS	<i>Oncideres cingulata</i> (Say) (Cerambycidae) ?	?	Freshly killed	Elevated / drier twigs had more adults
Blackman and Stage	1918	United States	Emergence, hand collecting	C	Succession of insects associated with dead American larch (<i>Larix laricina</i> (Du Roi) K. Koch)	25.4–50.8 mm	Dead	11 spp. Coleoptera, associated numerous galleries, predators, and parasites
Blackman and Stage	1924	United States	Emergence, hand collecting	C	Succession of insects associated with dead and dying hickory (<i>Carya glabra</i> (Mill.) Sweet)	<63.5 mm	Dead	16, 32, 20, 2 spp. Coleoptera in limbs 1–4 summers after tree death, numerous Hymenoptera, Diptera, and minor orders
Linsley	1940	United States	Emergence	C	<i>Oncideres</i> spp. (Cerambycidae)	20–40 mm	?	Summarizes available information on species of the genus
Beer	1949	United States	Emergence	SS	Buprestidae reared from various wood	?	Dead	Observations of long lived buprestid larvae

Table 1. Continued.

Author	Year	Country	Collection technique(s)	C / SS	Study system	Wood diameter	Plant vitality	Results (associated with emergence and twigs)
Elton	1966	United Kingdom	Artificial log traps	C	Ground and aerial artificial limbs compared with dead limbs	>7.62 cm	Artificial/dead	Artificial branches revealed many saproxylic species
Fager	1968	United Kingdom	Artificial log traps/dissection/Tullgren	C	Saproxylic invertebrate community in real and artificial branches	5-7.5 cm	Artificial/dead	Shows artificial logs work and provides a list of the saproxylic branch community
Polk and Ueckert	1973	United States	Dissection, emergence	C	Saproxylic community associated with <i>Oncideres rhodosticta</i> Bates (Cerambycidae)	5-20 mm	Freshly killed	Reported many emergent Coleoptera, Hymenoptera, Diptera
Rogers	1977	United States	Dissection	C	<i>Oncideres cingulata</i> (Say) (Cerambycidae)	8-15 mm	Freshly killed	Reports life history of species and some predators and parasites
Stevens <i>et al.</i>	1979	United States	Dissection	SS	<i>Pityophthorus opaculus</i> LeConte (Curculionidae)	?	Dying	Report outbreak of species
Hovore	1980	United States	Emergence	SS	<i>Nathriobrium methioides</i> Hovore (Cerambycidae)	?	Dead	Species was reared from small branches
Forcella	1981	United States	Dissection	SS	<i>Oncideres cingulata</i> (Say) (Cerambycidae)	?	Freshly killed	Limbs severed later in the season had more larvae

Table 1. Continued.

Author	Year	Country	Collection technique(s)	C / SS	Study system	Wood diameter	Plant vitality	Results (associated with emergence and twigs)
Hovore and Penrose	1982	United States	Emergence	C	<i>Oncideres pustulata</i> LeConte (Cerambycidae)	?	Dead	19 spp. of Cerambycidae that co-inhabit girdled twigs
Forcella	1984	United States	Looked at # of twigs only	SS	<i>Oncideres cingulata</i> (Say) (Cerambycidae)	7–11 mm	Freshly killed	Described per tree twig damage
Rice	1989	United States	Dissection	SS	<i>Oncideres pustulata</i> LeConte (Cerambycidae)	13–55 mm	Freshly killed	Described branch girdling and oviposition biology
Cramer	1998	United States	Dissection	SS	<i>Oncideres cingulata</i> (Say) (Cerambycidae)	5–11 mm	Freshly killed	Total mortality
Mecke <i>et al.</i>	2001	Brazil/Argentina	Emergence, beating, dissection	C	Insects associated with <i>Araucaria</i> trees	3–12 cm	Dead > living	34 spp. Coleoptera, 4 spp. Hymenoptera
Wang <i>et al.</i>	2002	New Zealand	Laboratory rearing	SS	<i>Oemona hirta</i> (Fabricius) (Cerambycidae)	50–60 mm	Living, dead	High mortality in desiccated twigs
Iwata <i>et al.</i>	2004	Japan	Laboratory rearing, emergence	SS	<i>Dinoptera minuta</i> (Gebler) (Cerambycidae)	5–25 mm	Living then dead	Larvae emerge to pupate in the soil
Petrice and Haack	2006	United States	Emergence	SS	<i>Agrilus planipennis</i> Fairmaire (Buprestidae)	6–37 (average 15) cm	Freshly killed	Desiccation major agent of mortality

Material and Methods

Study Area. The study was performed at Feliciana Preserve, a 61 ha tract located about 16 km east of St. Francisville, West Feliciana Parish, Louisiana (30°47.6'N, 91°15.2'W, WGS84). Feliciana Preserve encompasses a portion of the Tunica Hills at the southern extreme of the Blufflands, a belt of thick loess originally blown from the Mississippi River floodplain (Delcourt and Delcourt 1975). The resulting hills of easily erodible substrate have since formed a series of deep forested ravines. This area was a major refugium for mixed mesophytic forest species during the Wisconsin glaciation. Many taxa are holdovers from this Pleistocene event and occur nowhere else in Louisiana, or meet the southern limit of their range in the Tunica Hills (Delcourt and Delcourt 1975). This area also contains many subtropical elements not found further north, making this a unique collection of taxa in Louisiana.

