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Ecology and Systematics of Coleoptera in Woody Debris of Eastern North American Forests

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ECOLOGY AND SYSTEMATICS OF COLEOPTERA IN WOODY DEBRIS OF EASTERN NORTH AMERICAN FORESTS

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the formal
requirements for the degree of
Doctor of Philosophy

in

The Department of Entomology

by
Michael Leslie Ferro
B.S., Central Missouri State University, 2001
M.S., University of Missouri, Columbia, 2004
December 2011

In closing, gentle reader, I'd like to thank you.

`What's that?' you say? Me thanking you?

No, it's not a misprint, for you see, I enjoyed writing this book as much as you enjoyed reading it. The End.

-C. Montgomery Burns

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ABSTRACT

Dead wood is a largely unexplored reservoir of taxonomic diversity and its ecology is poorly known despite its use as fuel and its roles in the carbon cycle and healthy ecosystems. During this research 15 new species of dead wood associated rove beetles (Staphylinidae: Pselaphinae) in the genus *Sonoma* Casey were discovered and described. *Sonoma tolulae* (LeConte) was redescribed.

Taxonomic issues obfuscated the identity of another dead wood associate, *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae). Examination of holotypes resulted in the discovery of two nomenclatural synonyms: *T. longicollis* Motschulsky, and *T. fletcheri* Wendeler.

An inexpensive emergence chamber used to collect insects emergent from dead wood was designed using a modified 18-gallon plastic tote box. Five fundamental axes of emergence chamber design are identified and discussed.

A study was conducted to explore diversity and abundance of beetles utilizing dead twigs in Louisiana and how they are affected by twig position. A total of 414 specimens representing 35 species were collected. Ground level bundles had the lowest richness, aboveground bundles were highest, and propped bundles were intermediate.

Three simultaneous studies (totaling 12,406 specimens) took place at six sites (half primary, half secondary forests) in Great Smoky Mountains National Park (GSMNP), USA. Leaf litter and extremely decayed downed coarse woody debris (CWD5) were sampled for Coleoptera with a sifting/Berlese technique. A total of 4261 specimens, representing 216 species were collected. Leaf litter yielded more specimens than CWD5, but both habitats had equal species richness.

Coleoptera were collected from various decay classes of fine and coarse woody debris (FWD and CWD, respectively) using an emergence chamber. A total of 5673 specimens, representing 305 species were collected. Of 71 species available for statistical analysis, 27 were associated with fresh FWD, 11 with weathered FWD, four with CWD decay class I, 14 with CWD decay class II, and eight with CWD decay class III-IV.

A short-term flight intercept trap (FIT) survey was conducted at two sites and 2472 specimens, representing 217 species, were collected. Species overlap of FIT and emergence was too low to justify FITs as a surrogate technique to survey saproxylic Coleoptera.

CHAPTER 1: INTRODUCTION

The ecology of dead wood is largely unexplored. Attitudes toward dead wood, including its use as fuel, role in the carbon cycle, and the role it plays in a healthy ecosystem, changed greatly during the latter 1970s and early 1980s (Speight 1989; Thomas 2002). Studies of dead wood, in particular its role as a reservoir for biodiversity, have recently increased, largely due to a desire to use invertebrates as indicators of high quality forests and because many species of conservation concern are also dead wood dependent (Speight 1989, Grove 2002b).

However, taxonomic uncertainty represents a major impediment to ecological research. An inability to identify species may result in an under or overestimation of species richness that reduces the value of comparisons within and between studies. When undescribed species or species in need of taxonomic review are encountered attempts should be made, whenever possible, to rectify these issues. Rove beetles in the genus *Sonoma* Casey (Staphylinidae: Pselaphinae) are associated with well decayed dead wood and were collected during this research. Only a single nominal species was recognized in eastern North America, *Sonoma tolulae* (LeConte), but examination of specimens revealed numerous cryptic but morphologically diagnosable species, prompting a revision the eastern North America fauna of the genus (Chapter 2).

Taxonomic issues obfuscated the identity of another dead wood associate and one of the most numerous species collected in these studies, *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae). Three congeners are known from eastern North America, *T. brevicristatus* Horn, *T. longicollis* Motschulsky, and *T. fletcheri* Wendeler. A review was undertaken to determine if all available names were representative of unique species (Chapter 3).

A comprehensive study of the numerous organisms, particularly insects that reside within dead wood is virtually impossible in real time due to the small size of most insects and the matrix within which they reside. To overcome this difficulty, researchers use emergence chambers to quarantine dead wood samples, and during the following weeks or months collect the organisms that emerge. Emergence chamber designs used to collect insects from dead wood were reviewed and a new design for this research was proposed and tested (Chapter 4).

No general survey of the saproxylic beetles associated with fine woody debris (FWD) has been undertaken in the United States. However, several studies have shown considerable beetle richness in dead branches and twigs (Blackman and Stage 1918, 1924). A study of beetles emergent from twig bundles of southern red oak (*Quercus falcata* Michaux) in Louisiana was conducted to catalog which species are found in that habitat and how position of twigs affects species composition (Chapter 5). A review of literature on beetles in fine woody debris was also conducted.

The community within extremely decayed downed coarse woody debris, here referred to as decay class V (CWD5), has never been systematically sampled. The presumption has been that rotten wood is eventually overrun by surrounding soil and litter inhabitants. To determine differences in faunal composition, leaf litter and CWD5 were sampled for Coleoptera with a sifting/Berlese technique at three primary and three secondary forest sites in Great Smoky Mountains National Park, Tennessee, USA, during fall 2006 and spring 2007 (Chapter 6).

Despite previous studies on the ecology of dead wood in eastern North America (Savely 1939; Howden and Vogt 1951), basic knowledge required for good management decisions is still lacking. Most important are comprehensive lists of species (e.g. Coleoptera, Diptera) that require dead wood, an understanding of their natural history, and an understanding of how they have been impacted by past and current human endeavors. Diameter of woody debris, decay class, and land use history (specifically continuity of substrates) have all been shown to influence saproxylic beetle distributions. Thus a photoeclector emergence chamber was used to concentrate Coleoptera that emerged from various decay classes of fine and coarse woody debris collected in primary and secondary forest sites in Great Smoky Mountains National Park, Tennessee, USA (Chapter 7).

An accurate survey of the Coleoptera in a given area is difficult owing to the wide variety of species and their habits. To understand how different survey activities effect catch of target taxa three separate survey activities utilizing different collection methods (flight intercept trap, sifting/Berlese, and emergence) and targeting different habitats were used to collect beetles in Great Smoky Mountains National Park (Chapter 8). The ultimate goal of this work is to provide a better understanding of the ecology of dead wood and the Coleoptera that reside within it.

CHAPTER 2: FIFTEEN NEW SPECIES OF *SONOMA* CASEY FROM THE EASTERN UNITED STATES AND A DESCRIPTION OF THE MALE OF *SONOMA TOLULAE* (LECONTE) (COLEOPTERA: STAPHYLINIDAE: PSELAPHINAE)[1]

2.1. INTRODUCTION

Sonoma was described by Casey (1886) to include two species previously placed in *Faronus*, *S. tolulae* (LeConte) and *S. isabellae* (LeConte) (LeConte 1849, 1851). Casey did not designate a type species. Casey (1887) later described two more species (*S. corticina* Casey and *S. cavifrons* Casey) and moved *Euplectus parviceps* Mäklin (1852) into *Sonoma.* Casey refers to "*parviceps* Mäkl" in the diagnoses of the two new species but never mentions the genus *Euplectus* by name. In the first revision of the genus Casey (1893) described four more species (*S. grandiceps* Casey, *S. longicollis* Casey, *S. subsimilis* Casey, and *S. rubida* Casey), and *S. parviceps* (Mäklin) was redescribed. In that same publication Casey (1893) moved *S. tolulae* into a new genus, *Rafonus*, and was returned when Raffray (1904) synonymized *Rafonus* with *Sonoma*. Lucas (1920) designated *S. corticina* Casey as the type species for the genus; however, this designation is invalid, see below. For nearly three-quarters of a century no new species of *Sonoma* were described until Park and Wagner (1962) added three from the Pacific Northwest, *S. margemina* Park and Wagner, *S. hespera* Park and Wagner, and *S. olycalida* Park and Wagner. The genus was revised again by Marsh and Schuster (1962) who synonymized Casey's *S. longicollis* and *S. subsimilis* with *S. cavifrons*, and described nine additional species, *S. repanda* Marsh and Schuster, *S. spadica* Marsh and Schuster, *S. dolabra* Marsh and Schuster, *S. vanna* Marsh and Schuster, *S. triloba* Marsh and Schuster, *S. cuneata* Marsh and Schuster, *S. humilis* Marsh and Schuster, *S. dilopha* Marsh and Schuster, and *S. priocera* Marsh and Schuster. This brought the total number of valid species of *Sonoma* to 19, all but one of which were found on the Pacific coast of North America, leaving only one, *S. tolulae,* described from eastern North America. In their revision Marsh and Schuster (1962) redescribed *S. tolulae* and provided an illustration of a male genitalia even though the holotype of *S. tolulae* is female (MCZ Type Database 2009). They did not mention how many specimens of *S. tolulae* were studied and only one locality was given as a new distributional record, so presumably only one specimen, or a series of specimens from a single locality were examined (see comments below). Chandler (1983) described an additional species, *S. yahiorum* Chandler, from California, and five more species (Chandler 1986) from Oregon, *S. petersi* Chandler, *S. cascadia* Chandler, *S. quercicola* Chandler, *S. conifera* Chandler, and *S. russelli* Chandler. A survey of the pselaphid fauna of Tehama and surrounding counties in California resulted in the discovery of three more species, *S. tehamae* Chandler, *S. wintuorum* Chandler, and *S. konkoworum* Chandler (Chandler 2003). *Sonoma yahiorum* was transferred to *Megarafonus* (Chandler 2003). The most recently described species of *Sonoma*, from British Columbia, is *S. squamishorum* Chandler and Klimaszewski (McLean, et al. 2009). These later papers brought the total number of species to 28, all from western North America, with the exception of *S. tolulae* (Map 2.1).

Sonoma corticina Casey was not one of the originally included nominal species when Casey (1886) erected *Sonoma*. Therefore, Lucas' (1920) designation of *S. corticina* as type species

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[1] Reprinted with permission by Insecta Mundi

Map 2.1. Distribution of *Sonoma* spp.

for the genus is invalid under Article 69 (ICZN 1999). The authors herein designate *Sonoma tolulae* the type species for the genus *Sonoma* Casey 1886.

During 2001 researchers from the Louisiana State Arthropod Museum and collaborators began documenting the beetle diversity of Great Smoky Mountains National Park (GSMNP) (Bayless and Carlton 2005, Carlton and Bayless 2007). This renewed interest in the pselaphine fauna of the area and resulted in the collection of many more specimens. Don Chandler (pers. com.) suspected that there were several cryptic species of *Sonoma* in eastern North America based on genitalic differences and encouraged the senior author to pursue this line of inquiry further. The type locality of *Sonoma tolulae* was visited and male specimens were collected.

2.2. MATERIAL AND METHODS

The following institutions and curators loaned material on which this study is based with depositions of primary types as indicated: Field Museum of Natural History (FMNH, James Boone and Alfred F. Newton, Jr., Curators); Great Smoky Mountains Natural History Museum (GSMNP, Adriean J. Mayor Curator); University of New Hampshire Insect Collection (DENH, Donald S. Chandler, Curator); Museum of Comparative Zoology (MCZ, Philip D. Perkins, Curator); Louisiana State Arthropod Museum (LSAM, Victoria Bayless, Curator); James F. Cornell (JFCC, Charlotte, North Carolina). Verbatim label data are given for all male specimens examined, with specimens separated by an asterisks ("*"), label breaks indicated by a slash ("/"), and the lending institution and number of specimens indicated, e.g. "(FMNH) (4M)". All specimens from Louisiana State Arthropod Museum have a database number as a separate label (i.e. "/LSAM 0000000"). Those specimens are deposited in the LSAM unless otherwise indicated. All holotypes of newly described species are deposited in FMNH.

Collection of additional specimens by the authors (and others) was done using a sifting/Berlese technique as outlined in Schauff (2001).

Dissections of genitalia were performed after relaxing dried specimens in a warm water bath for 30 minutes. Alcohol preserved specimens were dissected with no additional preparation. Fine forceps were used to anchor the body, an insect pin was inserted between the fourth and fifth visible abdominal segments, the terminal segments of the abdomen were removed, and the aedeagus was extracted. Specimens were allowed to dry and repointed using Elmer's Glue-All®.

The aedeagus was placed directly into glycerin if clean, or cleared briefly in warm 10% KOH solution if contaminated with tissue, then placed into glycerin following an alcohol wash. Sometimes the genitalia of previously dried specimens contained air bubbles within the endophallus or parameres. These were removed by placing the aedeagus in a glass screw cap vial filled with enough alcohol to ensure no air bubbles would form when sealed. The cap was securely screwed down and the vial was left to set for several minutes. The bubble-less genitalia were then carefully recovered. Presumably the increased pressure allowed the air bubbles to dissolve into the alcohol or otherwise drove them from the aedeagus. A temporary glycerin slide mount was prepared and the aedeagi were examined using an Olympus BMax50 compound microscope and illustrated using a camera lucida. Aedeagi and any other detached parts of the specimens were stored in glycerin microwells or glued to cellulose acetate strips with dimethyl hydantoin formaldehyde and attached to the pins below point-mounted specimens.

For each species not represented by a unique specimen, one specimen was cleared in warm 10% KOH overnight, disarticulated, and mounted on a microscope slide in euparal. Head, pronotum, elytra, and antennal measurements were taken from these slide-mounted specimens when they were available, otherwise measurements were taken from the holotype. All measurements were taken in the dorsal view and represent the maximum value. The head was measured from the anterior margin of the clypeus to the back of the temples (area of greatest constriction of the occiput), and width was measured at the middle of the eyes. Total length was measured from the holotype and was from the anterior margin of the clypeus to the end of the fourth visible abdominal tergite. Tergite one refers to the first visible tergite.

Point-mounted specimens were examined using a Wild Heerbrugg stereo microscope. Whole specimens were photographed using a Syncroscopy® automontage system and images were optimized using Adobe Photoshop®. All measurements are in millimeters.

Maps were created using the mapping utility at <www.gpsvisualizer.com> (Schneider 2009). Markers represent collection events, not specimens. Where multiple specimens were taken at a single locality, only one marker is shown. Localities represented by circles are from coordinates taken with a Global Positioning System at the time of collection and may be considered as or more accurate than the map scale allows. Triangles are used to represent localities with verbal descriptions only (label data provided in Material Studied) and the degree of accuracy and precision of these records is unknown. Where multiple samples were taken at the same general location (i.e. Brasstown Bald) care was taken to slightly stagger triangles to illustrate that multiple collections occurred.

2.3. SYSTEMATIC ACCOUNTS

2.3.1. CLASSIFICATION OF *SONOMA* CASEY 1886

The 43 known species of *Sonoma* may be arranged into four species groups with distributions noted as state and province codes. For a full description of the genus see Marsh and Schuster (1963).

isabellae group

S. cascadia Chandler 1986 – OR
S. cavifrons Casey 1887 – CA, OR
S. conifera Chandler 1986 – OR
S. corticina Casey 1887 – CA
S. cuneata Marsh and Schuster 1962 – CA
S. dilopha Marsh and Schuster 1962 – CA
S. dolabra Marsh and Schuster 1962 – CA
S. grandiceps Casey 1894 – CA
S. hespera Park and Wagner 1962 – CA, OR
S. humilis Marsh and Schuster 1962 – CA
S. isabellae (LeConte 1851) – CA

S. konkoworum Chandler 2003 – CA
S. margemina Park and Wagner 1962 – BC, OR, WA
S. olycalida Park and Wagner 1962 – WA
S. parviceps (Mäklin 1852) – BC, OR, WA
S. petersi Chandler 1986 – OR
S. priocera Marsh and Schuster 1962 – OR
S. quercicola Chandler 1986 – OR
S. repanda Marsh and Schuster 1962 – CA
S. rubida Casey 1894 – CA
S. russelli Chandler 1986 – OR
S. spadica Marsh and Schuster 1962 – CA
S. squamishorum Chandler & Klimaszewski 2009 – BC
S. tehamae Chandler 2003 – CA
S. triloba Marsh and Schuster 1962 – CA
S. vanna Marsh and Schuster 1962 – CA
S. wintuorum Chandler 2003 – CA

cygnus group
S. baylessae **new species** – NC, TN
S. brasstownensis **new species** – GA
S. cygnus **new species** – GA, NC
S. parkorum **new species** – NC, TN

tolulae group
S. chouljenkoi **new species** – AL, GA, KY, NC, TN
S. gilae **new species** – GA, TN
S. gimmeli **new species** – NC, TN
S. nicholsae **new species** – NC
S. sokolovi **new species** – A,L GA
S. tolulae (LeConte 1849) – GA, NC, TN

tridens group
S. holmesi **new species** – NC, MD, PA, VA, WV
S. mayori **new species** – TN
S. nhunguyeni **new species** – AL
S. streptophorophallus **new species** – VA
S. tishechkini **new species** – GA, NC, SC
S. tridens **new species** – KY

2.3.2. KEY TO THE MALES OF *SONOMA* EAST OF THE MISSISSIPPI RIVER

External differences, such as body size, frontal foveae, elytral foveae, size of the eye, and relative width of the first and second antennal segments are not adequate to distinguish species. The only reliable method of identifying male species of *Sonoma* (Fig. 2.17) is direct comparison of the aedeagus (Fig. 2.18–2.33). Aedeagus extraction is a straight forward process requiring no special preparation to the specimen (see Materials and Methods) and provides an unambiguous feature for identification. The known range of any given species is probably a function of sampling rather than its actual distribution in nature, therefore the collection of a species far from previously known localities should not be cause for alarm. For the same reasons, the existence of several to many additional undescribed species in eastern North America is expected. Females may only be identified circumstantially by association with males.

1 Left paramere with apical half internally lobed (scoop shaped), short, only extending posteriorly to basal half of endophallus, never elongate or blade like (Fig. 2.18–2.21) (*cygnus* group) **2**

-- Left paramere never internally lobed, usually elongate with a mesal blade or hook, extending posteriorly beyond basal half of endophallus (Fig. 2.22–2.33). In *S. mayori* (Fig. 2.33) and *S. nhunguyeni* (Fig. 2.29) the left paramere is blunt, but never internally lobed **5**

2 (1) Apical half of endophallus thick, strongly recurved to left; right paramere with acute apex (Fig. 2.18); GA, NC .... 1. ***S. cygnus*** new species

-- Apical half of endophallus not recurved to left, either with large bulbous apex (Fig. 2.20), left lateral subapical process (Fig. 2.19), or wide apically expanded lamina (Fig. 2.21); right paramere with acute apex or not **3**

3 (2′) Apical half of endophallus with left lateral subapical process; apex of right paramere broad with blunt mesal hook (Fig. 2.19); NC, TN .... 2. ***S. parkorum*** new species

-- Apical half of endophallus without lateral subapical process, either with large bulbous apex (Fig. 2.20), or wide apically expanded lamina (Fig. 2.21); apex of right paramere acute.. **4**

4 (3′) Apical half of endophallus with large bulbous apex (Fig. 2.20), NC, TN .... 3. ***S. baylessae*** new species

-- Apical half of endophallus with wide apically expanded lamina (Fig. 2.21); GA .... 4. ***S. brasstownensis*** new species

5 (1′) Aedeagus compact, ratio of width to length ca. 0.7 – 0.8; endophallus often with sigmoidally curved apex (Fig. 2.24–2.27); right paramere often with apical hook or subapical lobe (Fig. 2.22, 2.24, 2.26, 2.27) or scythe shaped (Fig. 2.23) (*tolulae* group) **6**

-- Aedeagus elongate, ratio of width to length ca. 0.4 – 0.7; endophallus apex curved (Fig. 2.31) or not (Fig. 2.32), never sigmoidal; right paramere never with apical hook or subapical lobe, may have laterally curved claw (Fig. 2.28) (*tridens* group) **11**

6 (5) Left paramere with apical hook (Fig. 2.22); NC............. 5. ***S. nicholsae*** new species

-- Apex of left paramere without apical hook (Fig. 2.23–2.27) **7**

7 (6′) Endophallus with apex and subapical process connected by a thin membrane; right paramere scythe shaped (Fig. 2.23); GA, TN................. 6. ***S. gilae*** new species

-- Apex of endophallus sinuate (Fig. 2.25–2.26), or elongate and strongly curved right; right paramere often with apical hook or subapical lobe (Fig. 2.24, 2.26, 2.27), or acute (Fig. 2.25) **8**

8 (7′) Endophallus with subapical shelf, apex strongly curved right; right paramere as wide as left paramere at midpoint (Fig. 2.24); NC, TN ....7. ***S. gimmeli*** new species

-- Endophallus without subapical shelf, apex curved left; right paramere ca. ½ as wide as left paramere at midpoint (Fig. 2.25–2.27) **9**

9 (8′) Left paramere with distal third convergent to acute apex; lateral digitate process of endophallus wide at base, ca. 2x width of right paramere; right paramere without apical hook or subapical lobe (Fig. 2.25); GA, NC, TN .... 8. ***S. tolulae*** (LeConte)

-- Left paramere with distal third wide, blade like; lateral digitate process of endophallus narrow; right paramere with apical hook or subapical lobe (Fig. 2.26–2.27) **10**

10 (9′) Endophallus wide at base, basal left margin bulging, apex with wide, elongate sigmoidal curve to left; right paramere weekly angulate at midpoint, mesally curved to rounded apex (Fig. 2.26); AL, GA, KY, NC, TN .... 9. ***S. chouljenkoi*** new species

-- Endophallus narrow at base, basal left margin straight, apex with shallow sigmoid curve to left; right paramere sides parallel, except lateral angulate process at midpoint and evenly rounded subapical internal lobe, apex acute (Fig. 2.27); AL, GA .... 10. ***S. sokolovi*** new species

11 (5′) Left paramere with acute apex extending to level of endophallus; endophallus with apex "U" shaped in dorsal profile and curved ventrally; right paramere with laterally curved claw (Fig. 2.28); VA ..11. ***S. streptophorophallus*** new species

-- Left paramere with acute apex extending to level of endophallus (Fig. 2.30) or not (Fig. 2.29, 2.31–2.33); apex of endophallus with at most subapical process, not "U" shaped (Fig. 2.29–2.31); right paramere without apical hook (Fig. 29–34) **12**

12 (11′) Endophallus with subapical process (Fig. 2.29–2.31) **13**

-- Endophallus without subapical process (Fig. 2.32–2.33) **15**

13 (12) Left paramere 1/2 length of endophallus, apex truncate; right paramere with apex rounded (Fig. 2.29); AL .... 12. ***S. nhunguyeni*** new species

-- Left paramere at least 2/3 length of endophallus; right paramere with apex acute (Fig. 2.30–2.31) **14**

14 (13′) Left paramere nearly as long as endophallus, with apical blade elongate; right paramere with lateral setose process ca. 1/6 length of entire paramere (Fig. 2.30); KY .... 13. ***S. tridens*** new species

-- Left paramere shorter, ca 2/3 length of endophallus, apical blade not elongate; right paramere with lateral setose process elongate, 1/3 length of entire paramere (Fig. 2.31); NC, MD, PA, VA, WV .... 14. ***S. holmesi*** new species

15 (12′) Aedeagus long and thin, ratio of width to length 0.38; lateral digitate process on endophallus small; right paramere with low setose process (Fig. 2.32); GA, NC,

SC .... 15. ***S. tishechkini*** new species

-- Aedeagus wider, ratio of width to length 0.58; lateral digitate process of endophallus large, right paramere with large setose process (Fig. 2.33); TN .... 16. ***S. mayori*** new species

2.3.3. DESCRIPTION OF SPECIES GROUPS

The 43 species recognized in the present paper have been arranged into four species groups. The diagnostic characters used to distinguish the groups are based entirely on male aedeagal characters.

isabellae group

Diagnosis. Aedeagus compact, rarely with parameres as long as endophallus; the parameres are globose basally, with a distinct demarcation between base and any apical processes; often with thin elongate setae from one third to equal to length of paramere; parameres rarely with lateral blades or hooks.

Distribution. All species in this group are known from western North America and are not known to be sympatric with those from any other species group.

cygnus group

Diagnosis. Left paramere uniquely shaped with apical half internally lobed (scoop shaped); endophallus with an enlarged apex or elaborate subapical processes; and right paramere broad, as long as or longer than endophallus, usually with an acute apex or (*S. parkorum*) rounded process, but never a recurved hook.

Distribution. Species in this group form a small clump stretching from GSMNP in Tennessee south through the eastern tip of North Carolina to the northeast corner of Georgia. The *cygnus* group is sympatric with the *tolulae* and *tridens* groups.

tolulae group

Diagnosis. Aedeagus compact, ratio of width to length ca. 0.7 – 0.8; endophallus often with a sigmoidally curved apex that may be reduced to a hook (*S. nicholsae*) or further reduced and connected by a thin membrane to a subapical process (*S. gilae*); the right paramere has an apical hook or subapical lobe, or is acute apically and lacks a setose process.

Distribution. This group has the widest geographic range of the eastern species o*f Sonoma*. This is due in large part to *S. chouljenkoi*, which occurs from mid-western North Carolina, through the eastern two thirds of Kentucky, the eastern half of Tennessee, north eastern Alabama, north western Georgia, and into GSMNP in western North Carolina. *Sonoma chouljenkoi* overlaps the known ranges of all other species in this group, although not entirely. The range of *Sonoma sokolovi* extends across to northwestern Alabama; the range of *S. gilae* and *S. tolulae* extends into southwestern North Carolina and northeastern Georgia. The *tolulae* group is sympatric over the entire range of the *cygnus* group and most of the *tridens* group.

tridens group

Diagnosis. Aedeagus elongate, ratio of width to length ca. 0.4 – 0.7; left paramere with acute apex or truncate (*S. nhunguyeni* and possibly *S. mayori*), never internally lobed; endophallus straight or shallowly curved, may or may not have a subapical process; right paramere as long as endophallus or nearly so, with an acute or rounded apex, but never with a mesal hook or subapical lobe (*S. streptophorophallus* has a unique laterally curved claw at the apex of the right paramere).

Distribution. This group has a very wide geographic range, but none of the species appear to be sympatric, although three species are known from single specimens and further collection may show range overlap. *Sonoma holmesi* has the most northern range of any of the eastern *Sonoma* and is found from southwestern Pennsylvania south to northwestern North Carolina. The rest of the group is geographically dispersed, occurring from western Virginia, westward to eastern Kentucky, south to northeastern Alabama, and east to southeastern North Carolina.

2.3.4. DIAGNOSIS OF *SONOMA*

Throughout eastern North America members of the genus can be distinguished from those of all other genera of pselaphines by the following combination of characters: head with deep frontal depression between antennal insertions; antennae lacking club, at most weakly clavate; elytra bearing discal foveae in addition to usual basal foveae; tarsomeres 1 and 2 short and subequal, tarsomere 3 relatively much longer (Newton et al. 2001).

2.3.5. SPECIES ACCOUNTS

1. *Sonoma cygnus* new species (Fig. 2.1, 2.18; Map 2.5)

Description. Holotype, male. Measurements: head 0.33 long, 0.40 wide; pronotum 0.43 long, 0.48 wide; elytra 0.75 long, 0.33 wide; antennomeres 1–11 total, 0.96; total length 1.92.

Head. Eyes prominent, maximum length in dorsal view 4/5 length of first antennal segment, with approximately 50 facets. Antennomere 2 ~2/5 width of 1; 3 smallest.

Thorax. Elytra with row of three large sutural foveae in basal third; central row of ~10 foveae contained in basal 1/2. Winged.