The preserve consists of a secondary mixed mesophytic forest dominated by magnolia (*Magnolia grandiflora* L.), holly (*Ilex opaca* Aiton), beech (*Fagus grandifolia* Ehrhart), pine (*Pinus* spp.), and several species of oak (*Quercus* spp.). The area was clear-cut during the late 1950s (~55 years ago) and has remained largely undisturbed since. Feliciana Preserve is also the location of several studies focused on the Lepidoptera fauna of the area (Landau and Prowell 1999a, b; Landau *et al.* 1999; Prowell 2001).

Study Design. A single, healthy, ~30-year-old *Quercus falcata* Michaux (southern red oak) was felled 19 March 2006 in Feliciana Preserve. Following the cutting, 270 twigs averaging 36 cm (± 1 cm) in length and 14 mm (± 5 mm) in diameter were removed from the tree. Twigs were cut using saws and pruners so that ends were square, not splintered. These were placed in a single pile and later randomly assigned to one of 27 bundles of ten twigs each. Each bundle was tied with two lengths of twine. The 27 bundles were then randomly sorted into three groups of nine bundles each.

Three study sites, each situated ~300 m from each other, were used. Each site was within closed canopy forest and qualitatively similar with respect to stand size, age, substrate, amount of dead wood, litter, undergrowth, and distance from forest openings. At each site, three random twig bundles were placed directly on the ground (resting on top of the leaf litter), three twig bundles were propped at an approximately 45° angle, with the upper end against the trunk of a living tree and the lower end contacting the ground, and the remaining three bundles were tied horizontally against the limb of a small tree or woody shrub approximately 1.5 m above the ground. Bundles placed directly on top of the leaf litter, bundles propped against trees, and bundles tied 1.5 m above the ground are referred to as ground, propped, and aboveground, respectively. Bundles were 2–4 m from their nearest neighbor. A flag with an identity code was placed next to each bundle. The study was set up as quickly as possible (within about five hours) to ensure that insects did not oviposit on the twigs prior to being positioned at the study sites, and to ensure that any volatiles or chemical attractants would still be present in quantities strong enough to simulate a recent natural breakage event.

The bundles were left undisturbed until 28 January 2007 (*ca.* ten months later) when they were collected for emergence. Care was taken to “pounce” on each bundle and transfer it to a container quickly so as to minimize loss of fast-moving individuals fleeing the bundle. On site, each bundle was initially placed by itself into a clean white plastic ~19-L bucket (inside diameter 28 cm, height 36 cm), sealed, and removed to a central emergence area. Here, bundles were transferred to an emergence chamber that consisted of a similar bucket with an inverted foam

bowl in the bottom. A small amount of full-strength propylene glycol antifreeze (Prestone® Low Tox™ brand) was poured in the bottom of the chamber to serve as a killing and preservative agent. Twig bundles were transferred from their collecting bucket to the emergence chamber and positioned more or less vertically with the bottom end resting on the bowl so that the bundles were not in contact with the propylene glycol. Any material left in the transfer bucket was dumped into the emergence chamber. Emergence chambers were sealed, labeled, and randomly arranged in a covered, open air building.

On 12 July 2007 (*ca.* six months later), each chamber was opened and the twig bundles were shaken and visually inspected for adults. The propylene glycol/specimen/frass slurry was washed into a labeled Whirl-Pak® and removed to the laboratory for sorting. Adult Coleoptera were pinned or pointed as needed, and labeled. Identification to the finest level possible (typically species) was performed with the appropriate taxonomic literature and/or comparison with authoritatively identified reference specimens. All other macroinvertebrates were sorted from the debris, labeled, and preserved in 90% ethanol. Specimens are deposited in the Louisiana State Arthropod Museum (LSAM), LSU AgCenter, Baton Rouge, Louisiana.

Because of the exploratory nature of this study, several design aspects were somewhat arbitrary. Twigs of southern red oak were used because there is a concurrent study within Feliciana Preserve that is exploring aspects of Coleoptera communities within other portions of the same tree species. The twig diameter was chosen because it falls below the diameter of the smallest wood used in a different concurrent study, but was judged robust enough to harbor multiple insects. Twigs were placed in bundles of ten to reduce twig loss over time and because of convenient mathematical aspects. The length of the twigs was chosen so that the rearing chambers could comfortably accommodate them. Twigs were cut early in the spring to allow for ample colonization time, gathered before a putative spring pulse of emergence, and allowed to rear for an extended period of time to accommodate the emergence of as many adults as possible.