Abdomen. Tergite one with transverse patch of microtrichia narrowly interrupted at midline. Weak basal lateral foveae on ventrites. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: lobed internally (scoop shaped); short, basal half parallel sided; apical half bulbous, with apical margin mesally and mesal face concave; narrow posteriorly curved hooked process at midpoint of external margin, sub-apical setose process with 7 long stout setae, 3 inserted along lateral margin, 4 at apex of subapical process. Endophallus: base of lateral digitate process 4/5 width of base, basally broad, distally narrowed to broad truncate apex, ventrad from right paramere; apical one half thick, strongly re-curved to left. Right paramere: elongate, blade like; dorsolateral lobe on basal third with 6 long stout setae inserted distally; lateral constriction at level of digitate process of endophallus; lateral rounded lobe 1/3 from base; distal 2/3 twisted mesally, apically lamellate and ventral margin curved mesally. Parameres lacking tubercles.

Type Material. Holotype, male: *Rabun Bald, Ga. Rabun Co. 30.V.64 El. 2,500′ / Forest floor debris near dead wood / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). Deposited in FMNH.

Paratypes (n=3). **UNITED STATES: NORTH CAROLINA: Macon Co.:** *N.C.: Macon Co. 2 mi NW Highlands 19–III–1976 / berlese rhodo– dendron litter LEWatrous (DENH) (1M). *N.C. Macon Co. Coweeta Hydrologic Lab rhododendron litter 13 Apr. 1979 R. Turnbow (DENH) (1M); same data (1M) SLIDE.

Geographical Distribution. *Sonoma cygnus* has been collected at three localities, Rabun County in the extreme northeastern corner of Georgia, and two localities in neighboring Macon County, North Carolina. The only available elevational record is from 760 m.

Comments. *Sonoma cygnus* adults have been collected during March - May. Specimens were collected from "forest floor debris near dead wood," and "rhododendron litter" using a Berlese funnel.

Sonoma cygnus most closely resembles *S. baylessae* in aedeagal characters. The hooked process at the external margin of the left paramere, and the narrow digitate process and strongly recurved apex of the endophallus of *S. cygnus* will serve to separate it from *S. baylessae*. The strongly recurved apex of the endophallus is a unique feature in the genus.

Etymology. The specific epithet refers to the curved apical portion of the endophallus, which is reminiscent of curved neck of some species in the genus *Cygnus* (swan).

2. *Sonoma parkorum* new species (Fig. 2.2, 2.19; Map 2.2)

Description. Holotype, male. Measurements: head 0.33 long, 0.41 wide; pronotum 0.41 long, 0.48 wide; elytra 0.76 long, 0.36 wide; antennomeres 1–11 total, 1.00; total length 2.04.

Head. Eyes prominent, maximum length in dorsal view 4/5 length of first antennal segment, with approximately 30 facets. Antennomere 2 3/5 width of 1; 3 smallest.

Thorax. Elytra with row of 5 sutural foveae in basal 1/3; two foveae lateral sutural foveae in basal 1/4; central row of 5 foveae in basal 2/5. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: swollen at base, lobed internally (scoop shaped) then narrowed to sharply falcate apex; subapical shelf ventrad, curved right, with 2 thick lateral setae; apex with 4 setae pointed mesally, all setae apically minutely bifid. Endophallus: lateral digitate process elongate, ventrad of right paramere, apex rounded, sharply curved dorsally; base thick, parallel sided, large left lateral subapical process; apex elongate, pointed slightly right, tip blunt. Right paramere: broad throughout; dorsal lateral setose process small, near base, with 5 apical setae; lateral constriction at level of digitate process of endophallus thin, nearly same width distad level of lateral digitate process of endophallus; apex broad with blunt mesal process. Tubercles of left paramere fine, concentrated on ventral face, less numerous dorsally. Right paramere with coarse, sparse tubercles on mesal dorsal face.

Type Material. Holotype, male: *TENNESSEE: Blount Co. *GSMNP*, App. Tr. ~0.6 km W Mt. Thunderhead summit at 35°34.11′N 83° 42.00′W 1585m. Forest litter sifting 13 April 2006. A.K.Tishechkin / LSAM 0107285 (1M). Deposited in FMNH.

Paratype (n=2). **UNITED STATES: NORTH CAROLINA: Swain Co.:** *Smoky Mts., N. C. Bryson City Deep Ck., 2,000 ft. / Aug. 27 1930 Darlington (MCZ) (1M). *N CAROLINA: Swain Co. *GSMNP*, upper Eagle Creek Tr. at 35°33.03′N 83°43.98′W 1165m. Forest litter. 14 April 2006. A.K.Tishechkin / LSAM 0109115 (1M) SLIDE.

Geographical Distribution. *Sonoma parkorum* is known from three specimens, one from Blount County, Tennessee and two from Swain County, North Carolina. All specimens were collected within GSMNP. *Sonoma parkorum* was collected between 609 to 1585 m elevation.

Comments. Specimens were collected during April and August from leaf litter and extracted with Berlese funnels.

Sonoma parkorum has aedeagal characters unlike any other *Sonoma*. The large left lateral subapical process of the endophallus will serve to distinguish this species from all others in the genus.

Etymology. This species is named for: Orlando Park (1901-1969), a pselaphine specialist; and Jong-Seok Park, a staphylinid specialist and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

3. *Sonoma baylessae* new species (Fig. 2.3, 2.20; Map 2.2)

Description. Holotype, male. Measurements: head 0.32 long, 0.35 wide; pronotum 0.42 long, 0.45 wide; elytra 0.60 long, 0.32 wide; antennomeres 1–11 total, 0.95; total length 1.84.

Head. Eyes large, maximum length in dorsal view equal to length of first antennal segment, with approximately 20 facets. Antennomere 2 2/3 width of 1; 3 smallest.

Thorax. Elytra with row of 5 sutural foveae in basal 2/5, first fovea large; single fovea lateral and slightly basal to second sutural fovea; central row of 3 foveae in basal 2/5. Brachypterous.

Abdomen. Tergite one without transverse patch of microtrichia. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: swollen at base, lobed internally (scoop shaped); subapical setose process large, flattened, curved dorsomesad; 2 thick setae inserted on lateral margin; 4 thick setae inserted along obliquely truncate apex; large rounded mesal lobe; subapical shelf narrow and spine-like. Endophallus: lateral digitate process base as wide as endophallus base, ventrad of right paramere, sharply curved dorsally; large bulbous apex. Right paramere: dorsolateral setose process near base, long, with 5 apical setae; lateral constriction at level of digitate process of endophallus; apical 4/5 sinuate, apex acute. Tubercles on parameres fine and sparse, concentrated dorsally on left paramere, dorsomesally on right paramere.

Type Material. Holotype, male: *U.S.A., TN, Sevier Co. GSMNP, 0.5 km NE Newfound Gap, elv. 1600m 83°24′46″W, 35°38′9″N / forest liter Berlese 26 June 2001 C. Carlton, V. Moseley A. Tishechkin / LSAM0002288 (GSMNP) (1M). Deposited in FMNH.

Paratypes (n=4). **UNITED STATES: NORTH CAROLINA: Swain Co.:** *Gt.Smoky Mts.Nat.Pk. Newfound Gap Swain Co., N. C. 9.VI.60 Alt. 5000′ Leaf duff / W. Suter & J. Wagner Collectors / [male symbol] (FMNH) (2M). *N CAROLIA: Swain Co. *GSMNP*, Appalachian Tr. at Beech Gap. 35°28′27″N 83°42′27″W. 1650m. Forest litter / rotten wood 20 July 2003. A.Tishechkin / LSAM 0091887 (GSMNP) (1M). **TENNESSEE: Sevier Co.:** *USA Tenn. –N.Car.

Sevier Co. GSMNP, Newfound Gap to Clingmans Dome / Lot # 76–107 Oct. 11,1976 Berlesate R.Chenowith & R.T.Allen / LSAM0002046 (1M) SLIDE.

Geographical Distribution. *Sonoma baylessae* is known from the proximity of Newfound Gap in GSMNP, which is on the border of Sevier and Swain counties in Tennessee and North Carolina, respectively. One other specimen was collected ~30 km west at Beech Gap in GSMNP, Swain County, North Carolina. Specimens were collected between 1520 and 1650 m elevation.

Comments. Specimens were collected in June, July, and October from leaf litter and rotten wood and extracted using a Berlese funnel.

Sonoma baylessae has aedeagal characters unlike any other *Sonoma*. The large rounded mesal lobe of the left paramere and the large bulbous apex of the endophallus serve to distinguish this species from all others in the genus.

Etymology. This species is named for Victoria "Vicky-Loo" Lynn Moseley Bayless, co-collector of the holotype, curator of the Louisiana State Arthropod Museum, and participant and co-PI of the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

4. *Sonoma brasstownensis* new species (Fig. 2.4, 2.21; Map 2.3)

Description. Holotype, male. Measurements: head 0.31 long, 0.37 wide; pronotum 0.37 long, 0.44 wide; elytra 0.67 long, 0.35 wide; antennomeres 1–11 total, 0.85; total length 2.04.

Head. Eyes large, maximum length in dorsal view 9/10 length of first antennal segment, with approximately 25 facets. Antennomere 2 7/10 width of 1; 3 smallest.

Thorax. Elytra with row of 4 sutural foveae in basal 1/3, first fovea large, distance from 2nd to 3rd fovea 3x distance from 3rd to 4th; single fovea lateral to second sutural fovea; central row of 5 foveae in basal 2/5. Winged.

Abdomen. Thick transverse row of microtrichia narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: swollen at base, lobed internally (scoop shaped); apex blunt with long curved lateral spine; single thick distolateral seta adjacent to apical spine, single thick mesal subapical seta; truncate mesal setose process with 5 thick apically finely bifid setae on distal margin. Endophallus: lateral digitate process long and wide, ventrad from right paramere, strongly curved dorsally; strongly curved ventrally in distal 1/3 with apically expanded lamina. Right paramere: dorsolateral setose process near base, long, apex rounded, with 5 thick apical setae; lateral constriction at level of digitate process of endophallus; apex blade-like, acute. Tubercles weak and sparse concentrated on lateral and ventral surface of left paramere, and absent from right paramere.

Type Material. Holotype, male: *USA: Georg., Towns Co., 1 mi. S Brasstown Bald, (4000'), 15-V-1981, FMHD #81-169, ex litter under rhododen. on hillside 20 stream edge, L. Watrous (FMNH) (1M). Deposited in FMNH.

Paratypes (n=5). **UNITED STATES: GEORGIA: Towns Co.:** *USA: Georg., Towns Co., 1 mi. S Brasstown Bald, (4000'), 15-V-1981, FMHD #81-169, ex litter under rhododen. on hillside 20 stream edge, L. Watrous (FMNH) (1M). *USA: Georg., Towns Co., 1 mi. S. Brasstown Bald, 15-IV-1981, FMHD #81-172, ex damp litter at base of steep incline, L. Watrous (FMNH) (1M). **Union Co.:** *Brasstown Bald, GA. Union Co. 8.IX.63 El. 2,750' / Forest floor debris / H.R.Steeves,Jr. J.D.Patrick,Jr. Collectors / H. R. Steeves Jr. Collection / [male symbol] (FMNH)

(1M); same data, (FMNH) (1M) SLIDE. *Brasstown Bald Union Co., GEORGIA 9.VIII.1965 / Moss on log W.Suter leg. / [male symbol] (FMNH) (1M).

Geographical Distribution. *Sonoma brasstownensis* is only known from Brasstown Bald, which is bisected by Towns and Union Counties in northeastern Georgia, 830 - 1220 m elevation.

Comments. Specimens were collected during April, May, August, and September from litter under rhododendron, damp litter at the bottom of an incline, and from moss on a log.

Sonoma brasstownensis has aedeagal characters unlike any other *Sonoma*. The apically expanded lamina of the distal 1/3 of the endophallus will serve to distinguish this species from all others in the genus.

Etymology. This species is named for the type and only known locality, Brasstown Bald, Georgia.

5. *Sonoma nicholsae* new species (Fig. 2.5, 2.22; Map 2.2)

Description. Holotype, male. Measurements: head 0.30 long, 0.38 wide; pronotum 0.42 long, 0.42 wide; elytra 0.50 long, 0.32 wide; antennomeres 1–11 total, 0.90; total length 2.02.

Head. Eyes small, maximum length in dorsal view 2/3 length of first antennal segment, with approximately 25 facets. Antennomere 2 width of 1; 3 smallest.

Thorax. Elytra with row of ~5 small sutural foveae in basal 1/3; central row of 3 foveae in basal 2/5. Presumed brachypterous.

Abdomen. Tergite one without transverse patch of microtrichia. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Compact; apex of endophallus extending beyond parameres. Left paramere: robust; dorsolateral shelf 1/2 from apex with 6 thick setae; distal 1/3 evenly acuminate, apex hooked. Endophallus: lateral digitate process long, broad, ventrad from right paramere; sides divergent in apical 2/5; apex with large acute hook on left and rounded shelf on right. Right paramere: widened at base, dorsal lateral setose process elongate, with 5 apical setae; lateral constriction at level of digitate process of endophallus wide; apex abruptly curved mesally. Course, irregular tubercles present on mesal aspects of parameres.

Type Material. Holotype, male: *U.S.A., NC, Haywood Co. GSMNP, Chestnut Branch Trail 83°07′24″ W, 35°45′34″ N elv. 740m, leaf litter Berlese 1 August 2001, A. Tishechkin / LSAM0002378 (1M). Deposited in FMNH.

Paratype (n=1). **UNITED STATES: NORTH CAROLINA: Swain Co.:** *USA NC. Dirt Rd. from Heintooga Overlook to Cherokee / Lot #77-89 June 27, 1977 Berlesate 5100′-4900′ R.Chenowith & J.Heiss / LSAM0002044 (1M).

Geographical Distribution. Specimens have been collected in GSMNP in Haywood and Swain Counties, North Carolina between 740–1550 m elevation.

Comments. Specimens have been collected in June and August from leaf litter and extracted with a Berlese funnel.

Sonoma nicholsae has aedeagal characters unlike any other *Sonoma*, although it bears a superficial resemblance to *S. gimmeli.* The apical hooks on the parameres and endophallus of *S. nicholsae*, the lack of an apical hook on the left paramere, and the blunt subapical hook of the right paramere of *S. gimmeli* will serve to distinguish these two species.

Etymology. This species is named for Rebecca "Becky" Jo Nichols, Entomologist at GSMNP, and a supporter and promoter of the All Taxa Biodiversity Inventory in GSMNP.

6. *Sonoma gilae* new species (Fig. 2.6, 23; Maps 2, 6)

Description. Holotype, male. Measurements: head 0.30 long, 0.38 wide; pronotum 0.39 long, 0.45 wide; elytra 0.53 long, 0.28 wide; antennomeres 1–11 total, 0.92; total length 2.08.

Head. Eyes small, maximum length in dorsal view 7/10 length of first antennal segment, with approximately 30 facets. Antennomere 2 ~4/5 width of 1; 3 smallest.

Thorax. Elytra with row of three large sutural foveae in basal half; central row of 3 foveae in basal 1/2. Brachypterous.

Abdomen. Tergite one without transverse patch of microtrichia. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: base expanded in lower 1/3; evenly tapering to sharp acute apex; 6 subapical setae. Endophallus: lateral digitate process base 7/10 width of endophallus base, blunt, ventrad from right paramere; subapical process and apex wide, curved right apically, subapical process and apex connected by thin membrane which extends distally. Right paramere: longer than rest of aedeagus; basal third bulbous, bearing 5 thick setae on lateral face; lateral constriction at level of digitate process of endophallus; apical 2/3 scythe shaped, mesally arcuate, narrow and sharply acute. Parameres with scattered tubercles.

Type Material. Holotype, male: *TENNESSEE: Cocke Co. *GSMNP,* Albright Grove @ 35°44.11′N 83°16.78′W 970m. Forest litter. 1 Aug 2004. J.Ciegler, A.Tishechkin / LSAM 0094824 (1M). Deposited in FMNH.

Paratypes (n=23). **UNITED STATES: GEORGIA: Union Co.:** *Brasstown Bald, GA. Union Co. 27.IX.64 El. 2812′ / Forest floor debris nr. rotten wood / H.R.Steeves,Jr. J.D.Patrick,Jr Collectors / H.R.Steeves,Jr. Collection (FMNH) (1M). *Brasstown Bald, GA. Union Co. 24.X.65 El. 2415′ / Forest floor debris nr. rotten wood / H.R.Steeves,Jr. J.D.Patrick,Jr Collectors / H.R.Steeves,Jr. Collection (FMNH) (2M). **TENNESSEE: Blount Co.:** *Cade's Cove. Blount Co. Smoky Mts N.P. Tenn 13:IX:53, 5A·KO / Field Mus. Nat. Hist. Orland Park Pselaphidae Colln. (FMNH) (1M). *USA: TN: Blount Co. GSMNP, Cades Cove Parsons Branch Rd .5 mi from jct Force Creek Rd / 35°33.75′N 83°51.62′W Hemlock log litter 28 Jul 2004 SA Gil, J Hilten / LSAM 0146840 (GSMNP) (1M). *USA: TN: Blount Co. GSMNP, lower Gregory Ridge Tr 1 mi from trail–head / Berlese leaf litter 28 Jul 2004 A Tishechkin Beetle Blitz / LSAM 0146909 (1M). *TENNESSEE: Blount Co. *GSMNP,* lower Gregory Ridge Tr. @ 35°33.5′N 83°50.5′W. 630m. For. Litter 28 Jul 2004. A.K.Tishechkin / LSAM 0095574 (1M); same data LSAM 0095578 (1M). *TENNESSEE: Blount Co. *GSMNP,* lower Cooper Rd. Tr.@35°37.02′N 83°55.61′W 375m. Forest litter. 31 July 2004. J.Ciegler & S.Gil / LSAM 0094923 (GSMNP) (1M); same data, LSAM 0094925 (1M). *TENNESSEE: Blount Co. *GSMNP,* Parsons Branch Rd. 0.5mi from jct. with Forge Creek Rd. 605m. 35°33.75′N 83°51.62′W. Forest litter 31 Jul. 2004. J.Hilten & S.Gil / LSAM 0094934 (1M) SLIDE. *TENNESSEE: Blount Co., *GSMNP,* upper Long Hungry Ridge Tr. at 35°30.89′N 83°51.00′W. 1390m. For. litter 12 April 2006. A.K.Tishechkin / LSAM 0109118 (GSMNP) (1M). **Cocke Co.:** *USA: TN: Cocke Co. GSMNP Albright Grove N35°44.173′ W83°16.647′ 24 VI – 15 VII 2006 SP35C –CWD Rear 1 –M Ferro / LSAM 0167670 (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35°44.173′ W83°16.647′ 15 VII–17 VIII 2006 SP35A –CWD Rear 1 –M Ferro / LSAM 0167677 (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35°44.173′ W83°16.647′ 5

October 2006 SP3 CWD5 2 of 3 –M Ferro / LSAM 0152199 (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35º44.173′ W83º16.647′ 31 March 2007 SP3 CWD5 1 of 3 –M Ferro / LSAM 0152202 (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35º44.173′ W83º16.647′ 31 March 2007 SP3 CWD5 3 of 3 –M Ferro / LSAM 0152203 (1M); same data, LSAM 0152204 (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35º44.173′ W83º16.647′ 4X′06 – IV 2007 SP35A –CWD Rear 1 –M Ferro / LSAM 167678 (1M). **Sevier Co.:** *Tenn. :Sevier Co. Smoky Mtn. Natl. Pk., VI–17–1978 TPCopeland (DENH) (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35º43.147′ W83º23.349′ 18 V –24 VI 2006 SN15C –CWD Rear 1 –M Ferro / LSAM 0167680 (1M). *USA: TN: Sevier Co. GSMNP Laurel Falls N35º40.808′ W83º36.067′ 2 April 2007 SP1 CWD5 1 of 3 –M Ferro / LSAM 0152195 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek trail N35º41.42′ W83º23.56′ 6 October 2008 Sifting CWD5 M. Ferro / LSAM 0170163 (1M).

Geographical Distribution. Specimens have been collected from Cocke and Blount Counties in eastern Tennessee within GSMNP and Brasstown Bald in north central Georgia between 375–1390 m elevation.

Comments. Specimens have been collected in March, April, and June-October from "forest litter," "leaf litter," "hemlock log litter," coarse woody debris decay class III-IV and V, and "forest floor debris near rotten wood". Berlese funnels and dead wood emergence traps were used as a collection technique.

Sonoma gilae has aedeagal characters unlike any other *Sonoma*. The curved subapical and apical processes of the endophallus connected by a thin membrane and the smoothly curved scythe shaped right paramere will serve to separate this species from all others in the genus.

Individuals may have either fully formed flight wings, reduced flight wings, or be entirely brachypterous. Individuals with fully formed flight wings have a transverse patch of microtrichia narrowly interrupted at the midpoint on tergite one.

Etymology. This species is named for Stephanie Anne Gil, one of the co-collectors of the paratypes of this species and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

7. *Sonoma gimmeli* new species (Fig. 2.7, 2.24; Maps 2.2, 2.7)

Description. Holotype, male. Measurements: head 0.33 long, 0.40 wide; pronotum 0.42 long, 0.48 wide; elytra 0.55 long, 0.35 wide; antennomeres 1–11 total, 0.94; total length 1.96.

Head. Eyes prominent, maximum length in dorsal view 1.2 x length of first antennal segment, with approximately 30 facets. Antennomere 2 ~7/12 width of 1; 3 smallest.

Thorax. Elytra with row of three sutural crenulations in basal third; row of 4 foveae in center 2/5, distance from first to second twice distance from second to third. Brachypterous.

Abdomen. Tergite one without transverse patch of microtrichia. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Compact; apex of endophallus extending beyond parameres. Left paramere: base wide; parallel sided in basal half; apical half with wide, thin mesal blade; cluster of 6 thick elongate setae 1/3 from apex. Endophallus: basal 2/3 extremely asymmetrical; lateral digitate process at base 2/3 width of endophallus base, ventrad from right paramere; subapical shelf-like process directed ventrad; tip bowed, strongly curved right with expanded apex. Right paramere: base enlarged, rounded laterally; dorsolateral setose process short, rounded, with 4 setae along apex; lateral constriction at level of digitate process of endophallus; distal 1/3 as wide as left paramere, with straight outer margin; apex obtuse with blunt subapical hook mesad. Tubercles sparse, fine, scattered along mesal basal half of dorsal faces of both parameres.

Type Material. Holotype, male: *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 31 March 2007 SN1 Litter 2 of 3 –M Gimmel / LSAM 0152215 (1M). Deposited in FMNH.

Paratypes (n=14). **UNITED STATES: NORTH CAROLINA: Jackson Co.:** *NC: Jackson Co. Waterrock Knob, pitfall trap Spruce–fir forest, Ridge #8 648102N 763704E 06–20 June 2002, J. Robertson (GSMNP) (1M). **TENNESSEE: Cocke Co.:** *USA Tenn Cocke Co. GSMNP Cosly Crekk Trail / Lot #76–110 Oct. 15, 1976 Berlesate R.Chenowith & R.T.Allen / LSAM0002052 (GSMNP) (1M). *TN: Cocke Co. GSMNP ATBI Plot: Albright Grove Pitfall 85 83 16 50 35 43 60 Parker, Stocks, Petersen 16 FEB – 2 MAR 2001 (GSMNP) (1M). *USA: TN: Cocke Co. GSMNP Albright Grove N35°44.173′ W83°16.647′ 24 VI –15 VII 2006 SP35A –CWD Rear 1 –M Ferro / LSAM 0167674 (1M). **Sevier Co.:** *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 14 IV –18 V 2006 SN15B –CWD Rear 1 –M Ferro / LSAM 0170157 (1M); same data LSAM 0170158 (1M); same data LSAM 0170159 (1M) SLIDE. *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 14 IV –18 V 2006 SN12B –CWD Rear 1 –M Ferro / LSAM 0170160 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 14 IV –18 V 2006 SN15C –CWD Rear 1 –M Ferro / LSAM 0170161 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 5 October 2006 SN1 CWD5 3 of 3 –M Ferro / LSAM 0152194 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 4V′06 – 1 IV 2007 SN15C –CWD Rear 1 –M Ferro / LSAM 0167669 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 31 March 2007 SN1 Litter 1 of 3 –M Gimmel / LSAM 0152219 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 31 March 2007 SN1 Litter 2 of 3 –M Gimmel / LSAM 0152216 (1M). *USA: TN: Sevier C. GSMNP Porters Creek trail N35°41.42′ W83°23.56′ 6 October 2008 Sifting CWD5 M. Ferro / LSAM 0170162 (1M).

Geographical Distribution. Specimens have been collected from four locations in Sevier and Cocke Counties in the Tennessee side of GSMNP and from one location south of the park in Jackson County, North Carolina.

Comments. Specimens have been collected during March-July, and October from litter and coarse woody debris decay class 3-4 and 5. Berlese funnels and emergence traps were used as a collection technique. Two specimens were collected with pitfall traps; one set from February through early March, and the other set from early to late June.

Aedeagal characters of *Sonoma gimmeli* are similar to those of *S. chouljenkoi*. The wide lateral digitate process and subapical shelf of the endophallus, and width of the right paramere of *S. gimmeli* will serve to separate it from *S. chouljenkoi*.

Etymology. This species is named for Matthew Lincoln Gimmel, collector of the holotype specimen, phalacrid systematist, and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

8. *Sonoma tolulae* (LeConte, 1849) Fig. 2.8, 2.25; Maps 2.2, 2.13

Faronus tolulae LeConte 1849: 108-109. Holotype, female. Label: *[orange disc = Southern States; Gulf States; VA, NC, SC, eastern TN?, GA, AL, MS, FL, AR?, LA] / Type, [typed] 6184 [hand written] / Faronus tolulae [hand written] / HOLOTYPE [typed] Faronus tolulae LeConte [hand written]. Type locality: Tolulæ cataractam Georgiæ. Type deposition: Museum of Comparative Zoology, Harvard. LeConte 1851: 215. Brendel and Wickham 1890: 75-77.

Rafonus tolulae: Casey 1893: 441-442. Casey 1908: 257

Sonoma tolulae: Raffray 1904: 499-500. Bowman 1934: 6.

Description. Male. Measurements: head 0.30 long, 0.40 wide; pronotum 0.40 long, 0.45 wide; elytra 0.58 long, 0.29 wide; antennomeres 1–11 total, 1.04; total length 2.04.

Head. Eyes large, maximum length in dorsal view equal to length of first antennal segment, with approximately 40 coarse facets. Antennomere 2 ~3/4 width of 1; 3 smallest.

Thorax. Elytra with a row of five sutural foveae extending distad to midpoint; a second row of 4 foveae parallel and mesad to the sutural foveae, distance of the first and second foveae greater than 2x the distance from the second to third foveae; a third row of three smaller foveae laterad to the central row and contained within the middle one third of the elytra. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Compact; parameres and endophallus approximately same length. Left paramere: bulbous, distal 1/3 symmetrically convergent to acute apex, ventral longitudinal flange with 7 thick curved setae at distal 1/3. Endophallus: base half as wide as left paramere, wide lateral digitate process ventrad from right paramere, apex with sigmoid curve to left terminated posteriorly. Right paramere: lateral lobe short, rounded, with 5 thick curved setae along apex; lateral constriction at level of digitate process of endophallus; right lateral margin abruptly curved to produce acute apex with straight outer margin. Tubercles scattered along basal 3/4 of dorsal surface of left paramere, and basal half of dorsal face of right paramere.

Material Studied (n=63). **UNITED STATES: GEORGIA: Rabun Co.:** *USA:GA:Rabun Co., Satolah, V-29-1983 DSChandler, [?] Rhododendron & mixed leaf litter (DENH) (1M). *USA: Georgia: Rabun Co. Tallulah Falls N 34°44.360′ W 83°23.917′ 7 Oct 2008 M. Ferro Leaf Litter 475m / LSAM 0170147 (1M); same data, LSAM 0170165 (1M). **Towns Co.:** *USA: Georg., Towns Co., 1 mi. S Brasstown Bald, (4000′), 15-V-1981, FMHD #81-169, ex litter under rhododen. on hillside 20 stream edge, L. Watrous (FMNH) (4M). *USA: Georg., Towns Co. 1 mi. S. Brasstown Bald, 15-V-1981, FMHD #81-170, ex litter under rhododen. along stream, L. Watrous (FMNH) (1M). *USA: Georg., Towns Co., 1 mi. S. Brasstown Bald, 15-IV-1981, FMHD #81-172, ex damp litter at base of steep incline, L. Watrous (FMNH) (9M). **Union Co.:** *Brasstown Bald, GA. Union Co. II·VIII·63 El. 2750 B / H.R.Steeves Jr. J.D.Patrick Jr. Collectors/ Rhododendron and softwood debris/ H. R. Steeves Jr. Collection / [male symbol]. (FMNH) (2M). *GA.: Union Co. Blairsville (7 mi. E.?); below Brasstown Bald; VI:14:1973; 1400′. leg. W. Suter WS#73-60a; FM(HD)#73-243 Ber.: sawdust & pine litter on periphery of small pile. (FMNH) (1M). **NORTH CAROLINA: Macon Co.**: *USA: N. Carol., Macon Co., 3 mi NW Highlands, 15-V-1981, FMHD #81-174, ex litter under rhododen. and hemlock, L. Watrous. (FMNH) (1M). **Swain Co.:** *USA N.C. Swain Co. Dirt Rd. from Heintooga Overlook to Cherokee / Lot # 76-103 Oct. 14, 1976 Berlesate 5300′-5000′ R.Chenowith & J.Heiss / LSAM0002042 (1M). *USA N.C. Swain Co. Dirt

Rd. from Heintooga Overlook to Cherokee / Lot #77-89 June 27, 1977 Berlesate 5100’-4900’ R.Chenowith & J.Heiss / LSAM0002061 (1M). *N CAROLINA: Swain Co. *GSMNP*, Andrews Bald 1755m. 1m^2 litter. 27 June 1996. Coyle, Edwards, Stiles & Wright / LSAM 0096222 (1M). *N CAROLINA: Swain Co. *GSMNP*, Andrews Bald 1755m. 1m^2 litter. 6 Sept 1997. Aiken, Coyle, Davis & Edwards / LSAM 0096221 (1M); same data, LSAM 0096224 (GSMNP) (1M). *N CAROLINA: Swain Co. *GSMNP*, Appalachian Tr. at Beech Gap. 35°28’27”N 83°42’27”W. 1650m. Forest litter / rotten wood 20 July 2003. A.Tishechkin. / LSAM 0091889 (1M); same data, LSAM 0091890 (1M). *N CAROLINA: Swain Co. *GSMNP*, Thunderhead Mt. nr. summit @ 35°33.95’N 83°42.6’W 1615m. Forest litter. 30 July 2004 A.K.Tishechkin / LSAM 0095568 (1M); same data, LSAM 0095569 (1M) SLIDE; same data, LSAM 0095570 (1M); same data, LSAM 0095571 (1M); same data, LSAM 0095572 (1M). *USA: NC: Swain Co. GSMNP Near Pecks Corner Shelter Leaf litter, Berlese Funnel Mixed forest on ridge, 5396’ 35°39.064N, 83°18.566W 5 Oct 2004, WD Merritt / LSAM 0170146 (1M). **TENNESSEE: Blount Co.:** *Smoky Mts. N. C.-Tenn Newfound Gap 5,000-5,200 ft. / Aug. 30 1930 Darlington (MCZ) (1M). *USA NCSWAINCOGSMNP Indian Gap 17 VII 03 J&S Cornell Hemlock Liter w/ fungi JFC003-VII-17-2C (JFCC) (1M). *TENNESSEE / N. CAROL. Border. *GSMNP* Newfound Gap. 35.611°N 83.425°W. 5075’. Sift litter 19 July 2003. S.O’Keefe / LSAM 0091840 (1M) SLIDE. *TENNESSEE: Blount Co. *GSMNP*, lower Gregory Ridge Tr. @ 35°33.5’N 83°50.5’W. 630m. For. Litter 28 Jul 2004. A.K.Tishechkin / LSAM 0095579 (GSMNP) (1M); same data, LSAM 0095580 (1M). *TENNESSEE: Blount Co., *GSMNP*, App. Tr. ~0.6km W Mt. Thunderhead summit at 35°34.11’N 83°42.00’W 1585m. Forest litter sifting 13 April 2006. A.K.Tishechkin / LSAM 0107286 (1M). *TENNESSEE: Blount Co., *GSMNP*, Mt. Thunderhead nr. summit at 35°34.02’N 83°42.60’W. 1625m. Forest litter.30.vii.2004. A.Tishechkin / LSAM 0107295 (1M). *TENNESSEE: Blount Co. *GSMNP*, Mt. Thunderhead nr. Summit @ 35°34.1’N 83°42.5’W. 1650m. Litter 30 Jul 2004. A.K.Tishechkin / LSAM 0091947 (GSMNP) (1M); same data, LSAM 0091948 (1M); same data, LSAM 0091950 (1M). **Sevier Co.:** *U.S.A., TN: Sevier Co. GSMNP, 0.5 kn NE Newfound Gap, elv. 1600m 83°24’46”W, 35° 38’9” N / forest litter Berlese 26 June 2001 C. Carlton, V. Moseley A. Tishechkin / LSAM0002286 (1M); same data, LSAM0002287 (1M); same data, LSAM0002289 (1M); same data, LSAM0002290 (1M); same data, LSAM0002291 (1M). *U.S.A., TN, Sevier Co. Appalachian Trail at Beech Gap on Clingmans Dome Rd. 83°26’50” W, 35°36’36” N / elv. 1750 m, forest litter berlese 28 June 2001, C. Carlton, A. Tishechkin, V. Moseley / LSAM0002629 (1M). *USA, TN, Sevier Co. Great Smoky Mt. Nat. Pk. Beech gap on Clingmans Dome Rd. where Appal. / Trail crosses rd. 28 June 2001, C. Carlton, A. Tishechkin, V. Moseley / LSAM 0096334 (1M). *U.S.A., TN, Sevier Co. GSMNP, Laurel Falls Trail 83°35’36”W, 35°40’19”N / elev. 747m, Epifagus berlese 1 July 2001, C. Carlton, V. Moseley A. Tishechkin / LSAM0002546 (1M). *USA: TN: Sevier Co. GSMNP, Trillium Gap Tr. on Mt. Leconte 35°39.9’N 83°26.2’W / Berlese litter 29 Jul 2001 A Tishechkin / LSAM 0146470 (1M); same data, LSAM 0146471 (1M). *TENNESSEE: Sevier Co. *GSMNP*, Indian Head Tr. 35.60944°N 83.44659°W Sift litter. 5290’ 20 July 2003. S.O’Keefe / LSAM 0080774 (1M). *TENNESSEE: Sevier Co. *GSMNP*, Road Prong Tr. at 35°36’36”N 83°27’3”W 1580m. Leaf / moss mat litter. 20 July 2003 A. Tishechkin / LSAM 0091848 (1M); same data, LSAM 0091854 (1M); same data, LSAM 0091868 (1M). *Tennessee: Sevier Co. GSMNP, Trillium Gap Tr. @ 35°39.9’N 83°26.2’W 1400m. Forest litter. 29 July 2004. A.Tishechkin/ LSAM 0091968/ (1M). *Tennessee: Sevier Co. GSMNP, Trillium Gap Tr. @ 35°40.3’N 83°26.7’W 1420m. Forest litter. 29 July 2004. A.Tishechkin/ LSAM

0091968/ (1M). *Tennessee: Sevier Co. GSMNP, Alum Cave Bluff ~¼mi behind Alum Cave 35°38.6′N 83°26.8′W 1480m. Forest litter. 30 Jul 2004. JBrown & B.Pynn / LSAM 0094908 (GSMNP) (1M); same data, LSAM 0094915 (1M). *TENNESSEE: Sevier Co. *GSMNP*, App. Tr. ~2km W Derrick Knob Shelter 35°34.07′N 83°39.81′W 1450m. Forest litter. 7 June 2005. A.K.Tishechkin / LSAM 0094927 (1M).

Geographical Distribution. *Sonoma tolulae* is known from the central portion of the eastern border of Tennessee, across the western tip of North Carolina and into extreme northeastern Georgia. Specimens have been collected from elevations ranging from 425–1755 m.

Comments. Specimens have been collected every month from April through October from "leaf litter," "forest litter," "Leaf/moss mat litter," "*Epifagus* berlese," "Forest litter / rotten wood," "litter under rhododendron and hemlock," "sawdust & pine litter on periphery of small pile," and "damp litter". The senior author collected one female and two male specimens from rotted wood (decay class V).

The holotype described by LeConte is female (MCZ Type Database 2009) and was collected from "Tolulæ cataractam Georgiæ" (LeConte 1849). The senior author visited Tallulah Falls in Rabun County, Georgia in the fall of 2007 and the fall of 2008 and collected two male and one female specimens. The aedeagal characters of the two male specimens were identical. Based on the presumed type locality and absence of other species, we concluded that these specimens are conspecific with *S. tolulae*.

Aedeagal characters of *Sonoma tolulae* are similar to those of *S. sokolovi*. However, the acute apex of the left paramere and shape of the right paramere (right lateral margin abruptly curved to produce an acute apex with straight outer margin) and the lack of a subapical internal lobe on the apex of the right paramere in *S. tolulae* will distinguish these two species.

Individuals may have either fully formed flight wings, reduced flight wings, or be entirely brachypterous. Individuals with reduced or absent flight wings have no microtrichia on tergite one.

A disarticulated specimen of *Sonoma chouljenkoi* from Black Mountain, Buncombe County, North Carolina was in Orlando Park's collection labeled *Sonoma tolulae*. It appeared to be specifically prepared to be used as a model for external morphology illustrations. Park provided several illustrations of "*Sonoma tolulae*" in *A Study in Neotropical Pselaphidae* (1942) and we suspect that *S. chouljenkoi* was used as the model. However, the stylized form of the drawings and lack of noticeable differences in the external morphology between *S. chouljenkoi* and *S. tolulae* resulted in drawings that were not species specific.

The only previous illustration of an aedeagus attributed to *S. tolulae* is in Marsh and Schuster (1962). The illustration is clearly of *S. chouljenkoi* and the only additional locality given by them is "Black Mountain, Buncombe County, North Carolina." They do not say how or from whom they obtained the specimen or illustration, but probably the specimen or illustration came from Orlando Park and is based on a specimen from the same series from which his disarticulated model came. The authors found no examples of dissected genitalia labeled *Sonoma tolulae* in Orlando Park's material.

9. *Sonoma chouljenkoi* new species (Fig. 2.9, 2.26; Maps 2.2, 2.4)

Sonoma tolulae: Marsh and Schuster 1962 (not LeConte, 1849)

Description. Holotype, male. Measurements: head 0.33 long, 0.40 wide; pronotum 0.44 long, 0.50 wide; elytra 0.70 long, 0.35 wide; antennomeres 1–11 total, 0.89; total length 2.00.

Head. Eyes prominent, maximum length in dorsal view 6/10 length of first antennal segment, with approximately 50 facets. Antennomere 2 ~7/10 width of 1; 3 smallest.

Thorax. Elytra with row of 2 sutural foveae in basal 1/3; single fovea laterad of basal sutural fovea; row of five central foveae extending distad to midpoint. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Compact; apex of endophallus extending beyond parameres. Left paramere: curved, base parallel sided, blade-like in apical one third, row of 6 thick setae attached in lateral 1/3, apex acute. Endophallus: base bulbous; lateral digitate process equal to width of and ventrad from right paramere, sharply curved dorsally to rounded apex; sigmoidal and narrowing in apical third, apex with elongate sclerotized sigmoid curve to left followed by lightly sclerotized sigmoid curve terminated posteriorly. Right paramere: bulbous at base, width 3/5 length; dorsolateral setose process short, rounded, with 1 basal and 3 apical setae; lateral constriction at level of digitate process of endophallus; apical ½ narrow, weakly angulate at midpoint, mesally curved to rounded apex. Tubercles sparse, fine, scattered along basal half of dorsal faces of both parameres.

Type Material. Holotype, male: *TENNESSEE: Sevier Co. *GSMNP*, Porters Creek Tr. @ 35°40.1′N 83°23.6′W 850m. Forest litter. 31 July 2004. C.E.Carlton &N.Lowe / LSAM 0094971 (1M). Deposited in FMNH.

Paratypes (n=88). **UNITED STATES: ALABAMA: Cherokee Co.:** *ALA., Jackson Co. Indian Rocks Cave 5.5 mi. s Skyline 16.IX.67 x / Forest floor debris at rotten wood / T.G.Marsh W.M.Andrews Collectors / H.R.Steeves Collection / [male symbol] (FMNH) (1M). *Alabama: Cherokee Co. Desoto SP 34° 29.880′N 85° 37.152′W forest liter 20 Aug 2009 I.M.Sokolov / LSAM 0170154 (1M). **GEORGIA: Dade Co.:** *GA: Dade Co., 5mi SE of Cloudland Can. SP. [?]ogd's Lake April 20, 1983 [?]ing forest floor / 4.20.83 F CLC / (FMNH) (1M). **Walker Co.:** *GA: Walker Co. Pigeon Mtn. Nr. Rocky Lane at 34°39.972′ N 85°22.467′ W 495m / Litter Berlese I.M.Sokolov 24 March 2008 / LSAM 0170155 (1M); same data, LSAM 0170156 (1M). **KENTUCKY:** *Ky. / H. C. FALL COLLECTION (MCZ) (1M). **Bath Co.:** *USA :KY :Bath Co., Daniel Boone N. F. 4 mi from Clear / Ck. Rec. Area [??] [??] 918. XIII–5–1988 RMReeves sift rotten stump (DENH) (1M). **Edmonson Co.:** *KY. Edmonson Co. Mammoth Cave Nat. Park 8–APR–1950. L.J. Stannard Acc. 49602 / LSAM0002060 (1M). *KY.:Edmonton [Edmonson] Co.; Mammoth Cave Natl. Pk. Bruce Hollow VIII:24–27:1967 / leg.S.Peck, A.Fiske FM(HD)#67–145 Berlese log, stump litter / Field Mus. Nat. Hist. Orland Park Pselaphidae Colln. (FMNH) (11M). *KY.:Edmonson Co.; Mammoth Cave Natl. Pk. Cabin Woods h 24.III.1973 / Litter at log leg. W.Suter / [male symbol] (FMNH) (5M). *KY.:Edmonson Co.; Mammoth Cave Natl. Pk. Cabin Woods 24 March 1973 / Litter at log lowland leg. W.Suter / [male symbol] (FMNH) (1M). *USA: Ky., Edmonson Co., Mammoth Cave Natl. Pk., Cabin Woods, 20–IV–1983, FMHD #83–26, ex log, W. Suter (FMNH) (1M). *USA: Ky., Edmonson Co., Mammoth Cave Natl. Pk., Cabin Woods, 20–IV–1983, FMHD #83–119, litter pocket along stream, W. Suter (FMNH) (2M). **Meade Co.:** *Rockhaven KY [Meade Co.] 7/22/94 / LSAM0002053 (1M). **NORTH CAROLINA: Buncombe Co.:** *BlackMts. NC VII-15 1912 Beutenmuller (MCZ) (1M). *BlackMts. NC VII-30 1912 Beutenmuller (MCZ)

(1M). *BlackMts. NC VIII-27 1912 Beutenmuller (MCZ) (1M). *BlackMts. NC VIII-31 1912 Beutenmuller (MCZ) (2M). *BlackMts. NC X-11 1912 Beutenmuller (MCZ) (1M). *Mt. Mitchell St. Pk. Commissary Ridge Trail Buncombe Co., N. C. 2.VII.60 Alt. c6,600′ Rhododendron & spruce duff / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). *Bl. Mount [??]_N.C. / Field Mus. Nat. Hist. Orland Park Pselaphidae Colln. (FMNH) (1M). *Field Mus. Nat. Hist. Orland Park Pselaphidae Colln. / Faronus tolulae [male symbol] Black Mt., N.C. Sept. ABDOMEN (FMNH) (1M). *Bl. Mount N.C. / Sonoma tolulae LeC. (MCZ) (1M). **Haywood Co.:** *USA: NC: Haywood GSMNP BRPW nr. Cove Field Ridge Overlook; litter / 35°25.84′N 83°21.15′W 1420m 21 Sep. 2005 ATishechkin / LSAM 0092324 (1M). **Swain Co.:** *N Carolina: Swain Co. *GSMNP*, Lakeshore Tr. at 35°28′20″N 83°43′14″W 630m. Forest litter 18 July 2003. A.Tishechkin/ LSAM 0091822 (1M) SLIDE. **Yancy Co.:** *Mt. Mitchell N.C. 4-6000′ / June 1939 Quirsfeld / Sonoma tolulae LeC. / C. A. Frost Collection 1962 (MCZ) (1M). *N.CAR.:Yancy Co. Mt. Mitchill 31.V.1973 g / fern rhizome W.Suter leg. / [male symbol] (FMNH) (3M). *N.CAR.:Yancy Co. Mt. Mitchill 31.V.1973 g / fern rhizome fir, summit W.Suter leg. / [male symbol] (FMNH) (5M). *N.CAR.:Yancy Co. Mt. Mitchill 31.V.1973 [?] / fern rhizome fir, summit W.Suter leg. / [male symbol] (FMNH) (1M). *N.CAR.:Yancy Co. Mt. Mitchill 31.V.1973 [?] / Litter at log leg. W.Sute / [male symbol] (FMNH) (2M). **TENNESSEE: Bledsoe Co.:** *Fall Creek Falls St. Park, Bledsoe Co., TENNESSEE 1 September 1961 J.Wagner & W.Suter legs. / Floor Litter nr. Rhododendron W.Suter leg. / [male symbol] (FMNH) (4M). **Blount Co.:** *USA: TN: Blount Co. GSMNP, lower Gregory Ridge Tr 1 mi from trail-head / Berlese leaf litter 28 Jul 2004 A Tishechkin Beetle Blitz / LSAM 0146908 (GSMNP) (1M). *TENNESSEE: Blount Co., *GSMNP*, Grapeyard Ridge Tr. at. 35°41.68′N 83°27.77′W Litter sifting. 1 August 2004 V.Bayless & S.Gil / LSAM 0107302 (GSMNP) (1M). *USA: TN: Blount Co. GSMNP Tremont N35°37.308′ W83°40.447′ 4 October 2006 SN2 CWD5 2 of 3 –M Ferro / LSAM 0152196 (1M); same data, LSAM 0152197 (1M). *USA: TN: Blount Co. GSMNP Tremont N35°37.308′ W83°40.447′ 3 April 2007 SN2 CWD5 2 of 3 –M Ferro / LSAM 0152211 (1M). **Cocke Co.:** *USA: TN: Cocke Co. GSMNP Albright Grove N35°44.173′ W83°16.647′ 15 VII–17 VIII 2006 SP33B –CWD Rear 1– M Ferro / LSAM 0170153 (1M). **Fentress Co.:** *Jordan Motel TENN. Jamestown, Pickett Co. [Fentress Co.] 16.VI.62 A Forest Floor Debris / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (3M). *Jordan Motel TENN. Jamestown, Fentress Co. B 13–IV–63 / Forest floor debris nr. dead wood / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). **Pickett Co.:** *USA: Tenn., Pickett Co., Pickett St. Pk., 7–XII–1980, FMHD #80-120, conc. litter nr. stream (pine rhodod.), H. Dybas (FMNH) (1M). **Sevier Co.:** *Tenn.:Sevier Co., Smoky Mtn. Natl. Pk., VI–17–1978 TPCopland (DENH) (1M) SLIDE. *TN: Sevier Co., GSMNP Roaring Fork Motor Nature Trl. Dry leaf litter, 13 April 1995 / (GSMNP) (1M). *TENNESSEE: Sevier Co. *GSMNP*, Twin Creek ATBI Plot. FIT#1. 26 June – 1 July 2001. V.Bayless, C.E.Carlton & A.K.Tishechkin / LSAM 0113013 (1M). *TENNESSEE: Sevier Co. *GSMNP*, Twin Creek ATBI Plot. Malaise trap MT-0120010706. 21 June – 6 Jul 2001. I.C.Stocks / LSAM 0096225 (GSMNP) (1M). *U.S.A, TN, Sevier Co. GSMNP, Chimneys Picnic Area Nature Trail, 83°29′45″ W, 35°38′6″ N, elv.891 m / forest litter berlese 28 June 2001, C. Carlton, A. Tishechkin, V. Moseley / LSAM0002767 (GSMNP) (1M). *TENNESSEE: Sevier Co. *GSMNP*, Porters Creek Tr. @ 35°40.1′N 83°23.6′W 850m. Forest litter. 31 July 2004. C.E.Carlton &N.Lowe / LSAM 0094963 (1M) SLIDE; same data, LSAM 0094964 (1M); same data, LSAM

0094970 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek N35°40.790′ W83°23.855′ 12 IV -18 V 2006 SP25C –CWD Rear 1 –M Ferro / LSAM 0167675 (1M). *USA: TN: Sevier Co. GSMNP Greenbrier N35°43.147′ W83°23.349′ 24 VI -15 VII 2006 SN12A –CWD Rear 1 –M Ferro / LSAM 0167676 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek N35°40.790′ W83°23.855′ 24 VI -15 VII 2006 SP25C –CWD Rear 1 –M Ferro / LSAM 0170150 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek N35°40.790′ W83°23.855′ 15 VII-17VIII 2006 SP24C –CWD Rear 1 –M Ferro / LSAM 0167673 (1M). *USA: TN: Sevier Co. GSMNP Sugarlands QW N35°39.826′ W83°31.509′ 6 October 2006 SN3 CWD5 2 of 3 –M Ferro / LSAM 0152214 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek trail 6 October 2008 N35°40.79′ W83°23.85′ Sifting CWD5 M.Ferro / LSAM 0170149 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek N35°40.790′ W83°23.855′ 4X′06 – 1 IV 2007 SP25A –CWD Rear 1 –M Ferro / LSAM 0167672 (1M). *USA: TN: Sevier Co. GSMNP Porters Creek 5 April 2007 N35°40.790′ W83°23.855′ SP2 Litter 1 of 3 –M.Gimmel / LSAM 0152198 (1M). *USA: TN: Sevier Co. GSMNP Sugarlands QW N35°39.826′ W83°31.509′ 8 October 2008 Sifting Litter/CWD5 M.Ferro / LSAM 0170151 (1M); same data, LSAM 0170152 (1M). **Sulivan Co.:** *Tenn.: Sulivan Co. Bristol [?]–5–1978 TPCopland (DENH) (1M). **Locality Unknown:** *[?] / ex: Collection of Rev. Jerome Schmitt (1890–1904)? St. Vincent Archabby / Raf. tolulae L (FMNH) (1M).

Geographical Distribution. *Sonoma chouljenkoi* has the widest known distribution of any eastern species of *Sonoma*. It ranges from north central Kentucky south to northern Alabama and eastward to western North Carolina. Specimens have been collected from elevations ranging from 495–2011 m.

Comments. *Sonoma chouljenkoi* has been collected every month from March through October from "forest litter," coarse woody debris decay class V ("CWD5"), "dry leaf litter," "pine and rhododendron litter," "fern rhizome," "rhododendron & spruce duff," and "log, stump litter". A Berlese funnel was reported as a collection technique. This is the only eastern species of *Sonoma* to have been collected in Malaise and flight intercept traps indicating an active flight period. Both specimens were collected during a late June to early July trapping period.

Aedeagal characters of *Sonoma chouljenkoi* are similar to those of *S. sokolovi*. The wide base, wide digitate process, and shape of the apical 1/3 of the endophallus along with the shape of the right paramere (angulate at midpoint of apical 1/2) and the mesally curved to rounded apex will serve to separate it from *S. sokolovi*. The elongate sclerotized sigmoid curve at the apex of the endophallus is a unique feature in the genus.

Individuals may have either fully formed flight wings, reduced flight wings, or be entirely brachypterous. Individuals with reduced or lacking flight wings have no microtrichia on tergite one.

Etymology. This species is named for Dmitry "Mad Dog" Vladimirovich Chouljenko, one of the co-collectors of the paratypes of this species and a participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

10. *Sonoma sokolovi* new species (Fig. 2.10, 2.27; Map 2.10)

Description. Holotype, male. Measurements: head 0.32 long, 0.39 wide; pronotum 0.39 long, 0.45 wide; elytra 0.69 long, 0.43 wide; antennomeres 1–11 total, 1.00; total length 2.16.

Head. Eyes prominent, maximum length in dorsal view 9/10th length of first antennal segment, with approximately 35 facets. Antennomere 2 ~7/10th width of 1; 3 smallest.

Thorax. Elytra with basal row of ~8 sutural crenulations extending to distad 1/3; one distinct fovea laterad to base of crenulations; center with 7 foveae extending to distad 4/10. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Compact; apex of endophallus extending beyond parameres. Left paramere: curved, same width until apical 1/5, simple and blade-like in apical one third, ventral setose process with 6 thick elongate setae, apex acute. Endophallus: slightly thicker at base than left paramere, lateral digitate process 2/3 width of and ventrad from right paramere, apical 1/3 curved abruptly ventrally, then slightly anteriorly to bluntly rounded apex of main process, long slender secondary process originating subapically and with 5 spirally arranged curves, extends posteriorly. Right paramere: base bulbous, width 2/5 length; dorsolateral setose process short, rounded, with 6 setae along apex; apical 2/3 narrow, sides parallel, except lateral angulate process at midpoint and evenly rounded subapical internal lobe, apex acute. Tubercles sparse, fine, scattered along basal half of dorsal faces of both parameres.

Type Material. Holotype, male (slide mounted): *USA: GEORGIA, Dade Co., Cloudland Canyon State Pk. 34°48.88′N 85°29.10′W 510m. 17 Sept 2006. Forest litter sifting. I.M.Sokolov / LSAM 0108981 (1M) SLIDE. Deposited in FMNH.

Paratypes (n=27). **UNITED STATES: ALABAMA: Cherokee Co.:** *Rock Bridge Canyon Franklin Co. nr. Hodges, ALA. 21.V.61 Forest floor debris / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). *USA: Alabama: Cherokee Co. Desoto SP 34°29.880′N 85°37.152′W 20 August 2009 Forest Litter Col. I.M.Sokolov / LSAM 0170148 (1M). **Franklin Co.:** *The Dismals, Ala. Franklin Co. (B) 19.VII.59 Leaf mold / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (5M). *The Dismals, Ala. Franklin Co. (B) 19.VII.59 Wet leaf mold / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M); same data, Sonoma tolulae (Lec.) [male symbol] 59 Det. H.R. Steeves Jr. / Sonoma (Sonoma) horrenda Park (FMNH) (1M). **Lawrence Co.:** *Bee Branch Scenic Area Bankhead Nat'l Forest Lawrence Co., Ala. 30.IV.61 Oak tree hole / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). W**inston Co.** *AL: Winston Co. Sipsey R. Rec Area Bankhead Nat For 22 June 1985 RD Cave colr / taken in rotten log and leaf litter (DENH) (1M). **GEORGIA: Dade Co.:** *Cloudland Canyon S.Pk. Dade Co., GA. 3-IX-61 Debris nr. log / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (1M). *Cloudland Canyon St. Park, Trenton, Dade Co. GEORGIA 3 September 1961 W. Suter & J. Wagner legs. / stream debris / [male symbol] (FMNH) (2M). *Cloudland Canyon St. Park, Trenton, Dade Co. GEORGIA 3 September 1961 W. Suter & J. Wagner legs. / Floor Litter at Log on Slope W.Suter leg. / [male symbol] (FMNH) (1M). *Cloudland Canyon S.Pk. Dade Co., GA. 7-VII-62 B Forest floor debris / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (3M). *Cloudland Canyon S.Pk. Dade Co., GA. 7-VII-62 C Forest floor debris / H. R. Steeves Jr. Collector / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (3M). *Cloudland Canyon S.Pk. Dade Co., GA. 14-IV-63 / Forest floor debris nr. dead wood / H.R.Steeves,Jr. J.D.Patrick,Jr. Collectors / H. R. Steeves Jr.