Statistical Analysis. Statistical significance ($\alpha = 0.05$) was tested using Monte Carlo simulations to compare observed data to null expectations generated by appropriately randomizing those observed data (Manly 2007). Average species richness per bundle and total number of specimens for each site and treatment combination ($n = 9$ bundles for each site and treatment combination) were individually compared to null distributions, *i.e.*, distributions of expected values generated from 1,000 randomizations. Each randomization reassigned each bundle's observed species richness and number of specimens to a randomly chosen site and treatment combination (without replacement), whereupon nine randomized bundles' values were chosen at random to calculate one randomized value of average species richness and one randomized value of total number of specimens. The randomizations provided 1,000 randomized values for expected species richness per bundle and 1,000 randomized values for expected total number of specimens. A significant deviation from randomized expectations occurred when an observed value fell in the upper or lower 2.5% tail of the corresponding frequency distribution of expected (randomized) values; observed values in the upper 2.5% tail were significantly higher than expected, and vice versa (Prado and Lewinsohn 2004; Manly 2007).

Results

Richness. A total of 414 adult Coleoptera specimens were collected, representing 35 species in 33 genera and 16 families (Table 2). Twig bundles

Table 2. Coleoptera emergent from oak twig bundles in Louisiana. Taxa are grouped according to presence in treatments. Those present in all treatments appear at the top, those in only two treatments follow, and those present in only one treatment appear last.

Family	Species	Individuals emerged:				Totals
		Ground	Propped	Aboveground		
Biphylidae	<i>Diplocoelus rudis</i> (LeConte, 1863)	2	2	1	5	
Buprestidae	<i>Agrilus obsoletoguttatus</i> Gory, 1841	98	26	7	131	
Cerambycidae	<i>Anelaphus villosus</i> (Fabricius, 1792)	6	10	12	28	
Cerambycidae	<i>Liopinus alpha</i> (Say, 1827)	14	7	22	43	
Latrididae	<i>Melanophthalma distinguenda</i> (Comolli, 1837)	1	1	1	3	
Cerambycidae	<i>Neocyttus acuminatus</i> (Fabricius, 1775)	1	1	2	2	
Cerambycidae	<i>Anelaphus pumilus</i> (Newman, 1840)		5	2	7	
Cerambycidae	<i>Cyrtinus pygmaeus</i> (Haldeman, 1847)		8	17	25	
Cerambycidae	<i>Ecyrrus dasycerus</i> (Say, 1827)		12	7	19	
Curculionidae	<i>Hypothenemus californicus</i> Hopkins, 1915		4	24	28	
Curculionidae	<i>Laemosaccus nephele</i> (Herbst, 1797)		7	5	12	
Melyridae	<i>Attalus scincetus</i> (Say, 1825)		1	1	2	
Anobiidae	<i>Petalium debile</i> Fall, 1905	1			1	
Melandyridae	<i>Microtonus sericans</i> LeConte, 1862	1			1	
Monotomidae	<i>Monotoma longicollis</i> (Gyllenhal, 1827)	1			1	
Mordellidae	<i>Falsomordellistena hebraica</i> (LeConte, 1862)	1			1	
Mordellidae	<i>Mordella invisitata</i> Liljeblad, 1945	2			2	
Ptiliidae	<i>Acrotrichis</i> sp.	1			1	
Staphylinidae	<i>Sepedophilus macer</i> (Casey, 1895)	1			1	
Corylophidae	<i>Holopsis caroliniae</i> (Casey, 1900)		4		4	
Latrididae	<i>Corticarina</i> sp.		2		2	
Staphylinidae	<i>Biblopectus</i> sp.		1		1	
Anobiidae	<i>Calymnaderus nitidus</i> (LeConte, 1865)			1	1	
Buprestidae	<i>Chrysobothris chrysoela</i> (Illiger, 1800)			2	2	
Cerambycidae	<i>Euderces pictipes</i> (Fabricius, 1787)			4	4	
Cerambycidae	<i>Euderces pini</i> (Olivier, 1795)			1	1	
Cerambycidae	<i>Obrium maculatum</i> (Olivier, 1795)			4	4	
Cerambycidae	<i>Tessaropa tenuipes</i> (Haldeman, 1846)			10	10	

Table 2. Continued.

Family	Species	Individuals emerged:				Totals
		Ground	Propped	Aboveground	Totals	
Cleridae	<i>Macromella dislocatus</i> (Say, 1825)			1	1	
Cleridae	<i>Neorthopleura thoracica</i> (Say, 1823)			6	6	
Curculionidae	<i>Acalles clavatus</i> (Say, 1831)			1	1	
Curculionidae	<i>Pseudopityophthorus asperulus</i> (LeConte, 1868)			5	5	
Curculionidae	<i>Pseudothyssanoes dislocatus</i> (Blackman, 1920)			56	56	
Dermestidae	<i>Cryptorhopalum floridanum</i> Casey, 1916			1	1	
Laemophloeidae	<i>Charaphloeus</i> sp.			2	2	
Totals		130	91	193	414	
Total # species		13	15	24	35	

placed directly on the ground yielded 130 specimens, representing 13 species, 13 genera, and 10 families. Propped twig bundles yielded 91 specimens, representing 15 species, 14 genera, and 8 families. Aboveground bundles yielded 193 specimens, representing 24 species, 22 genera, and 10 families.