Collection / [male symbol] (FMNH) (4M). *GA.,Dade Co. Cloudland Canyon St.Park,16.V.72 S&JPeck,Ber.236 Rhododendron litter / [male symbol] / CNCI Ottawa, Canada (FMNH) (2M).

Geographical Distribution. *Sonoma sokolovi* is known from several localities across northern Alabama including numerous specimens from "The Dismals," Franklin County, and from Cloudland Canyon State Park, Dade County, in the extreme northwestern corner of Georgia. The only available elevational record is 510 m.

Comments. *Sonoma sokolovi* has been collected every month from April through September from "forest floor debris near dead wood," "rhododendron litter," "stream debris," "wet leaf mold," "rotten log and leaf litter," and an "oak tree hole". This is the only mention of a specimen of an eastern *Sonoma* species collected from a tree hole.

Aedeagal characters of *Sonoma sokolovi* are similar to those of *S. chouljenkoi*. The depth of spiral of the apical secondary process of the endophallus varies in *S. sokolovi* but is never as great as in *S. chouljenkoi*. The narrow base, narrow digitate process, shape of the apical 1/3 of the endophallus and the lateral angulate process at midpoint and evenly rounded subapical internal lobe of the right paramere of *S. sokolovi* will serve to separate it from *S. chouljenkoi*.

Etymology. This species is named for Igor Michailovitch Sokolov, collector of the holotype specimen, carabid systematist, and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

11. *Sonoma streptophorophallus* new species (Fig. 2.11, 2.28; Map 2.11)

Description: Holotype, male. Measurements: head 0.32 long, 0.39 wide; pronotum 0.42 long, 0.44 wide; elytra 0.64 long, 0.36 wide; antennomeres 1–11 total, 0.94; total length 2.10.

Head. Eyes large, maximum length in dorsal view 1.1x length of first antennal segment, with approximately 45 facets. Antennomere 2 3/5 width of 1; 3 smallest.

Thorax. Elytra with row of five sutural foveae in basal one half; central row of two large foveae in basal 1/4. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: base parallel sided; main body short; apical 1/3 dagger shaped, attached subapically to base, blade expended apex of endophallus, extremely acute; setose process bearing 8 thick setae. Endophallus: wide to apex; lateral digitate process wide, broadly emarginate along posterior margin, not curved; apex "U" shaped in dorsal profile and curved ventrally. Right paramere: base bulbous; setose process shallow with 8 apical setae, dorsolateral seta bifid at tip; apical 2/3 narrow, sinuate, lateral constriction at level of digitate process of endophallus deep; apex with laterally curved claw. Scattered moderately coarse tubercles on dorsal and lateral surface of left paramere and dorsal surface of right paramere and sparse fine tubercles on lateral process of endophallus.

Type Material. Holotype, male: *17 mi NW Amherst Amherst Co., Va. VIII–12–1975 DSChandler / shifting oak litter DSChandler (DENH) (1M). Deposited in FMNH.

Geographical Distribution. *Sonoma streptophorophallus* is represented by a single specimen collected in central Virginia (Amherst Co.).

Comments. *Sonoma streptophorophallus* was collected in August from "oak litter".

Sonoma streptophorophallus has aedeagal characters unlike any other *Sonoma*. The left paramere is very similar to *S. tridens* but the "U" shaped apex of the endophallus in *S. streptophorophallus* will separate the two species. Both the apex of the endophallus and the laterally curved claw at the apex of the right paramere are unique to *S. streptophorophallus* and serve to distinguish it from all other species in the genus.

Etymology. The specific epithet is derived from *streptophoros* (Greek, "collared"), and *phallus* (Greek, "penis"), referring to the unique form of the endophallus apex.

12. *Sonoma nhunguyeni* new species (Fig. 2.12, 2.29; Map 2.9)

Description. Holotype, male. Measurements: head 0.32 long, 0.40 wide; pronotum 0.40 long, 0.46 wide; elytra 0.70 long, 0.38 wide; antennomeres 1–11 total, 0.90; total length 1.92.

Head. Eyes prominent, maximum length in dorsal view 9/10 length of first antennal segment, with approximately 30 facets. Antennomere 2 7/10 width of 1; 3 smallest.

Thorax. Elytra with row of 4 sutural hemi-foveae in basal 2/5; 2 foveae laterad of second hemi-fovea; single fovea laterad of distal fovea; central row of 6 foveae in basal 2/5. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: short, blunt, parallel sided; sclerotized lateral apical spine directed posteriorly; apex with 6 thick setae. Endophallus: lateral digitate process, broad basally, narrowed apically, ventrad from right paramere, curved dorsally; apical 2/5 wide, parallel sided, bearing a dorsal lamina from right lateral margin curved obliquely across dorsal surface and terminating on left lateral margin, apex blunt. Right paramere: wide; dorsolateral setose process small, bearing 2 setae; lateral constriction at level of digitate process of endophallus shallow; apical half parallel sided, curved mesad; apex obliquely truncate. Parameres with few widely scattered tubercles.

Type Material. Holotype, male: *ALA.,Jackson Co. 5mi.N.Garth 19.V.1972 S.Peck.Ber.239 / CNCI Ottawa, Canada / [male symbol] (FMNH) (1M). Deposited in FMNH.

Paratypes (n=5): **UNITED STATES: ALABAMA: Jackson Co.:** *Horseshoe Cave Sink Jackson Co., Ala. 29.IV.61 Forest floor debris / H.R.Steeves,Jr. J.D.Patrick,Jr. Collectors / H. R. Steeves Jr. Collection / [male symbol] (FMNH) (2M). *ALA.,Jackson Co. 5mi.N.Garth 19.V.1972 S.Peck.Ber.239 / CNCI Ottawa, Canada / [male symbol] (FMNH) (1M) SLIDE. *USA: Ala., Jackson Co., 6 mi N Princeton, Hor-seshoe Cave, 30–VI–1976, FMHD #67–110, residue, outside cave, S. Peck & A. Fiske (FMNH) (2M).

Geographical Distribution. *Sonoma nhunguyeni* in represented by specimens collected in Jackson County in extreme northeastern Alabama.

Comments. *Sonoma nhunguyeni* has been collected in April through June from "residue, outside cave" and forest floor debris.

Aedeagal characters of *Sonoma nhunguyeni* are similar to those of *S. mayori*. The dorsal lamina on the apical 2/5 of the endophallus, small dorsolateral setose process of the right paramere, and the obliquely truncate apex of the right paramere of *S. nhunguyeni* will serve to distinguish it from *S. mayori*.

Etymology. This species is named for Nhu Huynh Nguyen, a mycoentomologist and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP. The specific epithet is pronounced "new-win-eye."

13. *Sonoma tridens* new species (Fig. 2.13, 2.30; Map 2.14)

Description. Holotype, male. Measurements: head 0.34 long, 0.42 wide; pronotum 0.46 long, 0.48 wide; elytra 0.76 long, 0.40 wide; antennomeres 1–11 total, 1.12; total length 2.38.

Head. Eyes large, maximum length in dorsal view 4/5 length of first antennal segment, with approximately 30 facets. Antennomere 2 3/4 width of 1; 3 smallest.

Thorax. Elytra with row of ~5 fine sutural foveae in basal 2/5; central row of ~3 large foveae in basal 1/4. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Lanceolate. Left paramere: base broadly oval; apical 1/3 dagger shaped, attached subapically to base, blade not extending to apex of endophallus, extremely acute; setose process bearing 4 thick mesal setae, and 3 lateral thick setae. Endophallus: lateral digitate process very wide, ventrad from right paramere, sharply curved dorsally; apical 1/2 sinuate to right; with small subapical dorsal shelf 1/5 from apex; apex blunt. Right paramere: setose process very large, 4 thick apical setae, dorsolateral seta bifid at tip; lateral constriction at level of digitate process of endophallus very deep; apex acute. Sparse fine tubercles scattered on dorsal surfaces of left and right parameres.

Type Material. Holotype, male: *USA: Ky., Powell Co., Natural Bridge St. Pk., 12–VII–1968, FMHD #68–41, log stump litter, S. Peck (FMNH) (1M). Deposited in FMNH.

Geographical Distribution. *Sonoma tridens* is known from a single specimen collected in Powell County, Kentucky from within Natural Bridge State Park.

Comments. *Sonoma tridens* was collected in July from log and stump litter.

Sonoma tridens is the only species of *Sonoma* in which both parameres and the endophallus have acute apices pointed posteriorly. However if the left paramere of *S. mayori* is damaged and possesses an elongate blade-like apex the two species may be distinguished by the presence of the subapical dorsal shelf in the apical 1/5 of the endophallus and the very deep lateral constriction of the right paramere at the level of the digitate process of the endophallus in *S. tridens*.

Etymology. The specific epithet of this species refers to the unique trident-like, elongate, posteriorly pointed parameres and endophallus of the aedeagus.

14. *Sonoma holmesi* new species (Fig. 2.14, 2.31; Map 2.8)

Description. Holotype, male. Measurements: head 0.32 long, 0.41 wide; pronotum 0.45 long, 0.52 wide; elytra 0.77 long, 0.37 wide; antennomeres 1–11 total, 0.97; total length 2.16.

Head. Eyes large, maximum length in dorsal view 9/10 length of first antennal segment, with approximately 35 facets. Antennomere 2 3/4 width of 1; 3 smallest.

Thorax. Elytra with row of two sutural foveae in basal 1/4; single foveae lateral of midpoint between sutural foveae; central row of 5 foveae in basal 2/5. Winged.

Abdomen. Transverse row of microtrichia on first visible tergite narrowly interrupted at midline. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Lanceolate. Left paramere: wide, gently curving mesad; apical blade broadly triangular with acute apex; outer lateral setose process with 5 thick setae inserted dorsally and 1 thick seta inserted apically. Endophallus: lateral digitate process ventrad of right paramere, broad at base and elongate, strongly curved dorsally at apex, infiltrated with complex canaliculi; distal 1/3 of endophallus forming a broad dorsally curved shelf terminating to reinforced knob; terminating a short distance beyond reinforced portion as a thin lightly sclerotized tube. Right paramere: sinuate above base, nearly bifurcate; lateral setose process elongate, 1/3 length of entire paramere, 6 thick setae along lateral margin; lateral constriction at level of digitate process of endophallus; apical 3/5 thin with a left sigmoidal curve, apex blunt. Tubercles sparse, fine, scattered along dorsal faces of both parameres.

Type Material. Holotype, male: *N CAROLINA: Wilkes Co., Blue Ridge Parkway, Sheets Gap. 1020m. 36°21.84′N 81°18.29′W. Litter sifting 30 Apr 2006. A.K.Tishechkin / LSAM 0170166 (1M). Deposited in FMNH.

Paratypes (n=20). **UNITED STATES: MARYLAND: Garrett Co.:** *MARYLAND;GarrettCo. 2.1mi.E.KeysersRidge 18.vi.1968, 2500′el S.Peck, Ber#129 log–stump litter 220 lbs, 231 liters / FM([?]D)68–46 (FMNH) (1M). **PENNSYLVANIA: Westmoreland Co.:** *St. Vinc. Penn. / 10/13-[18]97 / Liebeck Coll. / H. C. FALL COLLECTION (MCZ) (1M). *St. Vinc. Penn. / 10/13-[18]97 / 10 [yellow circular label] / Liebeck Collection (MCZ) (1M). *St. Vinc. Penn. / ½-[18]99 / H. C. FALL COLLECTION / Sonoma tolulae LeC. (MCZ) (1M). *Chestnut Ridge, E. of Youngstown, Westmoreland Co., PENNSYLVANIA 27.VI.1961 / Duff nr. Rhodod J. Wagner & W. Suter leg. / [male symbol] (FMNH) (2M). *Chestnut Ridge, E. of Youngstown, Westmoreland Co., PENNSYLVANIA 11.VII.1961 / Flood duff W.Suter, J.Wagner & D.Reichle legs. (FMNH) (2M). *Chestnut Ridge, E. of Youngstown, Westmoreland Co., PENNSYLVANIA 16.IX.1961 J. Wagner / Log Mold & Floor Berlese (FMNH) (1M). *Chestnut Ridge, E. of Youngstown, Westmoreland Co., PENNSYLVANIA 16.IX.1961 J.Wagner / Log Mold & Floor Berlese (FMNH) (1M); same data, / [male symbol] (FMNH) (1M). *Chestnut Ridge, E. of Youngstown, Westmoreland Co., PENNSYLVANIA 22.VI.1962 / Floor Litter J.Berry & W.Suter leg. (FMNH) (1M). *Chestnut Ridge, PENNA. Westmoreland Co. 16.IX.1964 / Litter at Log W.Suter leg. / [male symbol] (FMNH) (1M). **VIRGINIA: Tazewell/Bland Co.:** *USA: Va., Tazewell– Bland Cos., 4.4 mi S Burks Garden, 30–VI–1968, FMHD #68–34, log litter, S. Peck (FMNH) (1M). **WEST VIRGINIA: Pocahontas Co.:** *USA: WV: Pocah. [Pocahontas] Co. 16 mi East Richwood near For. Serv. Rd. 437; off Hwy 150 VIII– 23– 1990 / Sift hardwood litter near dead logs. S. O'Keefe (DENH) (2M); same data (DENH) (1M) SLIDE. *USA: WV. Pocahontas Co. 5mi N jct 150 & 39 on 150 V–17–1991 sift maple & conif. S. O'Keefe Collr. (DENH) (2M). **Wyoming Co.:** *Pineville WVa / Leng. / 536 / 1953 (MCZ) (1M).

Geographical Distribution. Specimens have been collected from southwestern Pennsylvania south through western Maryland, south central West Virginia, and western Virginia to northwestern North Carolina. Specimens have been collected from elevations ranging from 760–1020 m.

Comments. Specimens have been collected every month from April through September from "litter," "hardwood litter near dead logs," sifted maple and conifer, "flood duff," "log–

stump litter," and duff near rhododendron. A Berlese funnel has been used as a collection technique.

Aedeagal characters of *Sonoma holmesi* are similar to those of *S. tridens*. The short broadly triangular blade of the left paramere, the broadly curved knob on the distal portion of the endophallus, and the elongate lateral setose process of the right paramere in *S. holmesi* will distinguish these two species. The right paramere will serve to distinguish it from all other species in the genus.

Etymology. The specific epithet is in recognition of Orlando Park's enthusiasm for Sherlock Holmes, that culminated in *Sherlock Holmes, Esq., and John H. Watson, M.D.: an encyclopaedia of their affairs* (Park 1962). The specific epithet also celebrates the 160 year-old mystery surrounding the cryptic species of the genus *Sonoma* in Eastern North America.

15. *Sonoma tishechkini* new species (Fig. 2.15, 2.32; Map 2.12)

Description. Holotype, male. Measurements: head 0.32 long, 0.40 wide; pronotum 0.39 long, 0.45 wide; elytra 0.61 long, 0.29 wide; antennomeres 1–11 total, 0.87; total length 2.08.

Head. Eyes large, maximum length in dorsal view 9/10 length of first antennal segment, with approximately 50 facets. Antennomere 2 1/2 width of 1; 3 smallest.

Thorax. Elytra with row of five large sutural foveae in basal 2/5; single large fovea lateral of second sutural fovea; central row of 5 foveae in basal 2/5. Winged.

Abdomen. Tergite one with transverse patch of microtrichia narrowly interrupted at midpoint. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Elongate. Left paramere: broadly triangular in basal 1/2, distal 1/2 elongate, narrowly acuminate to extremely acute apex; 6 long stout setae on lateral low flange at midpoint. Endophallus: elongate, thin, weakly sinuate, 1.4 x length of left paramere; lateral digitate process short and sharply curved dorsally, ventrad of right paramere; apex blunt. Right paramere: elongate, slightly longer than endophallus; lateral setose process low with 5 thick setae; lateral constriction at level of digitate process of endophallus; apical 4/7 parallel sided, distal 1/3 weakly curved measly; apex blunt. With sparse tubercles on basal half of dorsal face of both parameres.

Type Material. Holotype, male: *N CAROLINA: Rutherford Co. Chimney Rock State Park at 35°26.07'N 82°15.27'W. 620m Deep litter/dead logs, Berlese 20 Sept 2005. A.K.Tishechkin / LSAM 0170164 (1M). Deposited in FMNH.

Paratypes (n=11). **UNITED STATES: GEORGIA: Rabun Co.:** *GA: Rabun Co., Satolah (3 mi S.) 15 April 1973 / Litter under Rhododendron leg. W.R.Suter / [male symbol] (FMNH) (1M). *USA:GA:Rabun Co., Satolah,V–29–1983 DSChandler, sift Rhododendron and mixed leaf litter (DENH) (1M); same data, no genitalia (DENH) (1M). **NORTH CAROLINA: Brunswick Co.:** *N. Carolina:Brun. [Brunswick] Co., nr. Mako [Maco?] X–15–1979 / JPCornell hardwood litter (DENH) (1M) SLIDE. **Jackson Co.:** *N.Car.:Jackson Co. Cashiers 7 mi SE 11.VI.1973 b / Pseudofork Elm-Maple Whitewater Falls W.Suter leg. / [male symbol] (FMNH) (1M). **Transylvania Co.:** *USANCTRANSYLVANIACONr Brevard PisgahNF PinkBedsPic nic Area N35°21'11"W82°43.557' El 2500' 4/5 Aug 09J.F.& TADCornell ExLitter/FloodDebr UnderRhododendrononBeaver Pond Trail Sift/Berlese (JFCC) (1M). **SOUTH CAROLINA**: **Greenville Co.:** *SC: Greenville Co. Paris Mtn. St. Park 373263 3867371 [zone 17] 6-VII-09 UV light (JFCC) (2M). **Oconee Co.:** *USA:SC:Oconee Co. 7 mi S NC state line on Hwy. 107 / V–29–1983 DSChandler, sift forest litter (DENH) (3M).

Geographical Distribution. Specimens have been collected from Rutherford and Jackson Counties in southwestern North Carolina, Oconee County in northwestern South Carolina, and Rabun County in northeastern Georgia. A single specimen was reportedly collected from Brunswick County in extreme southeastern North Carolina near the Atlantic Coast. This is an unexpected location as all other eastern *Sonoma* appear to be restricted to highland locations. Specimens have been collected from elevations ranging from 620–762 m.

Comments. Specimens have been collected in April–October from "deep litter/dead logs," "pseudofork elm-maple," "rhododendron and mixed leaf litter" using a Berlese funnel. Two specimens were collected at an ultraviolet light trap, this is the only record of *Sonoma* specimens being taken with this collection technique.

Sonoma tishechkini has aedeagal characters unlike any other *Sonoma*. A combination of the elongate, pointed left paramere, weak lateral digitate process of the endophallus, thin elongate endophallus lacking subapical modifications, low lateral setose process on right paramere and right paramere slightly longer than endophallus of *S. tishechkini* will serve to separate this species from all others in the genus.

Etymology. This species is named for Alexey Konstantinovich Tishechkin, collector of the holotype, histerid systematist, and participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

16. *Sonoma mayori* new species (Fig. 2.16, 2.33; Map 2.2)

Description. Holotype, male. Measurements: head 0.34 long, 0.44 wide; pronotum 0.44 long, 0.48 wide; elytra 0.56 long, 0.36 wide; antennomeres 1–11 total, 1.00; total length 2.14.

Head. Eyes large, maximum length in dorsal view equals length of first antennal segment, with approximately 40 facets. Antennomere 2 3/4 width of 1; 3 smallest.

Thorax. Elytra with row of ~5 fine sutural foveae in basal 2/5; central row of three large foveae in basal 1/4. Presumed brachypterous.

Abdomen. Tergite one without transverse patch of microtrichia. No abdominal foveae. Basal pubescence present on all visible ventrites.

Aedeagus. Asymmetrical. Left paramere: short; apical half bulbous, inner apical blade wide at base (apex possibly damaged in holotype); sub-apical lateral setose process with 5 stout setae, and 4 thick ventral setae. Endophallus: base of lateral digitate process wide, ventrad from right paramere, sharply curved dorsally; apical half sinuate, slightly recurved to left, apex blunt. Right paramere: elongate, blade like; dorsolateral setose process long with 5 thick setae along apex; lateral constriction at level of digitate process of endophallus shallow; distal 2/3 curved left, narrowed to acute apex. Scattered, sparse, fine tubercles on setose processes.

Type Material. Holotype, male: *USA: Tenn., Sevier Co., Gt. Smky. Natl. Pk., Clingman's Dome nr. tower, 29–V–1982, FMHD #82–48, at stump, u. fern, W. S. Suter (FMNH) (1M). Deposited in FMNH.

Geographical Distribution. *Sonoma mayori* is known from a single specimen collected near the tower at Clingman's Dome in Sevier County, Tennessee within GSMNP at 2020 m elevation.

Comments. *Sonoma mayori* was collected in June “at stump, u. [under?] fern”.

Aedeagal characters of *Sonoma mayori* are similar to those of *S. tridens* and *S. nhunguyeni*. The left paramere of the holotype may be damaged apically, and if it possesses an elongate blade-like apex it could be similar to the left paramere of *S. tridens*. However, the lack of a subapical dorsal shelf on the endophallus, the shallow constriction at the level of the digitate process of the endophallus on the right paramere, and the acute apex of the right paramere which extends distad of the endophallus in *S. mayori,* will serve to distinguish it from *S. tridens*. The lack of a dorsal lamina on the endophallus, and the acute apex of the right paramere extending distad of the endophallus of *S. mayori* will serve to distinguish it from *S. nhunguyeni*.

Etymology. This species was named for Adriean Johann Mayor, Museum Curator of the GSMNP Collection, melyrid specialist, and a participant in the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP.

2.4. BIOLOGY OF PSELAPHINES WITH AN EMPHASIS ON *SONOMA* SPP.

Very little is known about the bionomics of *Sonoma.* Park (1942) outlined two major lifestyles of pselaphines, “Myrmecocoles” and “Mold species.” *Sonoma* belongs to the latter and is found in logs in the Class V (advanced stage) of decay (Pyle and Brown 1999) and in the leaf litter (“mold”) of the forest floor (Marsh and Schuster 1962; Chandler 1983, 1986, 2003). Pselaphines are largely predators of earth-worms, insect larvae, small flies, Collembola, and mites (Denny 1825; Park 1932a; Jacot 1935; Park 1942, 1947a,b; Park et al. 1950; Engelmann 1956; Schomann et al. 2008). Park (1932a, 1947a) observed the feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte) that were associated with ants. They appeared to be scavengers of dead or injured ant larvae. When a potential food item was found the adult would wave its antennae and twirl its palpi around the item before feeding. Feeding mostly occurred every other day.

Schomann et al. (2008) and Engelmann (1956) observed the feeding behavior of pselaphines in the “Mold Species” group. While there were differences, all the species were active predators and readily ate Collembola, the main prey item offered in the studies. In general a foraging pselaphine would slowly advance waving its head and antennae side to side. Recognition of a prey item was made through fine tactile and/or chemical clues collected with the multitude of sensilla located on the antennae. After a prey item was “sighted” the hunter would immediately raise the front of its body, fling itself forward, attack (sometimes while guiding the prey item to its jaws with its antennae or raptorial forelimbs), and capture the prey with the mandibles and apparently sticky maxillary palps. Schomann et al. (2008) also observed ~1 to 3 prey capture events over two hours of observation, indicating that their study species eat frequently. While no direct observations have been made, it is likely that *Sonoma* exhibit similar feeding behavior. As we become more appreciative of the complex interactions that take place on small scales (Jacot 1935; Park 1947b; Schomann, et al. 2008) it may be more accurate to refer to the pselaphines as “litter lions” rather than the inarticulate nomen “short-winged mold beetles.”

Pselaphines have been collected using a multitude of techniques including hand collection, Berlese funnels, pitfall traps, flight intercept traps, Malaise traps, emergence chambers, Lindgren funnel traps, and ultraviolet light (Park 1942, 1947b; Wolda and Chandler

1996; Carlton et al. 2004; Chatzimanolis et al. 2004; Carlton and Leschen 2008; McLean et al. 2009). While more systematic sampling and observations are needed, *Sonoma* populations mostly occur in leaf litter or within or near well rotted hardwood logs, adults rarely fly or venture through the leaf litter, and are rarely attracted to ultraviolet light. In a study comparing the rotted log and leaf litter habitats in GSMNP, rotted logs yielded almost 4 times more *Sonoma* specimens than leaf litter (data not shown). Seven specimens of *S. gimmeli*, six of *S. chouljenkoi*, and four of *S. gilae* were collected from decay class V coarse woody debris during a systematic study in GSMNP using emergence traps. A single specimen of *S. sokolovi* was reportedly collected from a tree hole, although whether the tree hole was in contact with the ground or elevated is unknown. *Sonoma* adults have been collected in flight. Two specimens of *S. squamishorum* were collected using Lindgren funnel traps (McLean et al. 2009). One specimen of *S. chouljenkoi* was collected in a ground-level flight intercept trap and another was collected in a Malaise trap (where the collecting container is located above ground). Two specimens of *S. gimmeli* were collected in pitfall traps. Two *Sonoma tishechkini* specimens have been collected at an ultraviolet light trap, but no *Sonoma* spp. have been collected from the numerous light trap samples taken as part of the Coleoptera portion of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007).

Nothing is known about the egg, larval, or pupal stages of *Sonoma*. The immatures of pselaphines in general are poorly known (Carlton and Leschen 2008). The life history of *Pselaphophus atriventris* (Westwood) was studied by Martin (1983) and immatures were described by Carlton and Leschen (2008). Collection records indicated that the species passed through one generation per year, and, while adults were collected throughout the year, larvae only occurred for a short period during in the spring (Carlton and Leschen 2008). If *Sonoma* has a similar life history then frequent sampling throughout the year may be the best strategy when searching for immatures.

Sonoma adults have been collected during the spring, summer, and fall. The lack of specimens from the winter months is likely more a reflection of lack of collecting effort rather than adult absence. Adults may be very long lived. Engelmann's (1956) wild caught adults representing the genera *Cedius*, *Euplectus*, and *Bibloplectus* had remained alive for more than 100 days at the time of his publication. *Sonoma* caught while moving across the landscape (pitfall, flight intercept traps, ultraviolet light traps) were collected only in the spring and summer months (February-July), suggesting higher activity during spring.

2.5. DISCUSSION

The discovery of numerous undescribed *Sonoma* species, many represented by specimens collected 20 or more years ago, illustrates a larger problem in taxonomy and systematics called "Overlooked Syndrome" (OS) (Park et al. 2010). This syndrome presents when undescribed species across an otherwise familiar landscape persist because researchers are ignorant of their existence or are otherwise impotent to rectify the issue. Taxa suffering from OS are generally small, have slight or non-existent external morphological differences, obscure habits, little economic value, and are not considered charismatic by the public. Overlooked Syndrome is especially aggravated when taxonomic expertise is lacking. The results are artificially anemic estimates of total diversity in the region and lack of credibility of ecological research involving OS taxa at any functional or analytical levels. Bossart and Carlton (2002) showed that taxa with OS characteristics were much less likely to be considered for conservation or monitoring than other taxa, and Staphylinidae especially receive little conservation attention.

Extensive collecting in GSMNP yielded eight species of *Sonoma* (Map 2.2), the highest concentration of species of this genus anywhere in North America. *Sonoma chouljenkoi*, *S. gilae*, and *S. tolulae* were each collected from ten or more localities and have been collected from more localities outside of the park. In contrast *Sonoma baylessae*, *S. gimmeli*, *S. mayori*, *S. nicholsae*, and *S. parkorum* were collected from fewer than five localities, and all, except *S. gimmeli*, are only known from GSMNP. Four of the eastern species of *Sonoma* are only known from one or two male specimens, and five species have only been collected at one locality. Local abundance and habitat specificity of some species may account for their true or perceived rarity.

This publication represents a portion of a larger body of research, specifically the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007). This effort has resulted in a unique body of publications related by collectors, localities and even specific samples (e.g. species described in this publication and in Park et al. (2010) were originally collected as part of separate research (unpublished) by the authors). The overall research of the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP has resulted in publications on the following taxa: Carabidae: *Anillinus* (Sokolov et al. 2004, 2007; Sokolov and Carlton 2008), Cerylonidae: *Philothermus* (Gimmel and Slipinski 2007), Chrysomelidae: *Psylliodes* (Konstantinov and Tishechkin 2004), Leiodidae: *Ptomaphagus* (*Appadelopsis*) (Tishechkin 2007), Mycetophagidae: *Pseudotriphyllus* (Carlton and Leschen 2009), Staphylinidae: Aleocharinae: *Leptusa*: (Park et al. 2010), Pselaphinae: *Arianops* (Carlton 2008), *Reichenbachia* (Carlton 2010).

As more attention is given to diminutive fauna we should expect to discover more undescribed species even in taxonomically well-known eastern North America. Taxonomic expertise is essential if we wish to complete goals of inventorying, understanding, and conservation of the few complex ecosystems that are left on Earth.

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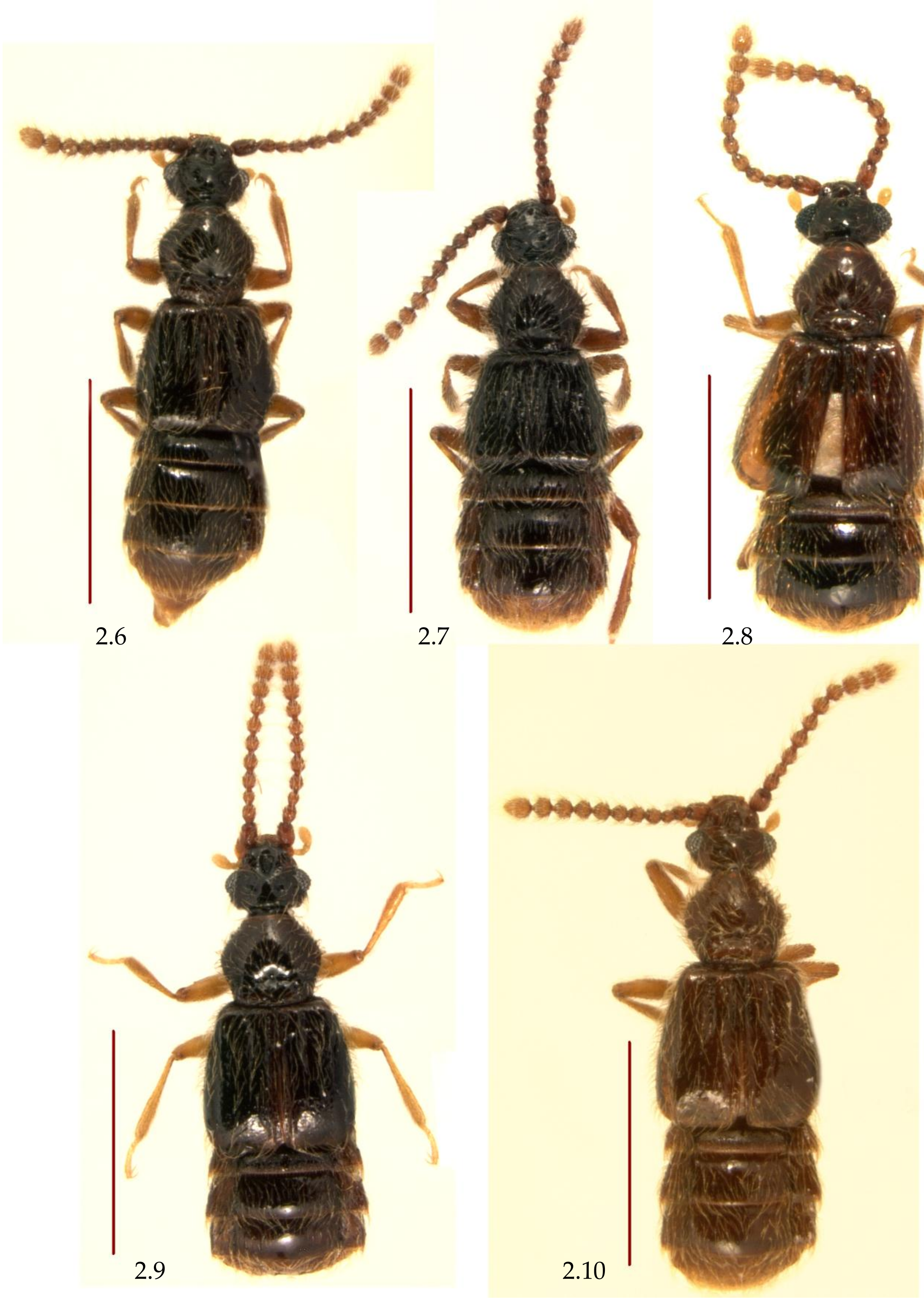
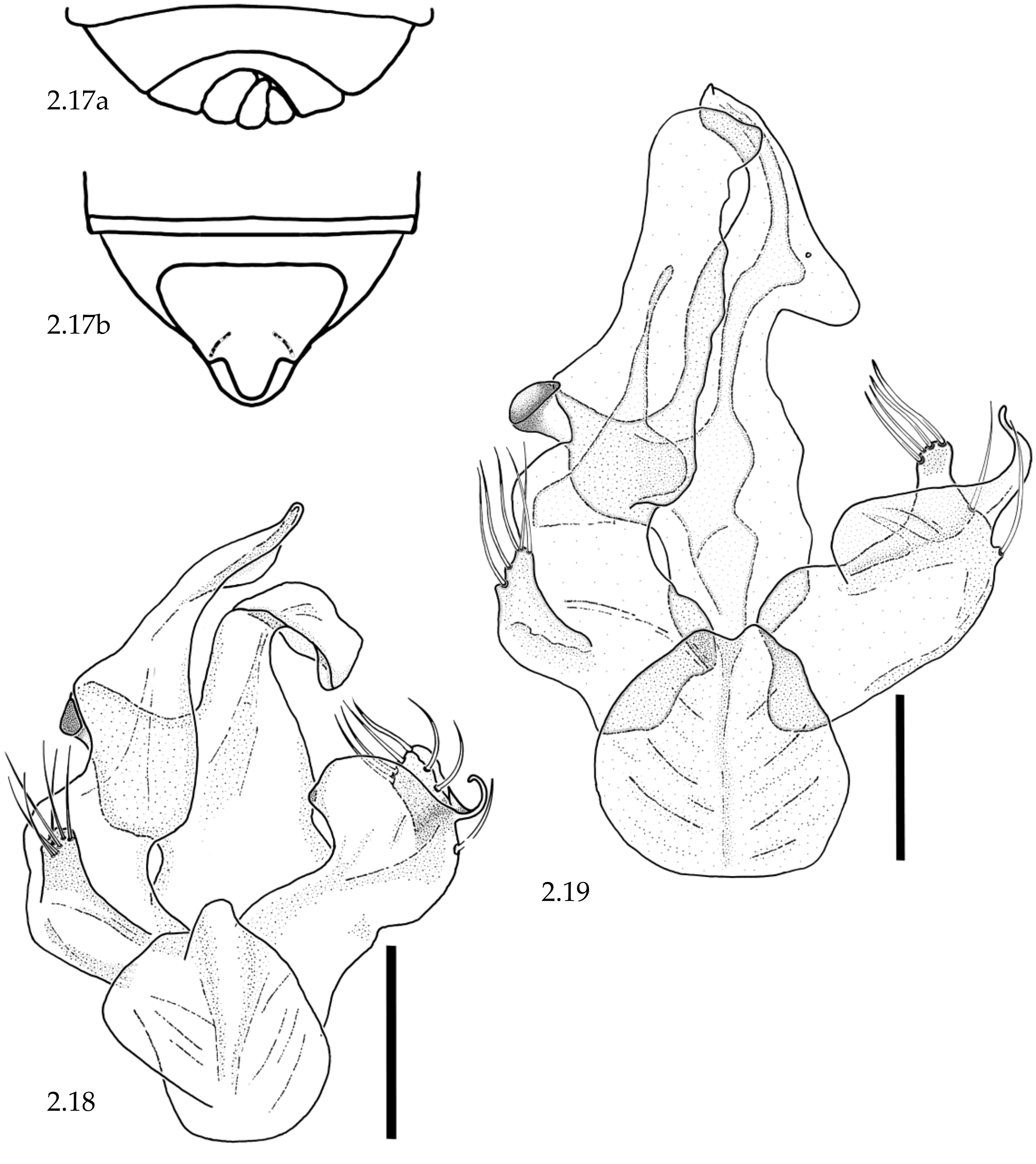
Figures 2.1-2.5. 2.1: *Sonoma cygnus*, holotype; 2.2: *Sonoma parkorum*, holotype; 2.3: *Sonoma baylessae*, holotype; 2.4: *Sonoma brasstownensis*, holotype; 2.5: *Sonoma nicholsae*, holotype. Scale lines equal 1.0 mm.

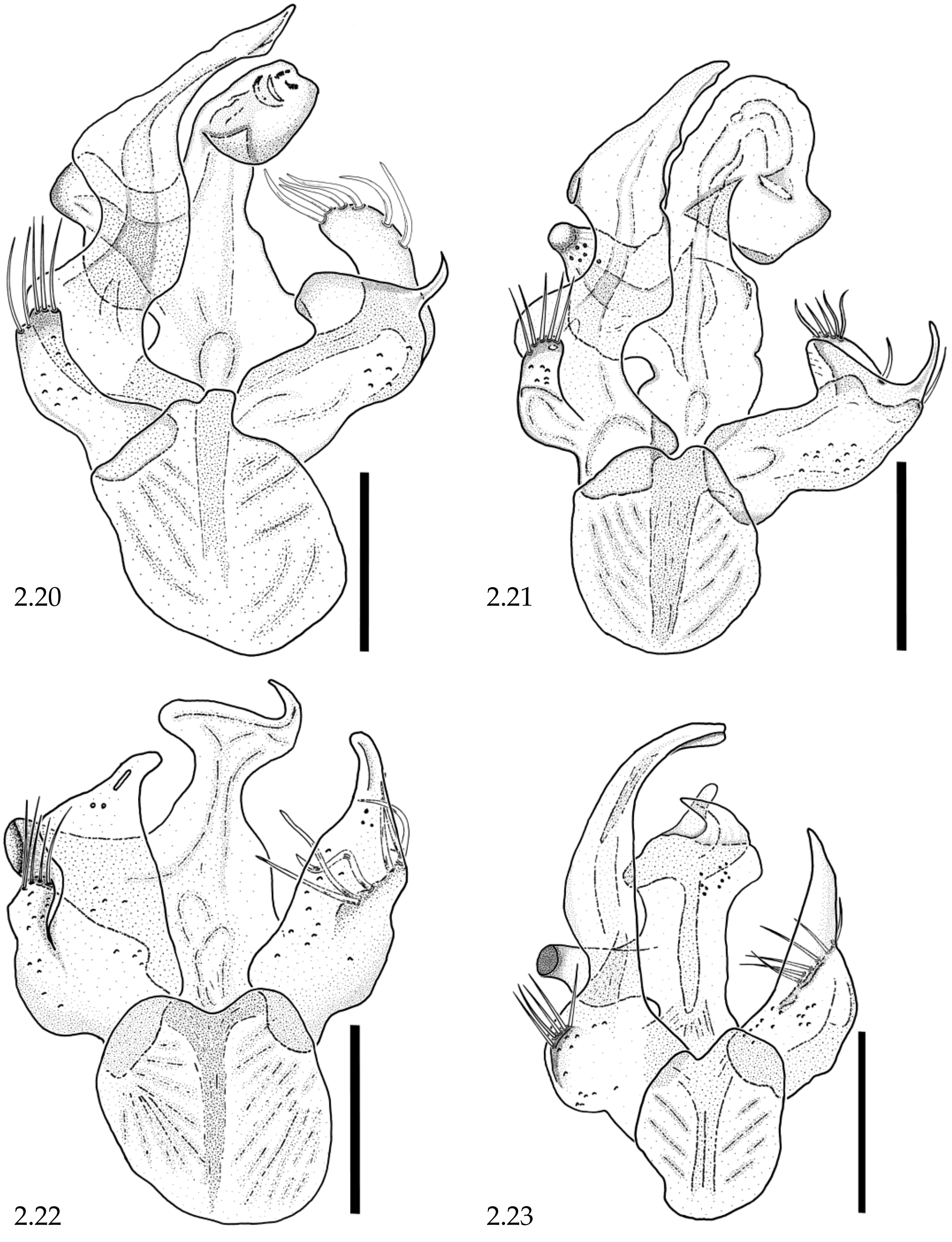


Figures 2.6-2.10. 2.6: *Sonoma gilae*, holotype; 2.7: *Sonoma gimmeli*, holotype; 2.8: *Sonoma tolulae* (♂); 2.9: *Sonoma chouljenkoi*, holotype; 2.10: *Sonoma sokolovi*, paratype. Scale lines equal 1.0 mm.

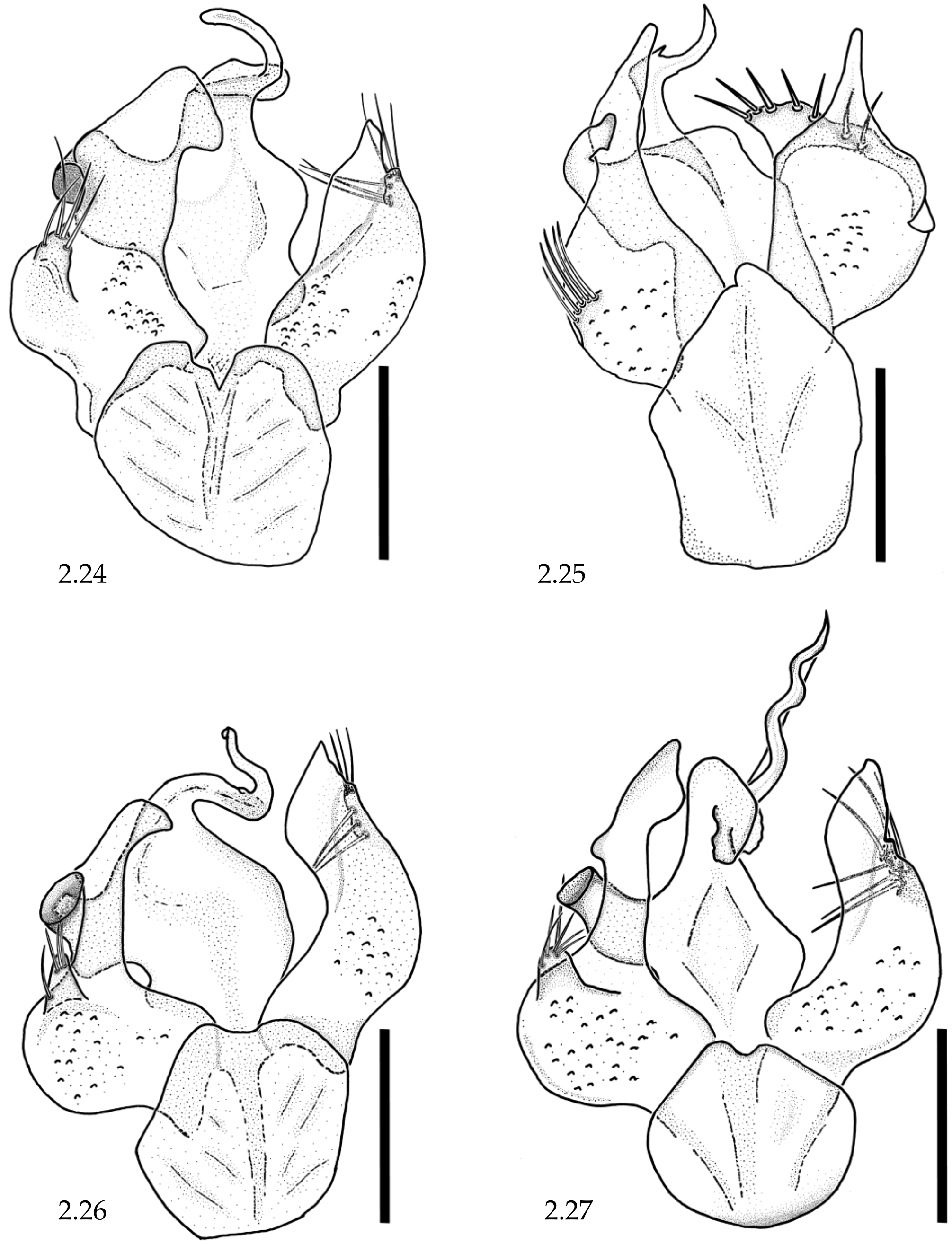
Figures 2.11-2.16. 2.11: *Sonoma streptophorophallus*, holotype; 2.12: *Sonoma nhunguyeni*, holotype; 2.13: *Sonoma tridens*, holotype; 2.14: *Sonoma holmesi*, holotype; 2.15: *Sonoma tishechkini*, holotype; 2.16: *Sonoma mayori*, holotype. Scale lines equal 1.0 mm.



Figures 2.17-2.19. 2.17a: ventral aspect of abdomen, male (redrawn from Park 1942); 2.17b: ventral aspect of abdomen, female; 2.18: *Sonoma cygnus*, aedeagus (dorsal view); 2.19: *Sonoma parkorum*, aedeagus (dorsal view). Scale lines equal 0.1 mm. Right side of figures 2.17–2.19 is anatomical left.



Figures 2.20-2.23. 2.20: *Sonoma baylessae*, aedeagus (dorsal view); 2.21: *Sonoma brasstownensis*, aedeagus (dorsal view); 2.22: *Sonoma nicholsae*, aedeagus (dorsal view); 2.23: *Sonoma gilae*, aedeagus (dorsal view). Scale lines equal 0.1 mm. Right side of figure is anatomical left.



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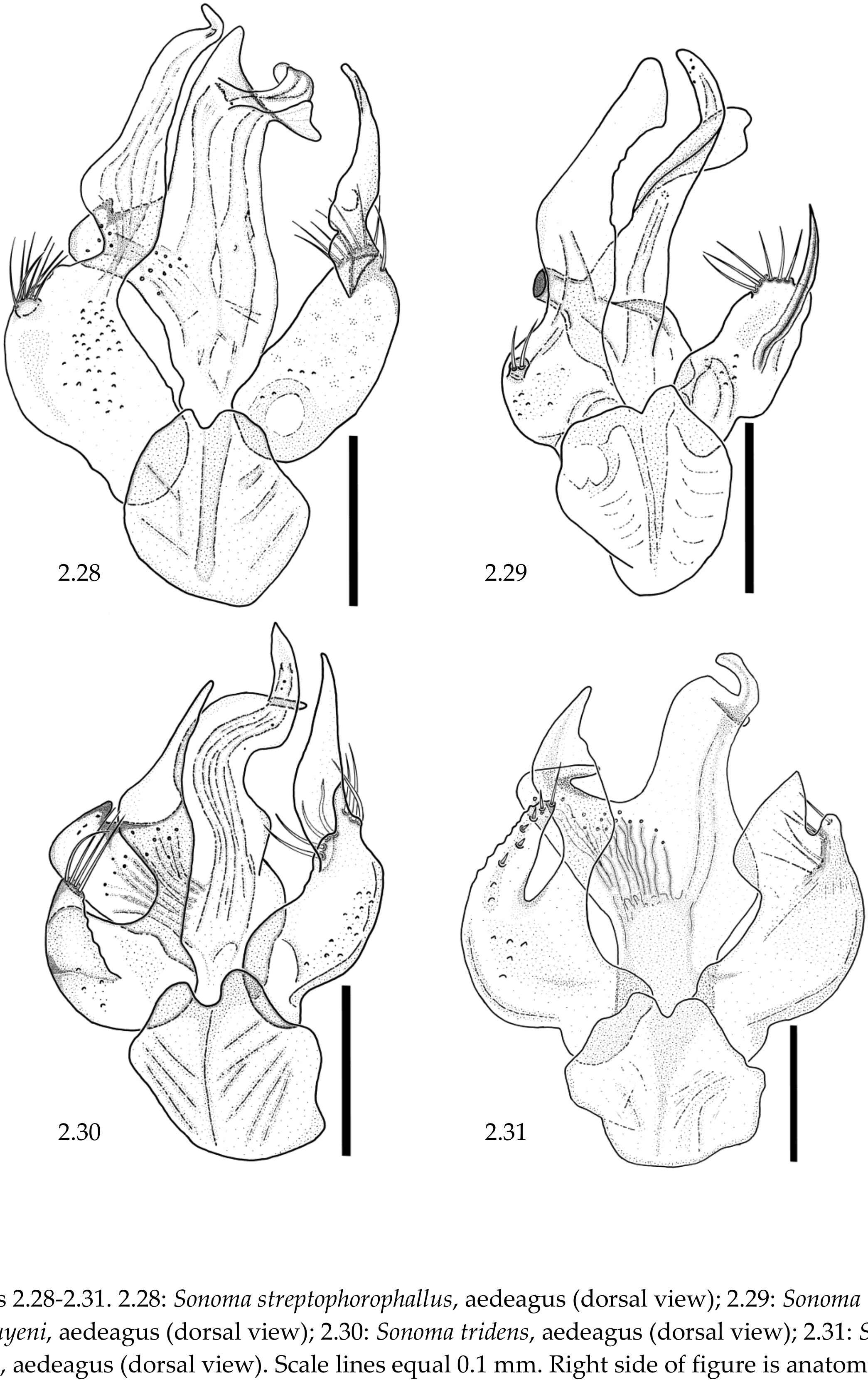
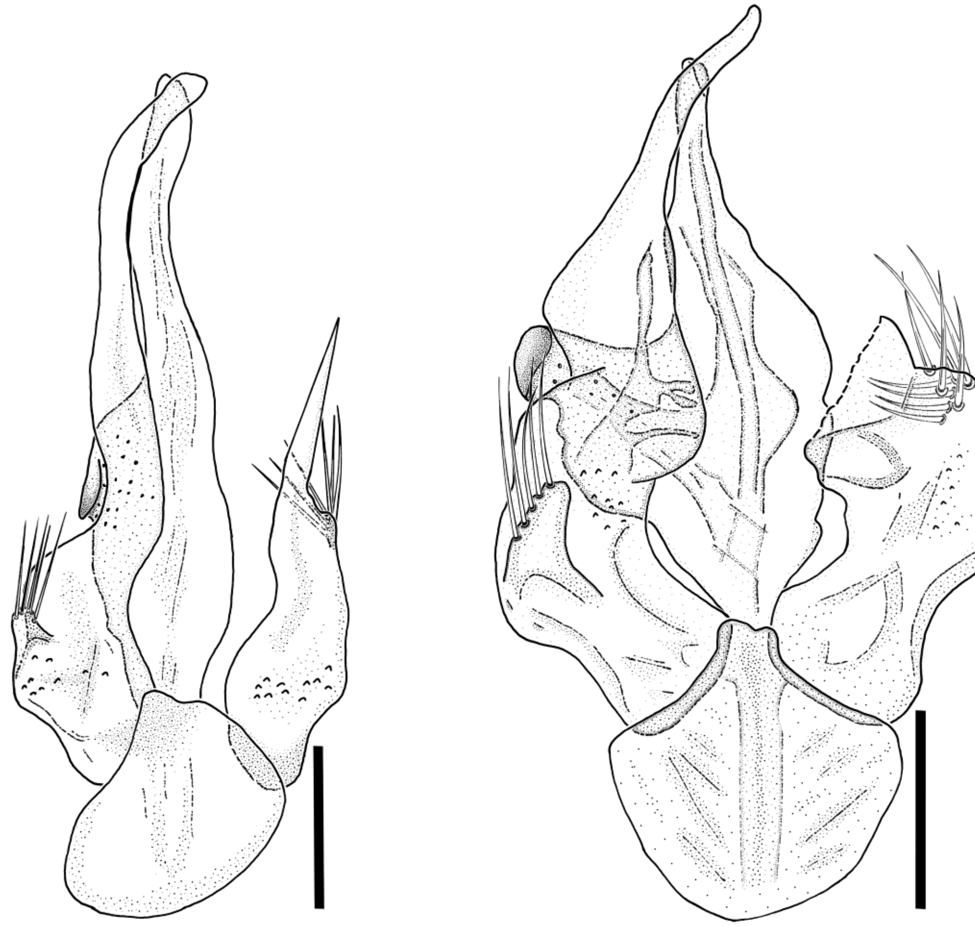
Figures 2.24-2.27. 2.24: *Sonoma gimmeli*, aedeagus (dorsal view); 2.25: *Sonoma tolulae*, aedeagus (dorsal view); 2.26: *Sonoma chouljenkoi*, aedeagus (dorsal view); 2.27: *Sonoma sokolovi*, aedeagus (dorsal view). Scale lines equal 0.1 mm. Right side of figure is anatomical left.



Figures 2.28-2.31. 2.28: *Sonoma streptophorophallus*, aedeagus (dorsal view); 2.29: *Sonoma nhunguyeni*, aedeagus (dorsal view); 2.30: *Sonoma tridens*, aedeagus (dorsal view); 2.31: *Sonoma holmesi*, aedeagus (dorsal view). Scale lines equal 0.1 mm. Right side of figure is anatomical left.