Within the entire collection, 13 species (37%) were represented by five or more individuals, whereas 22 species (63%) were represented by fewer than five individuals. Twelve species (34%) were represented by singletons. The number of species represented by fewer than five individuals was 10 (77%), 8 (53%), and 13 (54%) for twig bundles placed on the ground, propped, and aboveground, respectively.

The buprestid *Agrilus obsoletoguttatus* Gory was the most abundant species (131 specimens), accounting for 32% of all individuals, and having emerged from all three treatments. The scolytine curculionid *Pseudothysanoes dislocatus* (Blackman) had the second highest abundance with 56 individuals (13.5%), but only emerged from twig bundles that were aboveground. Five species, *A. obsoletoguttatus*, *Liopinus alpha* (Say), *Anelaphus villosus* (Fabricius), *Diplocoelus rudis* (LeConte), and *Melanophthalma distinguenda* (Comolli), emerged from all three treatments. A single species, *Neoclytus acuminatus* (Fabricius), was shared between ground and propped treatments, but was not found in the aboveground treatment. Six species, *Hypothenemus californicus* Hopkins, *Cyrtinus pygmaeus* (Haldeman), *Ecyrus dasycerus* (Say), *Laemosaccus nephele* (Herbst), *Anelaphus pumilus* (Newman), and *Attalus scincetus* (Say), were shared among propped and aboveground treatments, but did not emerge from bundles placed on the ground. Seven species that emerged from bundles placed on the ground were unique to that treatment, three species were unique to propped bundles, and 13 species were unique to aboveground bundles.

Species represented by five or more individuals within a particular treatment occurred in only four families: Buprestidae, Cerambycidae, Curculionidae, and Cleridae. However, Curculionidae were absent from ground bundles, and Cleridae were unique to aboveground bundles. Cerambycidae were represented by ten species, followed by Curculionidae with five species. Six families were represented by two species and the remaining eight families were each represented by a single species.

Sites Comparison. A total of 146 adult Coleoptera emerged from all bundles at Site I, 183 adult Coleoptera emerged from bundles at Site II, and 85 emerged from bundles at Site III. Numbers of specimens emerged per bundle were not significantly different among sites ($P > 0.05$). The average number of species per bundle was 4.0, 4.3, and 3.4 for Sites I, II, and III, respectively. Number of species emerged per bundle were not significantly different among sites ($P > 0.05$).

Treatments Comparison. A total of 130 adult Coleoptera emerged from all bundles placed on the ground, 91 adult Coleoptera emerged from propped bundles, and 193 emerged from aboveground bundles. Numbers of specimens were not significantly different among treatments ($P > 0.05$). The average number of species per bundle was 2.3, 3.8, 5.7, and 3.9 for ground, propped, aboveground, and all treatments combined, respectively. The average species richness per bundle placed on the ground was significantly less than expected ($P < 0.05$) from the null distribution. The average species richness per propped bundle was not significantly different ($P > 0.05$) from the null distribution. The average species richness per aboveground bundle was significantly more than expected ($P < 0.05$) from the null distribution. Thus, species richness per bundle ranked as follows: ground < propped < aboveground.

Discussion

While this may be likened to one of Charles Darwin's "fool's experiments" (Darwin 1887), the results of this research were astounding. From a smattering of finger-sized twigs we collected over 400 specimens and 35 species of beetles. Half the species collected were wholly absent (seven species) or were represented by five or fewer specimens (ten species) in the Louisiana State Arthropod Museum (which houses approximately 600,000 Coleoptera specimens from the region). This should be of great interest to researchers conducting comprehensive faunal inventories, and we highly recommend addition of this or a similar method to the biodiversity surveyor's and ecologist's toolkit.

Species richness results among treatments were also unexpected. Cramer (1998) reported complete mortality of the cerambycid *O. cingulata* caused by desiccation of twigs brought to the laboratory. However, Cerambycidae, while reared from all three treatments, showed the highest number of individuals and diversity in propped and aboveground bundles, presumably the driest treatments.

Aboveground twig bundles had the highest species richness, but presumably: 1) were more susceptible to desiccation; 2) experienced greater changes in daily temperature; and 3) were generally less accessible to potential colonists. In contrast, bundles placed on the ground had the lowest richness, but presumably none of the above limitations.

Interestingly, propped bundles, which were presumably more accessible to colonists than aboveground bundles but more prone to desiccation than ground bundles, showed a greater similarity to aboveground bundles. This initially suggests that desiccation of limbs may be more important at promoting species richness than accessibility to colonists. Petrice and Haack (2006) reported that desiccation was a major cause of mortality in *Agrilus planipennis* Fairmaire (the emerald ash borer), a congener of *A. obsoletoguttatus*. Perhaps *A. obsoletoguttatus* loses its dominance in drier wood, allowing other species to utilize the freed resources.

Increased exposure to predation, especially by ants (Formicidae), probably did not contribute to lower species richness of bundles placed in full contact with the ground or propped. When considering this question, predation and ability to colonize must be considered simultaneously. The number of specimens did not differ among treatments. This could occur if predation and ability to colonize were equal for all treatments, or it could occur if predation and ability to colonize differed among treatments, with predation increasing at the same rate as ability to colonize. The relative proportion of the two factors would have had to be equal across all treatments. This is unlikely due to great differences in ability to colonize among the bundles placed on the ground and those that were aboveground. Additionally, predation would probably not have resulted in the loss of all individuals of a given taxon within a treatment if sufficient numbers of that taxon had been present.

This research indicates that a rich, perhaps unique beetle fauna inhabits fine woody debris. Beetle communities among twigs that are in full contact with the ground appear to be distinct from those that remain in the tree after death. These basic observations may now be used to foster hypothesis-driven research.

Acknowledgments

We thank Dorothy Prowell (Louisiana State University) for allowing the study to be conducted on her property and access to the outbuilding-turned-emergence

facility. We thank Robert Rabaglia (Maryland Department of Agriculture) for the scolytine identifications, Stephanie Gil (Louisiana State University) for help with the corylophid identification, and Sarah Samson (University of Missouri, Columbia) for assistance in the field. This publication was approved by the Director, Louisiana Agricultural Experiment Station as manuscript number 2009-234-2782.

Literature Cited

- Beer, F. M. 1949.** The rearing of Buprestidae and delayed emergence of their larvae. The Coleopterists' Bulletin 3(6):81–84.
- Blackman, M. W., and H. H. Stage. 1918.** Notes on insects bred from the bark and wood of the American larch. The New York State College of Forestry, Technical Publication No. 10:11–115.
- Blackman, M. W., and H. H. Stage. 1924.** On the succession of insects living in the bark and wood of dying, dead, and decaying hickory. The New York State College of Forestry, Technical Publication No. 17:3–268.
- Cramer, K. L. 1998.** Effects of twig morphology on oviposition behavior and hatching success of the twig-girdling beetle *Oncideres cingulata* (Say) (Coleoptera: Cerambycidae). The Coleopterists Bulletin 52:186–193.
- Darwin, F. (ed.). 1887.** The life and letters of Charles Darwin, including an autobiographical chapter. Volume 1. John Murray, London. 558 pp.
- Elton, C. S. 1966.** The Pattern of Animal Communities. Methuen & Co. Ltd., London. 432 pp.
- Fager, E. W. 1968.** The community of invertebrates in decaying oak wood. Journal of Animal Ecology 37:121–142.
- Forcella, F. 1981.** Twig nitrogen content and larval survival of twig-girdling beetles, *Oncideres cingulata* (Say) (Coleoptera: Cerambycidae). The Coleopterists Bulletin 35:211–212.
- Forcella, F. 1984.** Trees size and density affect twig-girdling intensity of *Oncideres cingulata* (Say) (Coleoptera: Cerambycidae). The Coleopterists Bulletin 38:37–42.
- Hovore, F. T. 1980.** A new genus and species of Cerambycidae from southern Texas (Coleoptera). The Coleopterists Bulletin 34:115–119.
- Hovore, F. T., and R. L. Penrose. 1982.** Notes on Cerambycidae co-inhabiting girdles of *Oncideres pustulata* LeConte (Coleoptera: Cerambycidae). The Southwestern Naturalist 27:23–27.
- Iwata, R., Y. Hirayama, H. Shimura, and M. Ueda. 2004.** Twig foraging and soil-burrowing behaviors in larvae of *Dinoptera minuta* (Gebler) (Coleoptera: Cerambycidae). The Coleopterists Bulletin 58:399–408.
- Landau, D., and D. Prowell. 1999a.** A partial checklist of moths from longleaf pine savannas in Louisiana (Insecta: Lepidoptera). Transactions of the American Entomological Society 125:127–138.
- Landau, D., and D. Prowell. 1999b.** A partial checklist of moths collected from mixed mesophytic hardwood forests in Louisiana (Insecta: Lepidoptera). Transactions of the American Entomological Society 125:139–150.
- Landau, D., D. Prowell, and C. E. Carlton. 1999.** Intensive versus long-term sampling to assess lepidopteran diversity in a southern mixed mesophytic forest. Conservation Biology and Biodiversity 92:435–441.
- Linsley, E. G. 1940.** Notes on *Oncideres* twig girdlers. Journal of Economic Entomology 33:561–563.
- MacArthur, R. H. 1971.** Patterns of terrestrial bird communities [pp. 189–221]. In: Avian Biology, volume 1 (D. S. Farner and J. R. King, editors). Academic Press, New York. 586 pp.
- Manly, B. F. J. 2007.** Randomization, Bootstrap and Monte Carlo Methods in Biology. Third Edition. Chapman and Hall/CRC, New York. 455 pp.