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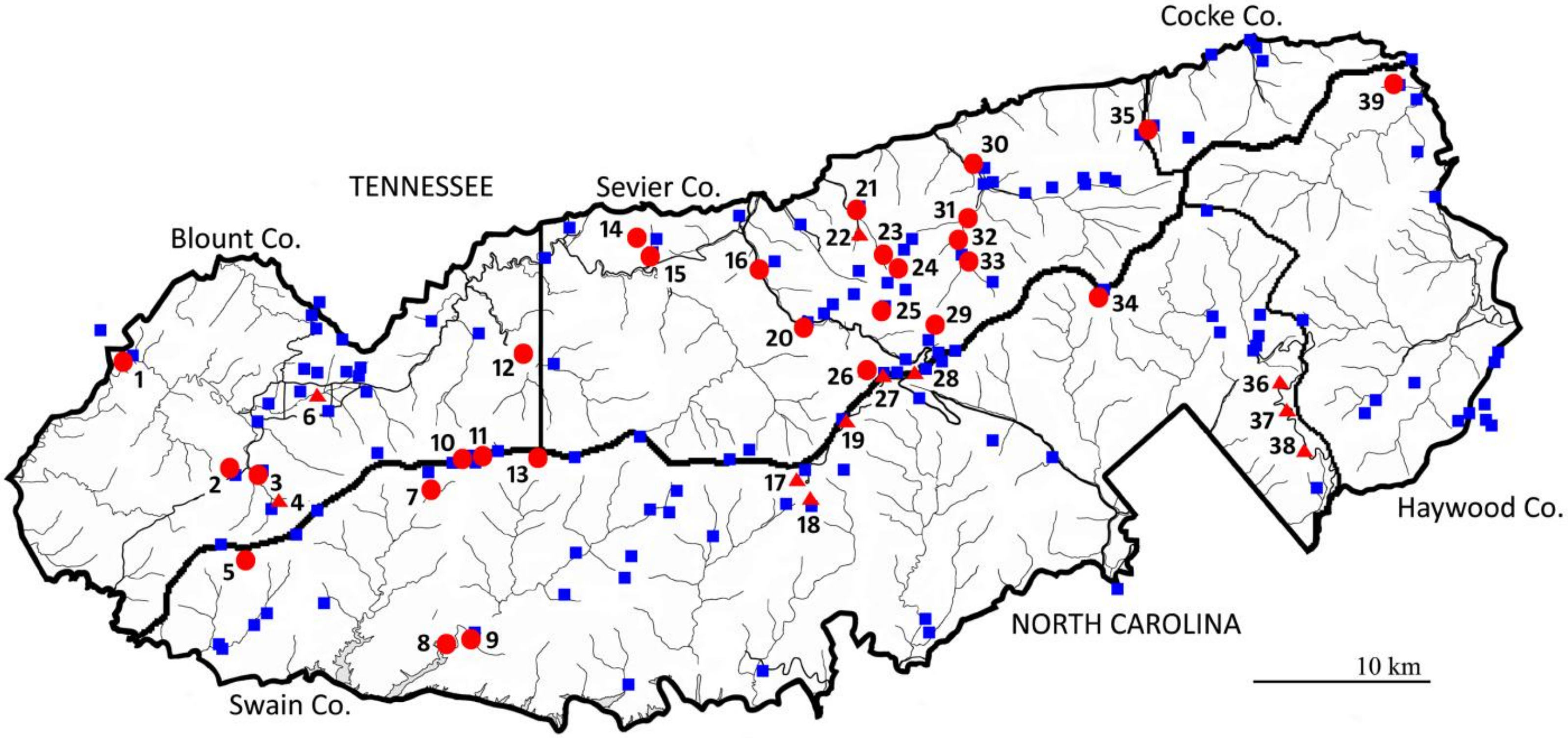
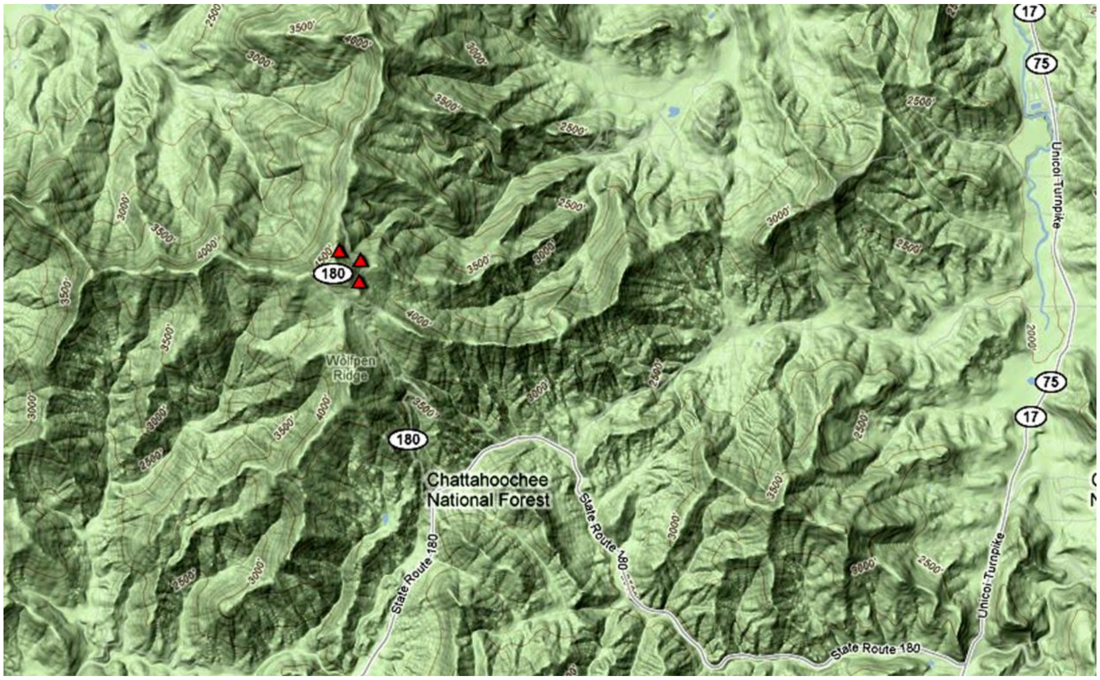
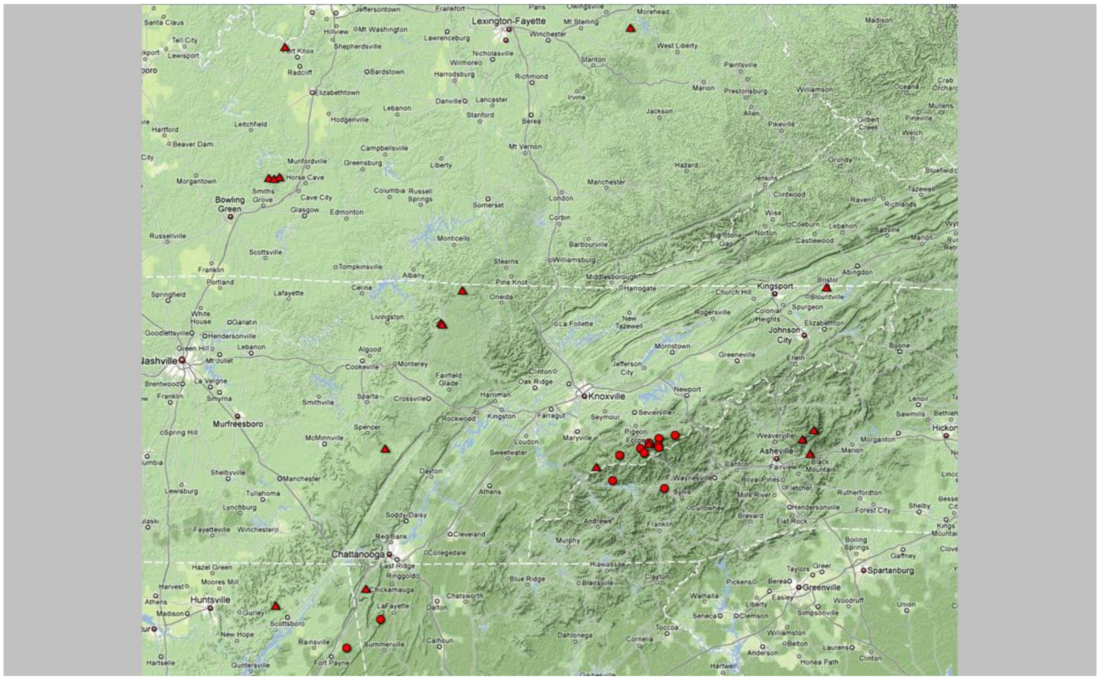
Figures 2.32-2.33. 2.32: *Sonoma tishechkini*, aedeagus (dorsal view); 2.33: *Sonoma mayori*, aedeagus (dorsal view). Scale lines equal 0.1 mm. Right side of figure is anatomical left.



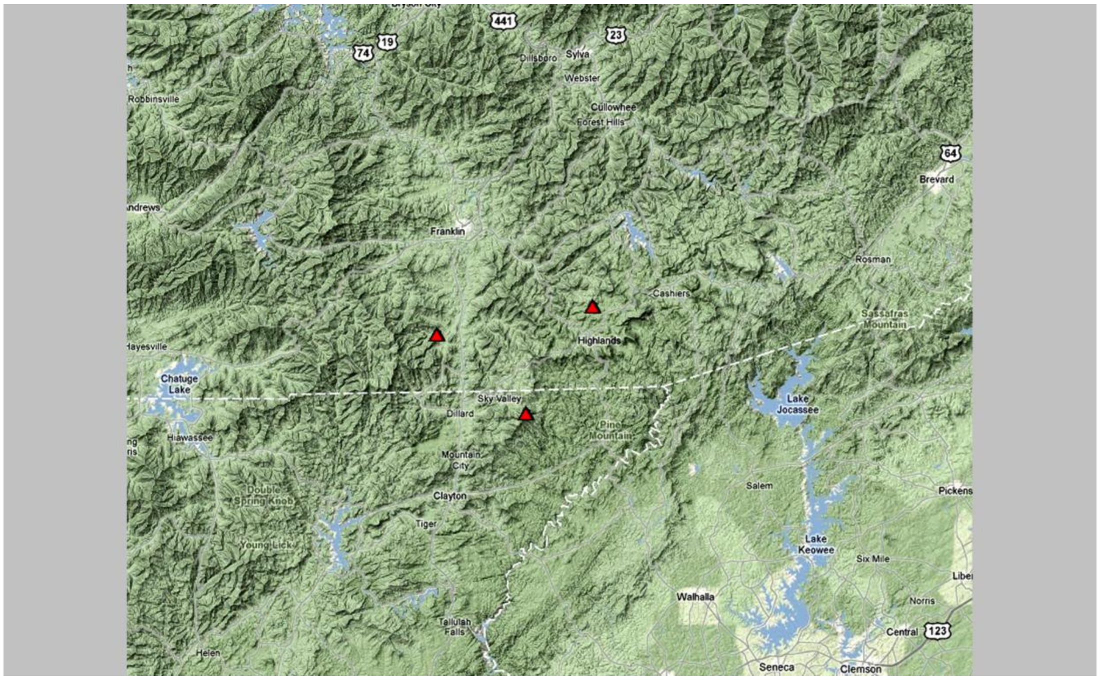
Map 2.2. Collection localities of *Sonoma* spp. in GSMNP. *Sonoma baylessae*: 9, 27, 28, 29; *S. chouljenkoi*: 4, 8, 12, 16, 20, 21, 22, 30, 32, 33, 35; *S. gilae*: 1, 2, 3, 4, 5, 6, 14, 30, 32, 35; *S. gimmeli*: 30, 31, 35; *S. mayori*: 17; *S. nicholsae* 38, 39; *S. parkorum*: 7, 11; *S. tolulae*: 3, 9, 10, 11, 13, 15, 18, 19, 23, 24, 25, 26, 29, 34, 36, 37. Red circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and red triangles represent localities with verbal descriptions only. Blue squares represent localities at which litter samples were taken as part of the Coleoptera component of the All Taxa Biotic Inventory.



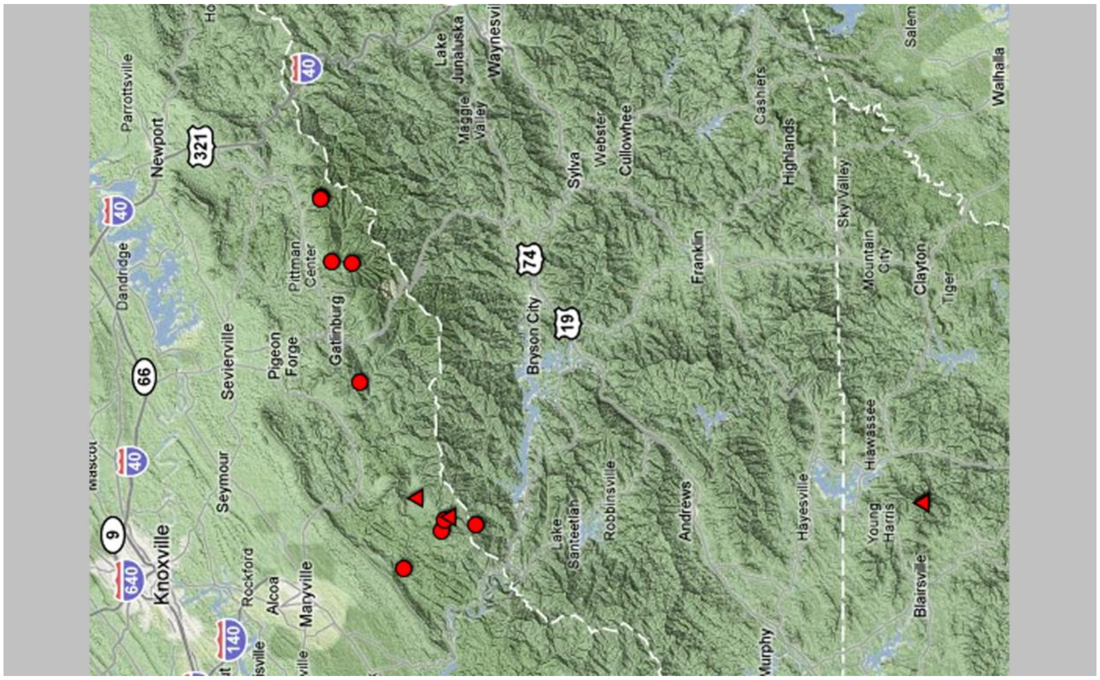
Map 2.3. Collection localities of *Sonoma brasstownensis*: Towns/Union County, Georgia. Triangles represent localities with verbal descriptions only.



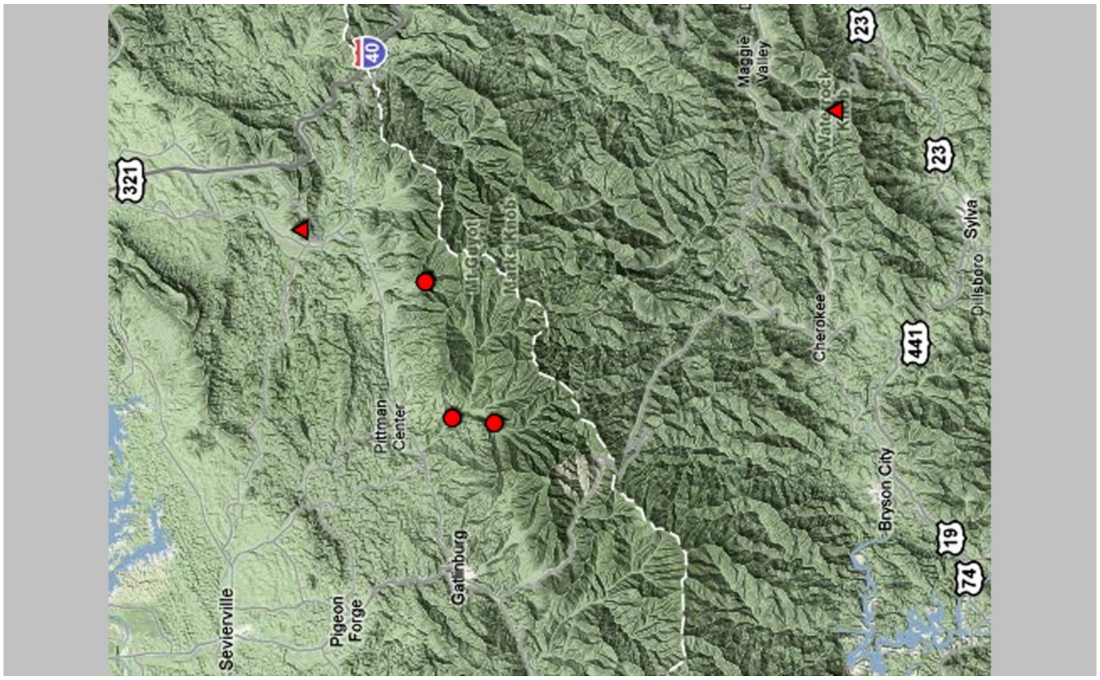
Map 2.4. Collection localities of *Sonoma chouljenkoi*: Alabama, Georgia, Kentucky, North Carolina, Tennessee. Circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



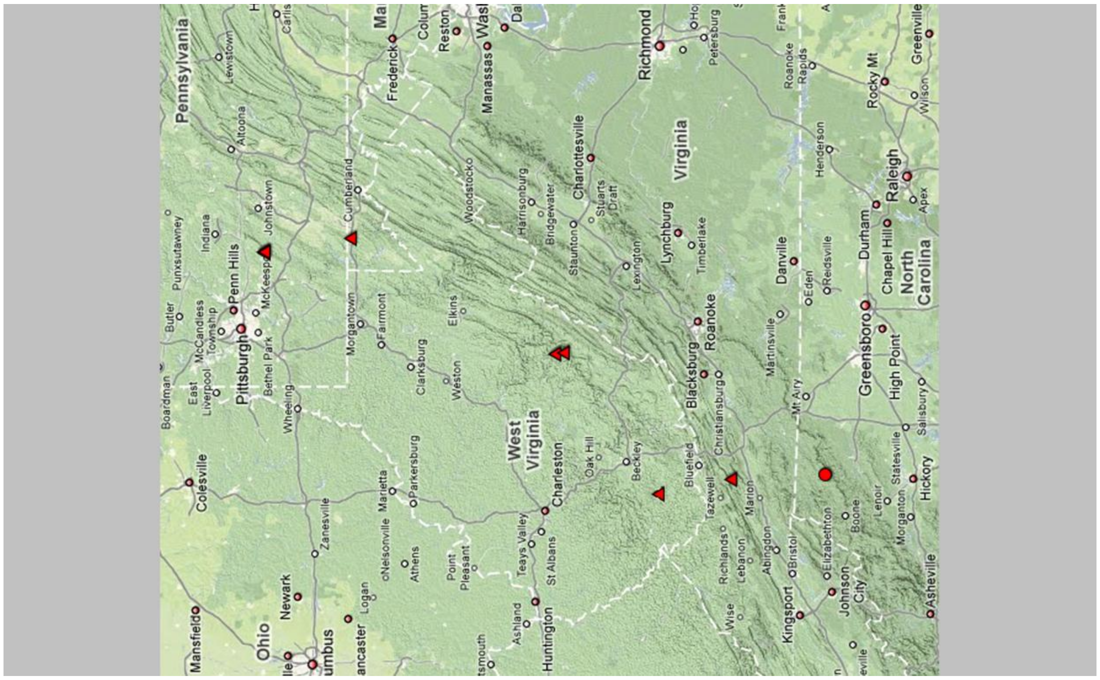
Map 2.5. Collection localities of *Sonoma cygnus*: Georgia, North Carolina. Triangles represent localities with verbal descriptions only.



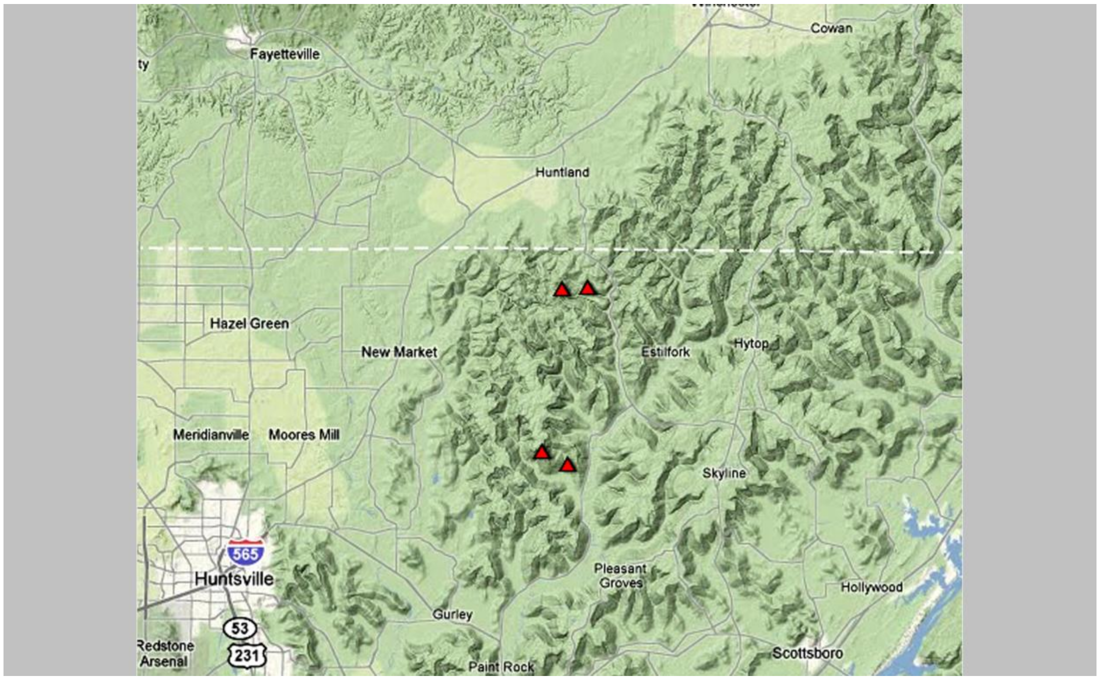
Map 2.6. Collection localities of *Sonoma gilae*: Georgia, Tennessee. Circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



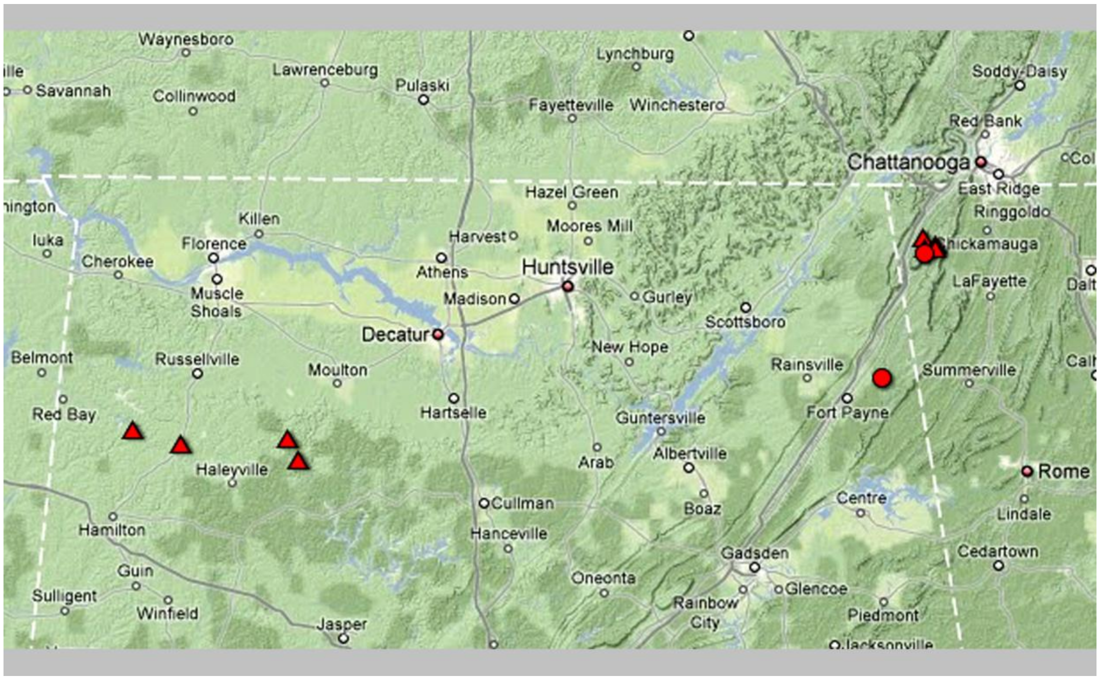
Map 2.7. Collection localities of *Sonoma gimmeli*: North Carolina, Tennessee. Circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



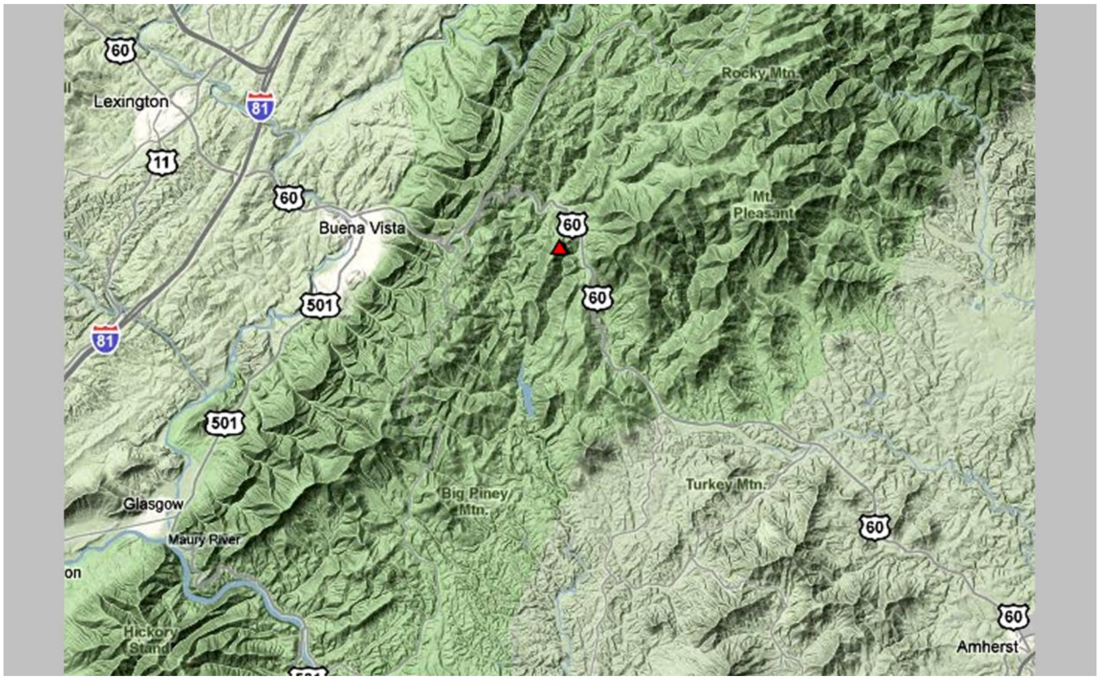
Map 2.8. Collection localities of *Sonoma holmesi*: North Carolina, Maryland, Pennsylvania, Virginia, West Virginia. The circle represents a locality from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



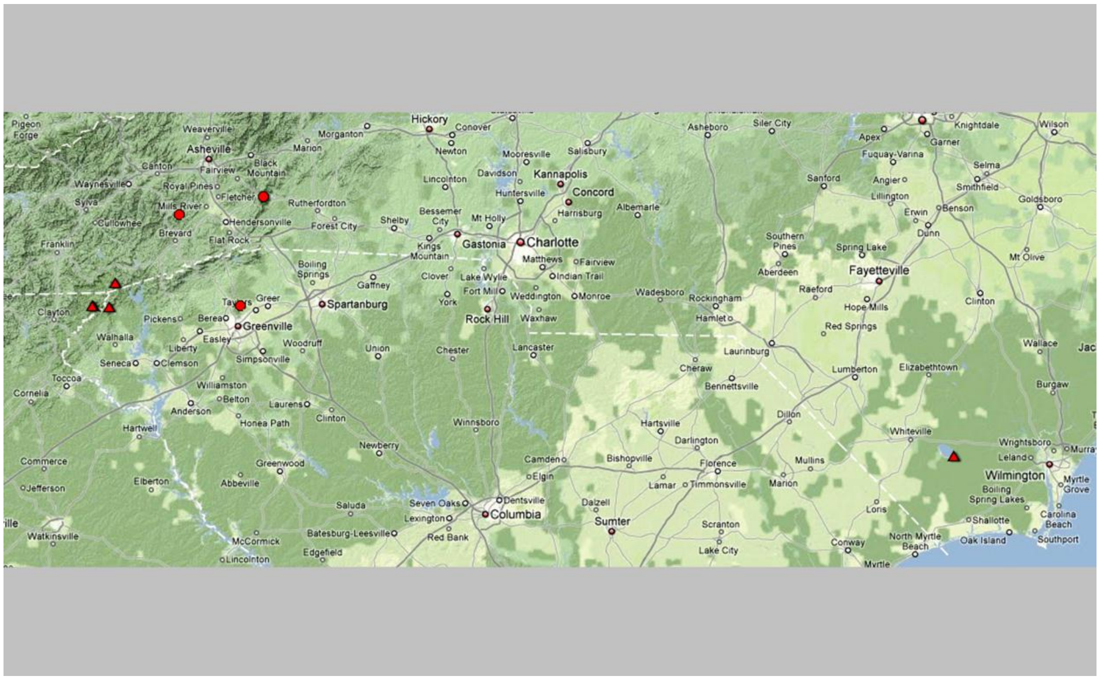
Map 2.9. Collection localities of *Sonoma nhunguyeni*: Jackson County, Alabama. Triangles represent localities with verbal descriptions only.