- Mecke, R., M. H. M. Galileo, and W. Engels. 2001. New records of insects associated with *Araucaria* trees: phytophagous Coleoptera and Hymenoptera and their natural enemies. *Studies on Neotropical Fauna and Environment* 36:113–124.
- Petrice, T. R., and R. A. Haack. 2006. Effects of cutting date, outdoor storage conditions, and splitting on survival of *Agrilus planipennis* (Coleoptera: Buprestidae) in firewood logs. *Journal of Economic Entomology* 99:790–796.
- Polk, K. L., and D. N. Ueckert. 1973. Biology and ecology of a mesquite twig girdler, *Oncideres rhodosticta*, in west Texas. *Annals of the Entomological Society of America* 66:411–417.
- Pollock, D. A. 1988. A technique for rearing subcortical Coleoptera larvae. *The Coleopterists Bulletin* 42:311–312.
- Prado, P. I., and T. M. Lewinsohn. 2004. Compartments in insect–plant associations and their consequences for community structure. *Journal of Animal Ecology* 73:1168–1178.
- Prowell, D. 2001. Additions and corrections to Macrolepidoptera in Landau and Prowell 1999 (a & b), partial checklists of moths from longleaf pine savannas and mesophytic hardwood forests in Louisiana. *Transactions of the American Entomological Society* 127:239–244.
- Rice, M. E. 1989. Branch girdling and oviposition biology of *Oncideres pustulatus* (Coleoptera: Cerambycidae) on *Acacia farnesiana*. *Annals of the Entomological Society of America* 82:181–186.
- Rogers, C. E. 1977. Bionomics of *Oncideres cingulata* (Coleoptera: Cerambycidae) on Mesquite. *Journal of the Kansas Entomological Society* 50:222–228.
- Sanborn, C. E. 1911. The twig girdler. *Bulletin of the Oklahoma Agricultural Experiment Station* 91:1–13.
- Solomon, J. D., F. I. McCracken, R. L. Anderson, R. Lewis, Jr., F. L. Oliveria, T. H. Filer, and P. J. Barry. 1987. [slightly revised October 1999] Oak Pests: A Guide to Major Insects, Diseases, Air Pollution, and Chemical Injury. Protection Report R8-PR7. USDA Forest Service, Southern Forest Experiment Station New Orleans. 69 pp.
- Stehr, F. W. 1991. *Immature Insects*. Volume 2. Kendall/Hunt Publishing Company, Dubuque, IA. 975 pp.
- Stevens, R. E., C. K. Lister, and J. L. Linnane. 1979. Outbreak of a twig beetle, *Pityophthorus opaculus* LeConte, in Colorado. *The Coleopterists Bulletin* 33:268.
- Wang, Q., G. Shi, D. Song, D. J. Rogers, L. K. Davis, and X. Chen. 2002. Development, survival, body weight, longevity, and reproductive potential of *Oemena* [sic] *hirta* (Coleoptera: Cerambycidae) under different rearing conditions. *Annals of the Entomological Society of America* 95:563–569.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6:1–1359.

(Received 8 September 2008; accepted 21 April 2009. Publication date 28 September 2009.)

Appendix A. North American Coleoptera emergent from fine woody debris. Only taxa from prior community-level surveys are included.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Anthribidae	<i>Discotenes nigrotuberculata</i> (Schaeffer, 1904)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Anthribidae	<i>Ischnocerus infuscatus</i> Fahraeus, 1839	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Anthribidae	<i>Omniscus eusphyroides</i> (Schaeffer, 1906)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Bostrichidae	<i>Amphicerus</i> sp.	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	Average 9.1 mm	Associated with twigs girdled by <i>Oncideres rhodosticta</i> Bates (Cerambycidae)	TX	Polk and Ueckert 1973
Bostrichidae	<i>Xylobiops basilaris</i> (Say)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Bostrichidae	<i>Xylobiops</i> sp.	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	Average 9.1 mm	Live twig girdled by parent	TX	Polk and Ueckert 1973
Bostrichidae	2 spp.	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	<i>Acmaeodera neoneglecta</i> Fisher, 1949	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	<i>Agrilus neoprosopidis</i> Knull, 1938	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	<i>Agrilus otiosus</i> Say, 1833	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Buprestidae	<i>Anthaxia quercata</i> (Fabricius, 1801)	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5-5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	<i>Anthaxia viridicornis</i> (Say, 1823)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	<i>Anthaxia viridifrons</i> Gory, 1841	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	<i>Chrysobothris analis</i> LeConte, 1860	<i>Leucaena puberulenta</i> (Schltdl.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	<i>Chrysobothris dentipes</i> (Germer, 1824)	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5-5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	<i>Chrysobothris femorata</i> (Olivier, 1790)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	<i>Chrysobothris rotundicollis</i> Gory & Laporte, 1837 [as <i>Chrysobothris blanchardi</i> Horn]	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5-5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	<i>Chrysobothris sexsignata</i> Say, 1839	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	<i>Chrysobothris sexsignata</i> Say, 1839	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5-5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	<i>Dicerca lurida</i> (Fabricius, 1775)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Buprestidae	<i>Phaenops fulvoguttata</i> (Harris, 1829) [as <i>Melanophila fulvoguttata</i> (Harris)] <i>Achryson surinamum</i> (Linnaeus, 1767)	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	<i>Achryson surinamum</i> (Linnaeus, 1767)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Linsley 1940
Cerambycidae	<i>Aegomorphus modestus</i> (Gyllenhal, 1817) [as <i>A. diciptens</i> Haldeman]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	NY	Hovore and Penrose 1982
Cerambycidae	<i>Anelaphus debilis</i> (LeConte, 1854)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	TX	Blackman and Stage 1924
Cerambycidae	<i>Anelaphus inermis</i> (Newman, 1840) [as <i>Anoplium truncatum</i> LeConte]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Astylopsis sexguttata</i> (Say, 1826) [as <i>Leptostylus sexguttatus</i> (Say)] <i>Ataxia crypta</i> (Say, 1831)	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	NY	Linsley 1940
Cerambycidae				Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae				Associated with twigs girdled by <i>Oncideres cingulata texana</i> Horn (Cerambycidae)		Linsley 1940