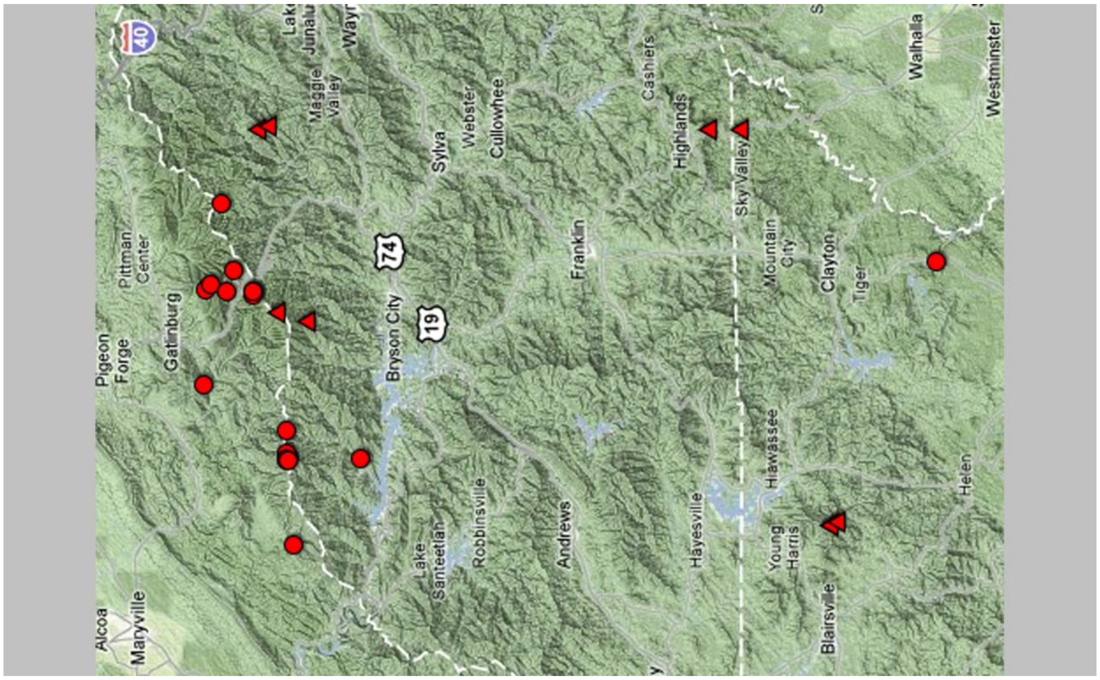
Map 2.10. Collection localities of *Sonoma sokolovi*: Alabama, Georgia. Circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



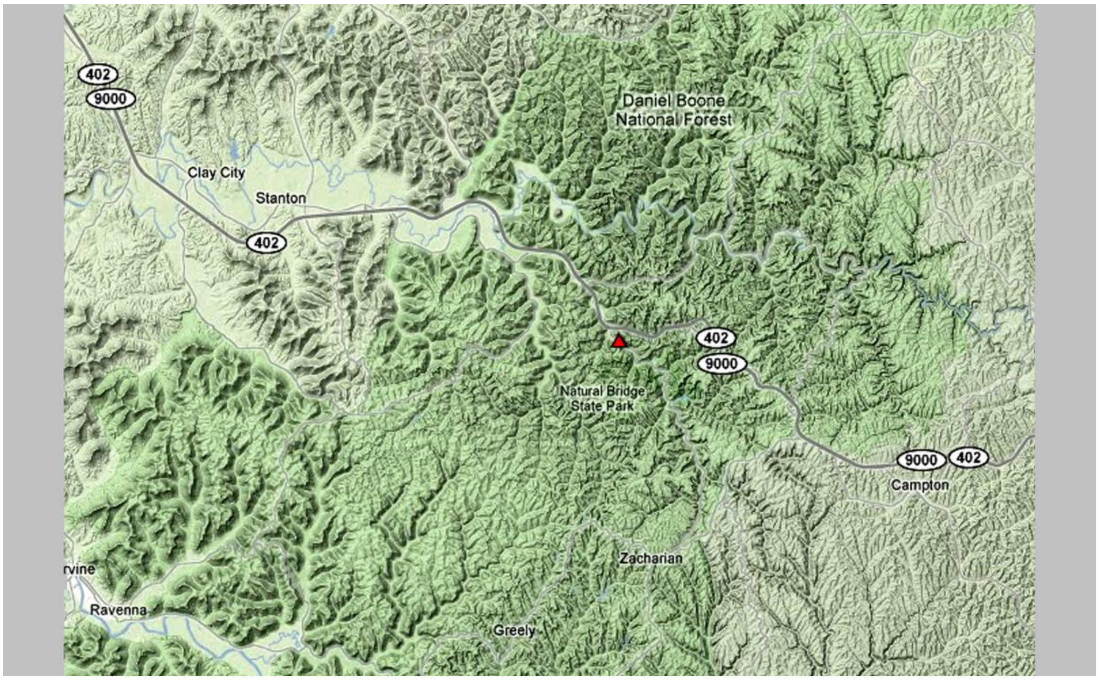
Map 2.11. Collection locality of *Sonoma streptophorophallus*: Amherst County, Virginia. The triangle represents a locality with a verbal description only.



Map 2.12. Collection localities of *Sonoma tishechkini*: Georgia, North Carolina, South Carolina. The circles represents a locality from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



Map 2.13. Collection localities of *Sonoma tolulae*: Georgia, North Carolina, Tennessee. Circles represent localities from coordinates taken with a Global Positioning System at the time of collection, and triangles represent localities with verbal descriptions only.



Map 2.14. Collection locality of *Sonoma tridens*: Powell County, Kentucky. The triangle represents a locality with a verbal description only.

CHAPTER 3. NEW SYNONYMIES AND RANGE EXTENSION FOR NORTH AMERICAN *THORACOPHORUS* MOTSCHULSKY (COLEOPTERA: STAPHYLINIDAE: OSORIINAE)

3.1 INTRODUCTION

The first author became interested in the genus *Thoracophorus* Motschulsky after collecting and curating 882 specimens during research (Ferro and Carlton 2011) associated with the Coleoptera component of the All Taxa Biodiversity Inventory that took place in Great Smoky Mountains National Park (Carlton and Bayless 2007). All of the specimens were identified as *T. costalis* (Erichson) based on illustrations and descriptions (Horn 1871; Irmler 1985) and comparison to authoritatively identified specimens. However, obtaining materials representing other nominal species of North American *Thoracophorus* proved difficult.

No key to the species of *Thoracophorus* in North America exists. Horn (1871) provided a diagnosis and illustrations to differentiate *T. costalis* from his *Thoracophorus brevicristatus*, which he described under the genus *Glyptoma* Erichson. Two other species have been described from America north of Mexico, *Thoracophorus longicollis* Motschulsky, 1860 from "Nouvelle-Orléans" (=New Orleans, Louisiana) and *Thoracophorus fletcheri* Wendeler, 1927 from Lake Minnetonka, Minnesota (Fletcher 1930).

3.2 MATERIAL AND METHODS

We examined the type series of *T. longicollis* housed in the Zoological Museum of Moscow State University, Moscow, Russia (ZMUM). The type series consists of four specimens glued to an elongate rectangular card. Motschulsky did not designate a holotype. We hereby designate the specimen furthest from the pin the **lectotype**, and a red dot was placed on the card next to this specimen. Motschulsky (1860) anticipated that this may be a southern variant of *T. costalis* within his description.

We also examined the holotype of *T. fletcheri* housed in the Museum für Naturkunde der Humboldt-Universität, Berlin Germany (ZMHB).

3.3 RESULTS AND DISCUSSION

Examination of the type material of *T. longicollis* and *T. fletcheri* revealed both to be indistinguishable from *T. costalis*. Details of the sculpturing of the head and pronotum (important for species recognition in the genus) and other aspects of external morphology are identical. Therefore, *Thoracophorus longicollis* Motschulsky, 1860 and *Thoracophorus fletcheri* Wendeler, 1927 are **new junior synonyms** of *Thoracophorus costalis* (Erichson, 1840).

While examining specimens of *Thoracophorus* in the Louisiana State Arthropod Museum, we found two specimens of *T. brevicristatus* collected in Louisiana. Blackwelder (1943) listed this species as having been collected in Florida and Arizona in America north of Mexico. Here we report *T. brevicristatus* in Louisiana as a **new state record**. Specimen label information is as follows: **USA: LA:** East Baton Rouge Parish, Baton Rouge, 12 Dec 1990, M. Sean Strother, under bark of dead sugarberry *Celtis laevigata* Willd.; Assumption Parish, Pierre Part, n. Lake Verret, 30 Dec 1992, D. R. Ganaway, coll. in rotten log.

Thoracophorus brevicristatus is also found throughout the West Indies (Blackwelder 1943; Irmler 1985), so the discovery of specimens midway between continental populations is not unexpected. Irmler (2010) reported that *T. brevicristatus* is an inquiline of termites.

CHAPTER 4. A PRACTICAL EMERGENCE CHAMBER FOR COLLECTING COLEOPTERA FROM ROTTING WOOD, WITH A REVIEW OF EMERGENCE CHAMBER DESIGNS TO COLLECT SAPROXYLIC INSECTS[2]

4.1. INTRODUCTION

Dead wood is an opaque habitat. Even the experienced collector, tramping through a forest, is easily rebuffed by an impenetrable log. Subcortical faunae may be easy prey, but the mass of life teeming within the heartwood is perfectly safe from the would-be assassin, biasing short-term survey results. To gain an appreciation of the "life" of dead wood we must step out of the day-collector's time scale. Only when we see months as if they were minutes, and years as if they were hours, can we truly see dead wood for the dynamic habitat that it really is.

A comprehensive study of the numerous organisms, particularly insects, that reside within dead wood is virtually impossible in real time due to the small size of most insects and the matrix within which they reside. To overcome this difficulty, researchers use emergence chambers to quarantine dead wood samples, and during the following weeks or months collect the organisms that emerge. Clever combinations of exposure or quarantine, substrate type, and time allow researchers to build a dynamic picture of the dead wood habitat.

Here we differentiate emergence from rearing. *Emergence* implies an attempt, with little or no intervention or addition of resources, to collect individuals from a given substrate, whereas *rearing* implies an attempt, often with intervention and addition of resources, to nurture organisms through life stages, for example from larva to adult, or through multiple generations. Emergence chambers are important tools in the study of the dead wood habitat because life cycles of most saproxylic insects involve emergence of adults after long periods of time inside the substrate.

Numerous emergence chamber designs have been used to collect saproxylic insects (Table 4.1). These designs vary greatly in size, ranging from the room of a house (Brues 1927) to much less than a cubic meter (Schauff 2001). They may enclose part of the wood (Derksen 1941) or all of it (Jonsell and Hansson 2007). Some designs may be placed within a closed building (Ulyshen et al. 2010), placed in an open building (Hedgren 2007), or left in the field (Hövenmeyer and Schauermann 2003). They may also require active external equipment (Ulyshen and Hanula 2009), or operate in a stand-alone fashion (Ferro et al. 2009). The specimen concentration method may be hand collection (Blackman and Stage 1924), photoeclection (Mecke et al. 2001), gravity (Hammond 1997) or a combination thereof. A photoeclector is a collecting device based on positive phototropism (Masner and García 2002). Additionally several publications describe numerous insect collection techniques, including emergence chambers (Aguilar 2010, Martin 1977, Peterson 1953, Schauff 2001, Southwood 1978).

To accommodate our specific research requirements, an emergence chamber was designed with the following attributes: 1) large enough to hold numerous pieces of dead wood, up to 20 cm diameter × 40 cm length; 2) robust enough to be left outdoors for several years; 3) easily defended against wild animals; 4) requiring no regular maintenance or active external

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Table 4.1. An annotated list of literature describing emergence chambers used to collect saproxylic insects. cut = wood death caused by humans; natural = wood death not caused by humans; CWD = coarse woody debris.

Publication	Country	Chamber type; size	Chamber location	Substrate type	Additional resources	Concentration method	Taxa, # specimens/species collected
Grove et al. 2008	Australia	wrap around substrate; 3 linear meters each	field	cut CWD	none	gravity/photoeclection lower, photoeclection higher	Coleoptera 11,816/346
Lachat et al. 2006	Benin	independent, self supporting; 0.18 and 0.20 m^3	field	natural CWD limbs > 5cm	none	photoeclection	Coleoptera 7474/469
Boulanger and Sirois 2007	Canada	wrap around suspended log; one sample per chamber	non-heated building	natural CWD produced by fire	building provided structure for chamber	gravity	Coleoptera 391/32
Hammond 1997	Canada	independent, self supporting; 1.5 m^3	laboratory	cut CWD logs and snags	none	gravity	Arthropoda 39,094 specimens, 13 orders, 113 families, 2000+ species
Hammond et al. 2001	Canada	independent, self supporting; 1.0 m^3	laboratory	cut CWD snag, log, and stump	none	gravity, photoeclection	Coleoptera 1049/49
Blackman and Stage 1918	USA	independent, self supporting	outdoors near laboratory	natural CWD snags, cut to size	water occasionally added	hand collection	Coleoptera ?/25; Diptera ?/4; Hymenoptera ?/15; Lepidoptera ?/1
Blackman and Stage 1924	USA	independent, self supporting; "cages" to "jars"	outdoors and inside insectary	natural CWD limbs and logs	none	hand collection	Coleoptera ?/105; Diptera ?/34+; Heteroptera ?/4; Hymenoptera ?/75; Lepidoptera ?/8; Thysanoptera ?/3

Table 4.1 cont.

Publication	Country	Chamber type; size	Chamber location	Substrate type	Additional resources	Concentration method	Taxa, # specimens/species collected
Brues 1927	USA	room of house where stove wood was stored	in building	cut CWD, seasoned (one year), split	climate control	photoeclection, hand collection	Coleoptera 385/34; Diptera 33/16; Heteroptera 5+/5; Hymenoptera 261/27; Psocoptera 12/4; Thysanoptera 3/2;
This research, in prep.	USA	independent, self supporting; 0.12 m^3	field	natural CWD, 2.5-20 cm	none	gravity, photoeclection	Coleoptera 5678/275+
Ferro et al. 2009	USA	independent, self supporting; 0.19 m^3	open air building	cut fine woody debris	none	gravity	Coleoptera 414/35
Ulyshen and Hanula 2009	USA	suspended bag; one sample per chamber	laboratory	cut CWD logs	ventilation with electric blower	gravity	Coleoptera 33,457/250+
Ulyshen et al. 2010	USA	suspended bag; one sample per chamber	laboratory	cut CWD logs	ventilation with electric blower	gravity	Coleoptera 3457/80
Mecke et al. 2001	Brazil	independent, self supporting; 0.043 m^3	laboratory (presumed)	cut dead CWD and fine woody debris	moistened every 1-3 days	photoeclection	Coleoptera 5787/35; Hymenoptera 64/5
Hövenmeyer and Schauermann 2003	Germany	independent, self supporting; one sample per chamber	field	natural CWD limbs	none	photoeclection	Diptera 11,616/163

Table 4.1 cont.

Publication	Country	Chamber type; size	Chamber location	Substrate type	Additional resources	Concentration method	Taxa, # specimens/species collected
Irmler et al. 1996	Germany	wrap supported by substrate; one sample per chamber (logs), partially surrounded substrate (stumps)	field	Cut CWD logs and stumps	none	photoeclection	Diptera: Mycetophilidae 1224/55; Sciaridae 5894/38; Coleoptera 3956/114
Økland 1996	Norway	wrap supported by substrate; partially surrounded substrate (75 cm linear distance)	field	natural CWD	none	gravity, photoeclection	Coleoptera 162/64
Gibb et al. 2006 a, b, Hilszczanski et al. 2005, and Stenbacka et al. 2010	Sweden	wrap supported by substrate; partially surrounded substrate (30 cm linear distance)	field	cut CWD logs and snags	none	photoeclection	Coleoptera 126,092/76; Ichneumonoidea (Hymenoptera) 949/24
Hedgren 2007	Sweden	suspended bag; one sample per chamber	open air building, then greenhouse	cut CWD low and high stumps	climate control	gravity, hand collection	Coleoptera 10,357/25+; Hymenoptera 797/10+; Heteroptera 168/1+
Jonsell and Hansson 2007	Sweden	Comparison of 1) independent, self supporting box; 2) suspended bag	1) and 2) laboratory	1) and 2) cut fine woody debris	1) none 2) Building provided structure for chamber	1) photoeclection; 2) gravity	Coleoptera 1) 433/92; 2) 1055/109

Table 4.1 cont.

Publication	Country	Chamber type; size	Chamber location	Substrate type	Additional resources	Concentration method	Taxa, # specimens/species collected
Lindhe and Lindelöw 2004	Sweden	wrap supported by substrate; one sample per chamber	field	cut high stumps	none	photoeclection	Coleoptera 47,038/316
Weslien 1992	Sweden	suspended bag; 0.13 m^3 - moved from bag to paper carton	bag left in field; bolts lay unprotected in the field during winter then placed in carton in laboratory	cut CWD logs	none	bag, gravity; carton, photoeclection	Arachnida: Pseudoscorpionida 8/1; Insecta: Coleoptera 23,373/21; Diptera 831/7+; Hymenoptera 953/8
Wikars et al. 2005	Sweden	suspended bag; each sample had 0.5 m^2 bark area	field	natural CWD	none	gravity	Coleoptera 1483/80
Scheigg 2001	Switzerland	wrap supported by substrate; partially surrounded substrate	field	natural CWD trunks and limbs	none	photoeclection	Diptera 30,095/426; Coleoptera 4906/228

equipment; 5) with a passive specimen concentration method; 6) mass producible; 7) and affordable to build in quantity.

4.2. MATERIAL AND METHODS

The main body of the emergence chamber is a grey Sterilite® 18-Gallon Tote Box model number 18158208. The external dimensions are 24.0 × 18.375 × 15.75 inches (~61 × 47 × 40 cm). The volume is 18 gal (~68 L) and each tote box masses ~1.7 kg. The central portion of the bottom of the tote box is raised and flat. This creates a trough ~4 cm wide and ~1 cm deep around the perimeter of the tote box. There is one ~5-mm diameter hole in the center of the molded handle on each end of the tote box placed here by the manufacturer. The central portion of the lid, starting ~6 cm from the edge, is lowered by ~1 cm. The lid clips on but does not entirely seal.

Modifications to the tote box were made as follows (Fig. 1).

1. A ~6-cm diameter hole was drilled in the trough of the bottom of the tote box directly under the molded handle (the end of the tote box) (Fig. 2). A band that fits a Kerr® wide-mouth half-pint (8-oz, ~0.24 L) mason jar was secured around the hole using two wide headed screws (truss washer lath). The screws were positioned in the distal and proximal edges of the band, not lateral. A generous amount of Liquid Nails® brand Heavy Duty Construction Adhesive (LN-901) was used to seal and fill any gaps between the band and the tote box. When the completed emergence chamber was in use, a Kerr® wide-mouth half-pint (8 oz, ~0.24 L) mason jar was placed here as the collection container.

2. The front ventilation hole was made by drilling one ~3-cm diameter hole in the center of the front side wall of the tote box ~10 cm above the bottom and directly over the collection jar (Fig. 1). Three layers of Weedblock® landscape fabric were placed over the hole and the edges were secured in place with Heavy Duty Construction Adhesive. The adhesive was covered with masking tape to keep nested chambers from becoming glued together. The landscape fabric has a closed mesh, allows ventilation, prevents light from entering, and blocks insects from entering or exiting the chamber.

3. The top ventilation holes were made by drilling two ~3-cm diameter holes side by side in the raised perimeter of the lid in the center of the left side (Fig. 1). On the underside of the lid three layers of landscape fabric were placed over the holes and secured in place with Heavy Duty Construction Adhesive.

4. Each hole in the center of the molded handle was covered with tape on the inside of the tote box.

5. After substrate was added, the lid was sealed to the bottom portion of the tote box with Duck Tape® duct tape.

6. When deployed in the field these emergence chambers could be safely stacked two high (Fig. 3). Landscaping timbers 3 × 4-in (~7.6 × 10-cm) were used to elevate and provide a stable platform for the lower chambers. The lower chambers were set side by side facing the same direction. A second chamber was placed on each lower chamber, facing the opposite direction and positioned so that its collection jar was just beyond the edge of the lid of the lower chamber. A 20-cm long piece of 2 × 2-in (~5 × 5-cm) lumber was placed on the lid of the lower chamber and against the back of the bottom of the upper chamber. Two 2.5-in (~6-cm) screws were used to secure the lumber to the lid of the lower chamber and one screw was used to

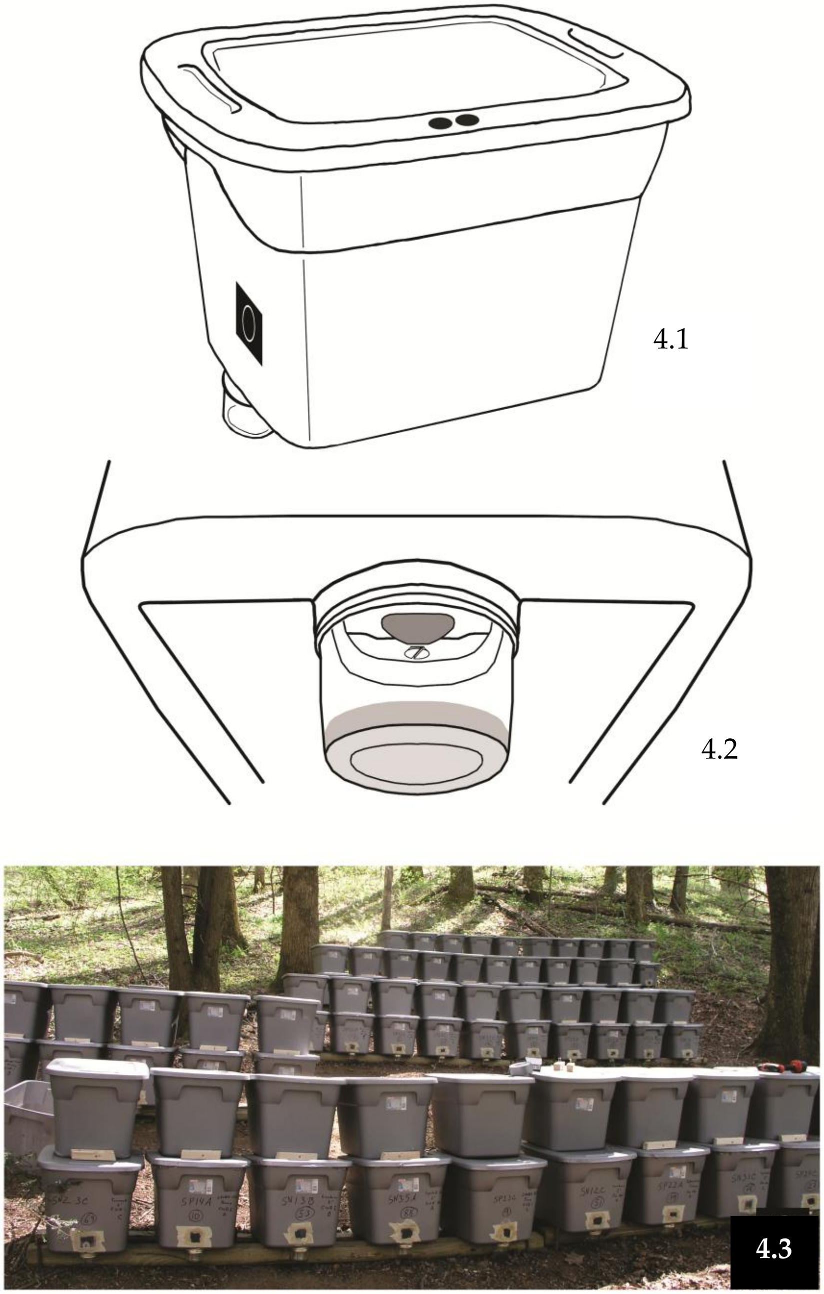

Fig. 4.1–4.3. Emergence chambers. **4.1)** Completed emergence chamber with collection jar and front and top ventilation holes; **4.2)** Detail of collection jar attachment, only the distal screw is shown; **4.3)** Stacked chambers in the field (GSMNP).

secure it to the back of the upper chamber, thus fastening the two together. A single 1.25-in (~3-cm) screw placed in the right front corner of the lid of the lower chamber was used to securely fasten it in order to prevent the lid from popping open due to strain from the slightly cantilevered upper chamber. No such screw was needed in the upper chamber.

7. After the emergence chambers were secured in place, an appropriate amount of propylene glycol antifreeze (Prestone® Low Tox™ brand) was added to each collection jar as a preservative.

The above design was used as part of the Coleoptera component of the All Taxa Biodiversity Inventory at Great Smoky Mountains National Park, Tennessee/North Carolina (GSMNP) (Carlton and Bayless 2007, for a summary of publications resulting from that project see Ferro and Carlton 2010). A complete description of the research indicated below with detailed results is in preparation, and the following outline is provided to place the generalized results of the use of the described chambers within context. During April 2006 dead wood from mixed species of deciduous trees of various decay classes and sizes was gathered at remote sites in GSMNP and transported to a single locality within the park. Ninety emergence chambers were each three-fourths filled with dead wood (2.5–20 cm diameter) and placed in a shady, forested location near the Twin Creeks Science and Education Center in GSMNP. This approximated the environment the wood was collected from and reduced the risk of overheating. The array was surrounded by a battery powered electrified fence to protect against bears and feral hogs. Chambers were serviced six times during the spring, summer, and early fall of 2006, and three more times during spring, summer, and fall of 2007, otherwise the chambers were left unattended. Servicing consisted of removal of specimens and old preservative, then addition of new preservative.

4.3 RESULTS

Production. Each emergence chamber cost approximately US$7 in supplies and building 90 units took about 10 days. Because the main bodies of the chambers can be nested, only about 6.5 m^2 of floor space were needed for the entire manufacturing process. The emergence chambers were loaded on a small trailer and transported ~1,100 km from Baton Rouge, Louisiana to GSMNP.

Integrity of the Design. No chambers fell over in the first year of use. During 2007, a dead tree crushed two stacked chambers and disturbed two others. Collection jars, even when left unattended through the winter, did not fall off, leak, or break. No lids came open and the ventilation holes remained "sealed".

At the end of the collection period all chambers were opened and inspected for defects or wear and tear. None of the holes made by screws in the lid of the lower chamber and base of the upper chamber showed signs of allowing water movement or insect entrance or escape. No chambers had holes or punctures caused by boring insects, falling sticks, or other mechanical abrasions. In some cases the Heavy Duty Construction Adhesive used to seal the collection jar band to the chamber began to separate from the chamber but remained firmly pressed against it. This separation was only evident when lateral pressure was placed on the collection jar but the chamber was effectively sealed again when pressure was removed.

The duct tape used to seal the lids was frayed, dried, and weathered on the top of the lid where it was exposed to the sun. However, it was surprisingly fresh, flexible, and strong under the edge of the lid where it sealed against the chamber.

Several times collection jars nearly filled with water, diluting the preservative, but not harming the specimens. Presumably, the central depression of the lid filled with water from a rain storm and debris (leaves and sticks) that had settled on the lid wicked the water over to the top ventilation holes.

When the chambers were opened, the underside of the lid tended to be covered in condensation, while the bottom of the chamber was typically dry. Several chambers had pieces of wood that were apparently saturated with water, while other pieces in the same chamber were dry. Several chambers had wood with extensive recent fungal growth.