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Cyrtophorus verrucosus</i> (Olivier, 1795)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Dorcaschema cinereum</i> (Olivier, 1795) [as <i>Hetoemis cinerea</i> (Olivier)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Dorcaschema nigrum</i> (Say, 1826)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Eburia mutica</i> LeConte, 1853	<i>Leucaena pulverulenta</i> (Schltdl.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Ecyrius arcuatus</i> Gahan, 1892 [as <i>Ecyrius texanus</i> Schaeffer]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Eudermes reichet</i> LeConte, 1873 [as <i>Eudermes exilis</i> Casey]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Eudermes picipes</i> (Fabricius, 1787)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Geropa concolor</i> (LeConte, 1873) [as <i>Achryson concolor</i> LeConte]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Geropa concolor</i> (LeConte, 1873)	<i>Leucaena pulverulenta</i> (Schltdl.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Gnaphalodes trachyderoides</i> Thomson, 1860	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Heterachthes quadrimaculatus</i> Haldeman, 1847	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Aneflaphus villosus</i> (Fabricius, 1792) [as <i>Hypermallus villosus</i> (Fabricius)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Knulliana cincta</i> (Drury, 1773) [as <i>Chiton cinctus</i> Drury]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Lepturges angulatus</i> (LeConte, 1852) [as <i>Lepturges angulatus</i> Casey]	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Lepturges inflatus</i> Bates, 1872	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Liopinus</i> nr. <i>alpha</i> (Say, 1827) [as <i>Leiotopus</i> nr. <i>alpha</i> (Say)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Liopinus mimeticus</i> (Casey, 1891) [as <i>Leiotopus houstoni</i> Casey and <i>Leiotopus texana</i> Casey]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte and <i>O. cingulata texana</i> Horn (Cerambycidae)		Linsley 1940

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Liopinus mimeticus</i> (Casey, 1891) [as <i>Sternidius mimeticus</i> (Casey) and <i>Sternidius texanus</i> (Casey)]	<i>Leucaena pulverulenta</i> (Schldl.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Liopinus wiltii</i> (Horn, 1880) [as <i>Leiopus wiltii</i> Horn]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte and <i>O. cingulata texana</i> Horn (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Lochmaeocles cornuticeps</i> Schaeffer, 1906	<i>Leucaena pulverulenta</i> (Schldl.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Molorchus bimaculatus</i> Say, 1824	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Neolytus acuminatus</i> (Fabricius, 1775)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Neolytus leucozonus</i> Laporte & Gory, 1835 [as <i>Neolytus longipes</i> (Kirby)]	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	<i>Neocompsa exclamatoris</i> (Thomson, 1860) [as <i>Ibidion exclamatoris</i> Thomson]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Neocompsa exclamatoris</i> (Thomson, 1860)	<i>Leucaena puberulenta</i> (Schltld.) Benth.	56 mm	Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Neocompsa mexicana</i> (Thomson, 1865) [as <i>Ibidion townsendi</i> Linell]			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Neocompsa mexicana</i> (Thomson, 1865)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Obrium maculatum</i> (Olivier, 1795)			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte and <i>O. cingulata texana</i> Horn (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Obrium maculatum</i> (Olivier, 1795)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Obrium mozinnae</i> Linell, 1897	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Oncideres cingulata</i> texana Horn, 1885 [as <i>Oncideres texana</i> Horn]	<i>Acacia</i> , probably also <i>Prosopis</i> and <i>Ebenopsis</i> [as <i>Pithecolobium</i>]		Live twig girdled by parent		Linsley 1940

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Oncideres pustulata</i> LeConte, 1854	<i>Acacia farnesiana</i> (L.) Willd., <i>Ebanopsis</i> <i>ebano</i> (Berl.) Barneby & Grimes [as <i>Pithecolobium</i> <i>flexicaulis</i> (Benth.) J.M. Coult.], <i>Prosopis</i> <i>glandulosa</i> Torr., <i>Acacia berlandieri</i> Benth., <i>Parkinsonia</i> <i>aculeata</i> L., <i>Mimosa</i> <i>aculeaticarpa</i> Ortega [as <i>Mimosa lindheimeri</i> A. Gray]	20–40 mm	Live twig girdled by parent		Linsley 1940
Cerambycidae	<i>Oncideres pustulata</i> LeConte, 1854	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Live twig girdled by parent	TX	Hovore and Penrose 1982
Cerambycidae	<i>Oncideres rhodosticta</i> Bates, 1885	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	Average 9.1 mm	Live twig girdled by parent	TX	Polk and Ueckert 1973
Cerambycidae	<i>Placosternus difficilis</i> (Chevrolat, 1862)			Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Pogonocherus mixtus</i> Haldeman, 1847	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	<i>Pyrrassa unicolor</i> (Randall, 1838) [as <i>Pseudibidion unicolor</i> (Randall)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria</i> <i>glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus</i> <i>quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Purpuricenus axillaris</i> Haldeman, 1847	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria</i> <i>glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus</i> <i>quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Saperda discoidea</i> Fabricius, 1798	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Sphaenothecus bivittata</i> Dupont, 1838			Associated with twigs girdled by <i>Oncideres cingulata texana</i> Horn (Cerambycidae)		Linsley 1940
Cerambycidae	<i>Sphaenothecus bivittata</i> Dupont, 1838 [as <i>Taranomis bivittata</i> (Dupont)]	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Stenosphenus lugens</i> LeConte, 1862	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Stenosphenus notatus</i> (Olivier, 1795)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Thyralis undatus</i> (Chevrolat, 1834)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Trachyderes mandibularis</i> (Dupont in Audinet-Serville, 1834) [as <i>Dendrobias mandibularis</i> (Audinet-Serville)]	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	<i>Urteptes celtis</i> (Schaeffer, 1905)	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	<i>Urgleptes querci</i> (Fitch, 1858) [as <i>Lepturges querci</i> (Fitch)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	<i>Xylotrechus colonus</i> (Fabricius, 1775)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	<i>Chariessa pilosa</i> (Forster, 1771)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	<i>Cymatodera inornata</i> (Say, 1835)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	<i>Enoclerus quadrisignatus</i> (Say, 1835)	<i>Leucaena puberulenta glabra</i> Mill.]		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cleridae	<i>Enoclerus</i> sp.	<i>Prosopis glandulosa</i> Torr. var. <i>glandulosa</i>	Average 9.1 mm	Associated with twigs girdled by <i>Oncideres rhodosticta</i> Bates (Cerambycidae)	TX	Polk and Ueckert 1973
Cleridae	<i>Madoniella dislocatus</i> (Say, 1825) [as <i>Phyllobaenus dislocatus</i> (Say)]	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cleridae	<i>Madoniella dislocatus</i> (Say, 1825) [as <i>Phyllobaenus dislocatus</i> (Say)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	<i>Monophylla pallipes</i> Schaeffer, 1908	<i>Leucaena puberulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cleridae	<i>Monophylla terminata</i> (Say, 1835)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	<i>Pyticeroidea laiticornis</i> (Say, 1835) [as <i>Neichnea laiticornis</i> (Say)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Chramesus hicoriae</i> LeConte, 1868	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Cophes fallax</i> (LeConte, 1876) [as <i>Cryptorhynchus fallax</i> LeConte]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Hylocurus rudis</i> (LeConte, 1876) [as <i>Hylocurus biorbis</i> Blackman]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Magdalis pandura</i> (Herbst, 1797)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Magdalis pandura</i> (Say, 1831)	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	<i>Polygraphus rufipennis</i> (Kirby, 1837)	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Curculionidae	<i>Sciaphilus asperatus</i> (Bonsdorff, 1785) [as <i>Sciaphilus muricatus</i> (Fabricius)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924

Appendix A. Continued.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Curculionidae	<i>Scolytus piceae</i> (Swaine, 1910) [as <i>Eccoptogaster piceae</i> Swaine]	<i>Larix laricina</i> (Du Roi) K. Koch.	2.5–5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Curculionidae	<i>Scolytus quadrispinosus</i> Say, 1824 [as <i>Eccoptogaster</i> <i>quadrispinosus</i> (Say)]	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria</i> <i>glabra</i> Mill.]	<6.4 cm		NY	Blackman and Stage 1924
Melandyridae	<i>Orchesia castanea</i> Melsheimer, 1846	<i>Carya glabra</i> (Mill.) Sweet [as <i>Hicoria</i> <i>glabra</i> Mill.]	<6.4 cm	Tree killed by <i>Scolytus</i> <i>quadrispinosus</i> Say (Scolytinae)	NY	Blackman and Stage 1924
Mordellidae	1 sp.	<i>Leucaena pulverulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i>	TX	Hovore and Penrose 1982
Tenebrionidae	1 sp.	<i>Leucaena pulverulenta</i> (Schltld.) Benth.		LeConte (Cerambycidae) Associated with twigs girdled by <i>Oncideres pustulata</i>	TX	Hovore and Penrose 1982
Trogossitidae	<i>Tennoscheila</i> sp.	<i>Leucaena pulverulenta</i> (Schltld.) Benth.		Associated with twigs girdled by <i>Oncideres pustulata</i> LeConte (Cerambycidae)	TX	Hovore and Penrose 1982