Performance. Identifications are ongoing for difficult taxa, and some are identified only to family or genus. Therefore, the true number of genera and species is expected to be higher than what is reported here.

A total of 5,678 adult beetle specimens were collected. These comprised 50 families, 226 genera, and 275 species (Table 4.2). During 2006, the six collection events resulted in 1,580 specimens in 44 families, 174 genera, and 197 species (Table 4.3). Of these, 13 families, 74 genera, and 97 species were collected exclusively during the first year. During the second year, three samples were taken that resulted in 4,098 specimens in 37 families, 155 genera, and 178 species. Of these, 6 families, 53 genera, and 77 species were collected exclusively during the second year.

4.4 DISCUSSION

Emergence Chamber Described in This Paper. This emergence chamber design was low-cost, easy to manufacture, stable, resisted weathering and breakage, required no upkeep, and concentrated/preserved a wide variety of taxa. This is an excellent trap design for researchers with little indoor or laboratory space to devote to emergence chambers. Additionally, the design is robust enough to be left unattended for many months. The diversity of taxa collected was impressive: 74 beetle families with possible saproxylic species occur in GSMNP and specimens from 50 (68%) of these were collected using the emergence chambers.

The number of specimens increased by 250% during the second year, indicating that at least some species may have undergone multiple generations in the emergence chambers. Twenty-eight percent of all species collected were only collected during the second year. This indicates that at the very least the chamber did not contain a design flaw that sterilized the contents (e.g. overheating) and species requiring more than one year to develop could do so within the environment of the chamber.

This study resulted in the fourth highest species richness of all saproxylic Coleoptera emergence studies reviewed and the second highest species richness of saproxylic Coleoptera emergence using a self supporting chamber (Table 4.1). Meaningful comparisons across studies are difficult because each study looked at different faunas, used different volumes of substrate, and collected over differing amounts of time. However, standardization of studies of fauna in deadwood using emergence chambers would require an emergence chamber that is compatible a wide variety of taxa.

Table 4.2. Coleoptera families and number of species collected from emergence chambers in GSMNP. Scydmaenids are considered separately (as Staphylinidae: Scydmaeninae) because they were widely recognized as a family until recently (Grebennikov and Newton 2009).

Family	# spp.	Family	# spp.
Aderidae	1	Lucanidae	1
Anobiidae	9	Lycidae	1
Anthribidae	2	Lymexylidae	1
Buprestidae	2	Melandryidae	8
Carabidae	11	Melyridae	2
Cerambycidae	29	Monotomidae	1
Cerylonidae	5	Mordellidae	7
Chrysomelidae	2	Mycetophagidae	1
Ciidae	7	Nitidulidae	3
Cleridae	1	Oedemeridae	1
Colydiidae	2	Ptiliidae	3+
Corylophidae	1	Ptilodactylidae	1
Cryptophagidae	3	Pyrochroidae	3
Cucujidae	1	Salpingidae	1
Cupedidae	1	Scarabaeidae	1
Curculionidae	28	Scraptiidae	1
Elateridae	10	Silvanidae	3
Endomychidae	5	Staphylinidae	62+
Erotylidae	1	Scydmaeninae	7+
Eucinetidae	1	Stenotrachelidae	1
Eucnemidae	7	Synchroidae	1
Histeridae	4	Tenebrionidae	13
Hydrophilidae	1	Tetratomidae	1
Laemophloeidae	4	Throscidae	1
Lampyridae	1	Trogossitidae	2
Leiodidae	9	Total spp.	275+

Table 4.3. Total taxa and unique taxa collected by year.

	2006 total # taxa (%)	2006 only # taxa (%)	2007 total # taxa (%)	2007 only # taxa (%)	Total
Specimens	1583 (28%)		4109 (72%)		5692
Family	44 (88%)	13 (26%)	37 (74%)	6 (12%)	50
Genus	174 (77%)	74 (33%)	155 (69%)	53 (23%)	226
Species	197 (72%)	97 (35%)	178 (65%)	77 (28%)	275

Reviewed Emergence Chamber Designs. The reviewed emergence chamber designs (Table 4.1) differed on five major axes: 1) full or partial enclosure of dead wood; 2) self supporting or supported by substrate; 3) final location of chamber/environmental control; 4) resource requirements for chamber operation; and 5) concentration method. These axes are not meant to represent every conceivable aspect of chamber design, only the most fundamental. Depending on the research question(s) other aspects may be as or more important (e.g. incorporation of data loggers and other sensor equipment), but those specific aspects will not be discussed in this general review.

1. Enclosure of Dead Wood. This axis has two states: fully enclosed or partially enclosed (not given in Table 4.1). The substrate is typically not fully enclosed in the following situations: the substrate is too large to fully enclose (snags, large logs); portions of the substrate are inaccessible (stumps); and/or the researcher wishes to leave a portion of the substrate open to colonization while another section is being surveyed. Full enclosure of the substrate in principle provides a better seal and reduces loss of enclosed organisms or contamination from outside organisms. Other axes are largely independent of this axis, except axis 3 where a decision to not fully enclose the substrate may reduce where and how the substrate may be stored.

2. Chamber Self Supporting of Supported by Substrate. This axis represents a continuum of states ranging from a rigid chamber whose structure is independent of the substrate, to a completely flaccid chamber that is fully supported by the substrate (Table 4.1: Chamber type). Where the substrate is small, not structurally sound, samples are intended to be stacked, and/or complete or partial climate control is desired (e.g. in a laboratory), a rigid chamber may be best. Rigid chambers provide an easily standardized volume and may be easier to monitor for damage or holes than some types of partially or fully flaccid chamber. However, a chamber (typically consisting of cloth-like material or netting) supported by the substrate may be best used in situations where the substrate is very large (lying or standing), when the study area is far from vehicular access and the substrate will be left in the field (thus rigid material would be heavy/cumbersome to transport to the site), or when portions of the substrate are to be left exposed. This axis is largely influenced by axis 3 (see below).

3. Final Location of Chamber and Environmental Control. This axis represents a continuum from the chamber being left in the field with no additional attempts to control the substrate's environment, to the chamber removed to a laboratory where multiple aspects of the environment are strictly controlled actively or passively (Table 4.1: Chamber location). Any emergence chamber, regardless of design or material used, will alter the microclimate of the substrate, affecting, at the very least, the boundary layer of air surrounding the dead wood, which in turn will influence the temperature and humidity of the substrate. Presumably, chambers left at the study site or completely outdoors will experience large environmental effects, such as daily temperature changes, similar to the undisturbed substrate. However it should be expected that the rate or magnitude of these changes will be dampened by the increased boundary layer created by the chamber. As the chamber is further removed from the outside environment—placed in an open-sided building or a climate-controlled laboratory—the influence of the outside environment will necessarily decrease. Thus the final location of the chamber and environmental control over the substrate are inseparably linked.

Environmental factors such as the possibility of the chamber flooding, overheating, being destroyed by animals (e.g. bears, rodents), being vandalized, and accessibility should be taken into account when deciding the final location of the chamber and any environmental controls used. Chamber location influences axis 1 (see above) and axis 2 where transportation, stacking, or otherwise storing samples is affected by chamber size and shape. Location is influenced by axes 4 and 5 (see below).

4. Resource Requirements for Chamber Operation. This axis takes into consideration the labor, energy, and materials used during the entire life of the chamber (Table 4.1: Additional resources, exclusive of servicing). Typically resources are associated with environmental control, such as laboratory space for stacking or hanging chambers (axis 2), ventilation, and addition of water. Servicing a chamber (e.g. specimen removal) is a labor resource and should be taken into account when considering the final location of the chamber (axis 3) especially if there is a possibility that student workers or volunteers will be used. Resource requirements are also influenced by axis 5, see below.

5. Concentration Method. When an emergence chamber is sealed specimens within the substrate have, in a sense, been collected. This axis involves methods to sequester specimens after they have emerged from the substrate (Table 4.1: Concentration method). Concentration methods can be active or passive. The most straightforward active concentration method is hand collection. This method has obvious benefits, including allowing for precise association of specimens with emergence holes and galleries, and association of parasitoids with hosts. However, hand collection may result in small specimens being overlooked, requires that chambers be very accessible (axis 3), and is labor intensive (axis 4). Most concentration methods are passive, based on the design of the chamber, and exploit specific aspects of insect behavior. Photoeclection (concentration of insects based on positive phototropism) is accomplished by constructing an opaque emergence chamber where the only light available is from a transparent collection container. Placement of such a collection container at the top of the chamber exploits the flying or crawling up behavior of certain insects. However, not all insects associated with dead wood can fly or detect directionality of light, so these techniques may not be appropriate for some taxa. Many substrate-supported chambers have funnels leading to collection containers incorporated into their design. Here, collection is based on organisms actively moving around within the chamber and randomly falling into the collection container. Another passive collection method is the use of gravity, where a collection container is placed under the substrate to collect anything falling or moving downward. This is certainly an effective concentration method (see below) and does not rely on organisms actively moving around the chamber, but for maximum efficiency requires that the chamber have a funnel-shaped bottom. That requirement may limit final location of the chamber (axis 3) and may add to resource requirements (axis 4), e.g. laboratory space for hanging chambers.

Design Comparisons. Jonsell and Hansson (2007) compared three sampling methods for saproxylic beetles involving two different styles of emergence chambers. One chamber was a self-supporting box with a photoeclection concentration method. The collection vial was inserted in the side of the box several centimeters above the bottom. The other chamber was a suspended bag with a collecting vial at the bottom (gravity concentration). The suspended bag was "somewhat more efficient" than the box (Jonsell and Hansson 2007). Of 119 species collected, 55 were represented by five or fewer individuals. The box produced 60% fewer specimens and 15% fewer species. Thirty-eight species were exclusively collected using the bag, and 19 were exclusively collected from the box. But their comparison involved at least two variables (chamber support and concentration method) so which had the greater influence over chamber performance is difficult to determine.

The design described in this paper combines the two concentration methods of photoeclection and gravity. The chamber (including ventilation holes) is opaque; therefore, the transparent glass collection jar acts as a photoeclector. Additionally, by placing the collection jar in the trough at the bottom of the chamber, species that are wingless, blind, or otherwise indifferent to light are more likely to enter the collection jar. For example, two rarely collected wingless species, *Adranes lecontei* Brendel (Staphylinidae) and *Tohlezkus inexpectus* Vit (Eucinetidae), were both collected in very high numbers, 40 and 163 specimens respectively. Collecting specimens of those two species would have been unlikely using an elevated collection container such as the one used in Jonsell and Hansson (2007).

Certainly, more comparative studies are needed to show what, if any, systematic biases exist among emergence chamber designs. This pertains not only to concentration methods, but also the effects of microclimate (such as temperature and humidity) and substrate position (horizontal vs. vertical) on the diversity of catch. The level of appropriateness for various emergence chamber designs depends on how the five design axes relate to the specific study question and the resources available to the researcher. Due to the highly complex nature of any biological or ecological research extreme care should be taken to ensure that the observations being made relate in a biologically significant manner to the questions being asked and are not simply based on an idealized statistical scenario.

CHAPTER 5: THE BEETLE COMMUNITY OF SMALL OAK TWIGS IN LOUISIANA, WITH A LITERATURE REVIEW OF COLEOPTERA FROM FINE WOODY DEBRIS[3]

5.1 INTRODUCTION

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 & 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 5.1) 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.

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Table 5.1. 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	*Oncideres cingulata* (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 (*Larix laricina* (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 (*Carya glabra* (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	*Oncideres* spp. (Cerambycidae)	20-40 mm etc.	?	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
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

Table 5.1 cont.

Author	Year	Country	Collection Technique(s)	C / SS	Study System	Wood Diameter	Plant vitality	Results (associated with emergence and twigs)
Polk and Ueckert	1973	United States	dissection, emergence	C	saproxylic community associated with *Oncideres rhodosticta* Bates (Cerambycidae)	5-20 mm	freshly killed	reported many emergent Coleoptera, Hymenoptera, Diptera
Rogers	1977	United States	dissection	C	*Oncideres cingulata* (Say) (Cerambycidae)	8-15 mm	freshly killed	reports life history of species and some predators and parasites
Stevens et al.	1979	United States	dissection	SS	*Pityophthorus opaculus* LeConte (Curculionidae)	?	dying	report outbreak of species
Hovore	1980	United States	emergence	SS	*Nathriobrium methioides* Hovore (Cerambycidae)	?	dead	species was reared from small branches
Forcella	1981	United States	dissection	SS	*Oncideres cingulata* (Say) (Cerambycidae)	?	freshly killed	limbs severed later in the season had more larvae
Hovore and Penrose	1982	United States	emergence	C	*Oncideres pustulata* LeConte (Cerambycidae)	?	dead	19 spp. of Cerambycidae that co-inhabit girdled twigs
Forcella	1984	United States	looked at # of twigs only	SS	*Oncideres cingulata* (Say) (Cerambycidae)	7-11 mm	freshly killed	described per tree twig damage
Rice	1989	United States	dissection	SS	*Oncideres pustulata* LeConte (Cerambycidae)	13-55 mm	freshly killed	described branch girdling and oviposition biology
Cramer	1998	United States	dissection	SS	*Oncideres cingulata* (Say) (Cerambycidae)	5-11 mm	freshly killed	total mortality
Mecke et al.	2001	Brazil/ Argentina	emergence, beating, dissection	C	insects associated with *Araucaria* trees	3-12 cm	dead>living	34 spp. Coleoptera, 4 spp. Hymenoptera
Wang et al.	2002	New Zealand	laboratory rearing	SS	*Oemona hirta* (Fabricius) (Cerambycidae)	50-60 mm	living, dead	high mortality in desiccated twigs

Table 5.1 cont.

Author	Year	Country	Collection Technique(s)	C / SS	Study System	Wood Diameter	Plant vitality	Results (associated with emergence and twigs)
Iwata et al.	2004	Japan	laboratory rearing, emergence	SS	*Dinoptera minuta* (Gebler) (Cerambycidae)	5-25 mm	living then dead	larvae emerge to pupate in the soil
Petrice and Haack	2006	United States	emergence	SS	*Agrilus planipennis* Fairmaire (Buprestidae)	6-37 (average 15) cm	freshly killed	desiccation major agent of mortality

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 1).

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.

5.2 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 (N 30˚ 47.6′, W 91˚ 15.2′, 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* Ehrh.), pine (*Pinus* sp.), 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 1999*a*, *b*; Landau *et al.* 1999; Prowell 2001).

Study Design. A single, healthy, ~30-year-old *Quercus falcata* Michx. (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 (α= 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 1000 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 1000 randomized values for expected species richness per bundle and 1000 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).

5.3 RESULTS

Richness. A total of 414 adult Coleoptera specimens were collected, representing 35 species in 33 genera and 16 families (see Table 5.2). Twig bundles 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.

Table 5.2. 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.

		Individuals emerged:			
Family	**Species**	**Ground**	**Propped**	**Aboveground**	**Total**
Biphyllidae	*Diplocoelus rudis* (LeConte, 1863)	2	2	1	5
Buprestidae	*Agrilus obsoletoguttatus* Gory, 1841	98	26	7	131
Cerambycidae	*Anelaphus villosus* (Fabricius, 1792)	6	10	12	28
Cerambycidae	*Liopinus alpha* (Say, 1827)	14	7	22	43
Latridiidae	*Melanophthalma distinguenda* (Comolli, 1837)	1	1	1	3
Cerambycidae	*Neoclytus acuminatus* (Fabricius, 1775)	1	1		2
Cerambycidae	*Anelaphus pumilus* (Newman, 1840)		5	2	7
Cerambycidae	*Cyrtinus pygmaeus* (Haldeman, 1847)		8	17	25
Cerambycidae	*Ecyrus dasycerus* (Say, 1827)		12	7	19
Curculionidae	*Hypothenemus californicus* Hopkins, 1915		4	24	28
Curculionidae	*Laemosaccus nephele* (Herbst, 1797)		7	5	12
Melyridae	*Attalus scincetus* (Say, 1825)		1	1	2
Anobiidae	*Petalium debile* Fall, 1905	1			1
Melandryidae	*Microtonus sericans* LeConte, 1862	1			1
Monotomidae	*Monotoma longicollis* (Gyllenhal, 1827)	1			1
Mordellidae	*Falsomordellistena hebraica* (LeConte, 1862)	1			1
Mordellidae	*Mordella invisitata* Liljeblad, 1945	2			2
Ptiliidae	*Acrotrichis* sp.	1			1
Staphylinidae	*Sepedophilus macer* (Casey, 1895)	1			1
Corylophidae	*Holopsis carolinae* (Casey, 1900)		4		4
Latridiidae	*Corticarina* sp.		2		2
Staphylinidae	*Bibloplectus* sp.		1		1
Anobiidae	*Calymmaderus nitidus* (LeConte, 1865)			1	1

Table 5.2 cont.

Family	Species	Ground	Propped	Aboveground	Total
		Individuals emerged:			
Cerambycidae	*Euderces picipes* (Fabricius, 1787)			4	4
Cerambycidae	*Euderces pini* (Olivier, 1795)			1	1
Cerambycidae	*Obrium maculatum* (Olivier, 1795)			4	4
Cerambycidae	*Tessaropa tenuipes* (Haldeman, 1846)			10	10
Cleridae	*Madoniella dislocatus* (Say, 1825)			1	1
Cleridae	*Neorthopleura thoracica* (Say, 1823)			6	6
Curculionidae	*Acalles clavatus* (Say, 1831)			1	1
Curculionidae	*Pseudopityophthorus asperulus* (LeConte, 1868)			5	5
Curculionidae	*Pseudothysanoes dislocatus* (Blackman, 1920)			56	56
Dermestidae	*Cryptorhopalum floridanum* Casey, 1916			1	1
Laemophloeidae	*Charaphloeus* sp.			2	2
	Totals	130	91	193	414
	Total # species	13	15	24	35

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.

5.4 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.

CHAPTER 6: COMPARISON OF THE COLEOPTERA COMMUNITIES IN LEAF LITTER AND ROTTEN WOOD IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

> Do not go gentle into that good night,
> Old age should burn and rave at close of day;
> Rage, rage against the dying of the light.
> —Dylan Thomas, *Do not go gentle into that good night*
>
> Behold this compost! behold it well!
> —Walt Whitman, *This Compost*

6.1 INTRODUCTION

The last moments in the "life" of a rotten log are a mystery. The organisms within extremely decayed downed coarse woody debris and their relationships to surrounding forest litter are virtually unexplored. In contrast, dead wood in early decay stages has been much more thoroughly investigated and is known to contain a diverse assemblage of saproxylic organisms that account for an important part of the biodiversity of the landscape (Blackman and Stage 1924; Ferro et al. 2009; Grove 2002b; Harmon et al. 1986; Speight 1989).

Numerous decay classifications exist. Decay class V (CWD5), based on the decay classification of coarse woody debris (CWD) by Pyle and Brown (1999), is the stage we focused on in this study. Logs in CWD5 are composed of predominantly powdery wood, are easily crushed, are generally flattened, and are beginning to become integrated into the forest floor. At the end of this decay stage coarse woody debris will lose its individuality and disappear as small fragments to the O and A soil horizons, also known as mould, humus, or duff by earlier authors.

The community within CWD5 has never been systematically sampled, but the presumption is that the well-rotted log is eventually overrun by surrounding soil and litter inhabitants. Here the term community is meant to refer to the organisms inhabiting a particular habitat *sensu* MacArthur (1971) (''… any set of organisms currently living near each other and about which it is interesting to talk''). Shelford (1913: 247) characterized the final decay stage of rotten wood by commenting, "Such a log is only shelter for the regular inhabitants of the forest floor…" Adams (1915: 149) stated, "There is thus with the decay of wood a progressive increase in the kinds of animals characteristic of humus." Graham (1925: 397) wrote, "There is a regular progression from truly wood eating (xylophagous) forms toward an association of organisms characteristic of the duff strata of forest soils." Savely (1939: 360) wrote about pine, "The final stages in the decomposition of the wood, in which it becomes a part of the soil has not been studied, but it is reasonable to assume that insects characteristic of the soil fauna (termites, etc.) replaced those found only in rotten wood." Maser and Trappe (1984) described CWD5 in western North American forests as becoming permeated with roots of overstory trees and listed centipedes, salamanders, and small mammals as important predators within CWD5. However, their review concentrated on vertebrates and large invertebrates and may have overlooked smaller ones.

We are not aware of any survey focused on the invertebrate community of CWD5. Adams (1915: 153) listed seven taxa from "much decayed wood": *Odontotaenius disjunctus* (Illiger) (as *Passalus cornutus* Fabricius) (Coleoptera: Passalidae); *Dendroides* larvae (Coleoptera: Pyrochroidae); *Neopyrochroa* larvae (as *Pyrochroa*) (Coleoptera: Pyrochroidae); *Camponotus herculeanus* (Linnaeus) (Hymenoptera: Formicidae); *Scolecocampa liburna* Geyer (Lepidoptera: Noctuidae); *Meracantha contracta* (Beauvois) (Coleoptera: Tenebrionidae); and immature *Myrmeleon* sp. (probably *Myrmeleon immaculatus* DeGeer) (Neuroptera: Myrmeleontidae) which makes pits in the dry "brown meal" on the top of much decayed wood. However, with the exception of *Myrmeleon,* these species are more associated with the penultimate decay class than with CWD5 as here defined.

Only two direct comparisons of the invertebrate community between leaf litter and CWD were found. Chandler (1987) compared the Pselaphinae (Staphylinidae) fauna between leaf litter and rotten wood ("could be easily worked apart by hand") in both an old-growth and a 40-year-old regrowth forest in New Hampshire. He collected 9 species, three of which were associated with leaf litter, four associated with rotten wood, and two were intermediate.

Irmler et al. (1996) collected specimens using emergence traps from multiple classes of CWD in a beech forest in northern Germany. Each emergence trap was 1 m^2 in area, but the authors do not make clear whether logs were placed entirely in emergence traps or if 1 m^2 of only the outer surface of the log was covered. Additionally, emergence traps covering 1 m^2 were placed over leaf litter at the same locations. Of the Mycetophilidae (Diptera) species collected, 46% were collected only from CWD, 32% only from leaf litter, and 22% from both habitat sites. Respective Sciaridae findings were 30%, 45%, and 25%. These findings indicate that the Diptera community within CWD and leaf litter may be quite distinct. However, Irmler et al. (1996) sampled from less decayed wood, not CWD5, so there may be more overlap between the CWD5 and leaf litter than indicated by their results.

Several researchers have studied invertebrate communities within leaf litter near and far from CWD. Results have been contradictory. In a Florida, USA, forest Hanula et al. (2009) used pitfall traps to sample litter arthropods near (immediately against) and distant (10 m) from CWD. In general more total arthropods and a greater biomass of arthropods were collected in pitfalls away from CWD. They identified specimens to genus (932 total) and found that of the 297 taxa that were collected in sufficient numbers to be analyzed, 73 taxa were captured in significantly higher numbers in pitfalls away from CWD, and 28 were captured in higher numbers near CWD.

Andrew et al. (2000) found no differences in Berlese samples of ant communities near (against) and far (3 m) from CWD in burned and unburned forests in New South Wales, Australia.

Marra and Edmonds (1998) took Berlese samples from locations near (0-10 cm) and distant (100-110 cm) from CWD in forested and logged sites in Washington, USA. Distance from CWD had no influence on densities of Acari, Collembola, or Coleoptera. Of 123 species for which there were sufficient data to perform an analysis, five had significantly higher densities near CWD and two had higher densities distant from CWD.

In a study by Evans et al. (2003), 71 families and 41 mite "recognizable taxonomic units" were collected using Tullgren funnels from leaf litter in a New Zealand forest from sites near and distant from CWD (0, 1.5, and 2.5 m). Two families increased in abundance with increased distance from CWD, while three families and four mite "recognizable taxonomic units" showed an increase in abundance near CWD.

Topp et al. (2006) collected specimens using a Tullgren funnel in four forests in Slovakia and found higher beetle richness in leaf litter samples close to CWD (<10 cm) than those taken further away (>200 cm).

In South Carolina, USA, leaf litter invertebrates were sampled using Berlese funnels and found to be more numerous near CWD (<15 cm) than away (>2 m) (Ulyshen and Hanula 2009b). Taxa were only identified to order.

Jabin et al. (2007), working in Germany, used Tullgren funnels to sample macro-arthropods in leaf litter near (<10 cm) and distant (> 500 cm) from CWD, in edge and interior forest habitats, in summer and winter. All taxa occurred in higher numbers near CWD than distant from it. They also found some effect of season on densities of some taxa. Specimens were only identified to the level of order or family.

The above studies are difficult to compare, but some generalities can be highlighted. Pitfall traps may not be appropriate for use in these comparisons because they may bias for large vagile organisms that move on or near the leaf litter surface and against smaller less mobile organisms that stay under leaf litter or within wood. Across all studies "near" CWD was designated as 0 – 15 cm and "distant" was 1 – 10 m. Where distant samples were less than 2 m from CWD, few taxa showed differences in density. Studies that identified taxa below order tended to find that taxa within an order responded differently to distance from CWD, implying a direct positive correlation between identification to low taxonomic levels and an accurate understanding of the system.

The daily or seasonal movement of organisms between leaf litter and CWD is not well studied. Jackson et al. (2009) studied the saproxylic beetle *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae) in Louisiana, USA. While *O. disjunctus* can fly, it tends to move from one piece of CWD to another by walking through the surrounding leaf litter. Dispersal was highest in spring and fall and individuals were 3.5 times more likely to disperse during the day than at night. Additionally temperature and relative humidity were positively related to movement rate.

The general consensus holds that many organisms overwinter in CWD, which is expected for those organisms that live in CWD. However, organisms that actively seek CWD as an overwintering site but are otherwise not generally associated with it in warmer months are poorly documented. Maser and Trappe (1984) commented that centipedes overwinter in CWD. Penney (1967) documented a litter dwelling species of Carabidae that hibernates and aestivates in specially excavated cells in dead wood.

Banerjee (1967) studied the natural history of the millipede *Cylindroiulus punctatus* (Leach) and showed that season and age of individuals dictated whether they resided in logs or leaf litter. Adults migrated into logs in the spring to mate and lay eggs, then left the logs in the fall. After hatching, the first to third instars remained under bark, but the remainder of instars, fourth to seventh, resided in the leaf litter. As the natural history of more organisms becomes known we should expect to see more dynamic habitat use such as this.

Lloyd (1963) performed two experiments on the movement of invertebrates between beech leaf litter and fallen branches in Wytham Woods near Oxford, England. The branches had an average diameter of about 5 cm and still had bark, although it had separated from the heartwood. One experiment showed that during a 4 day period, as the temperature rose from 0°C to 8°C, organisms moved from the leaf litter to the branches, which contradicts the overwintering hypothesis. Another of his experiments tested for diurnal rhythms but failed to find any significant movement of organisms between leaf litter and branches over a 20 hour period. Both experiments have been cited often, but suffer from small sample sizes. There is no indication they have been reproduced by other researchers, and should be before any general conclusions can be made.

If overwintering in CWD5 is important for litter dwelling species, then CWD5 should have the highest species richness in winter. Collecting in winter is not practical within our chosen study location, Great Smoky Mountains National Park (GSMNP), because of deep snow and road closures. However, an increase in the number of taxa in CWD5 in the fall as individuals congregate in anticipation of winter, and maintenance of this diversity in the early spring before individuals move back to the leaf litter, should be expected. Thus fall and spring collections should provide samples with the greatest overlap of taxa between the two habitats and may provide evidence of seasonality for particular species.

As older forests are reduced and more forested land becomes managed, CWD is dwindling, as are the saproxylic species dependent upon it (Grove 2002b; Speight 1989). In North America there is some research on how anthropogenic forest disturbance affects CWD dwelling organisms. Chandler (1991) collected a greater abundance of Eucinetoidea (=Coleoptera: Scirtoidea) and Cucujoidea (Coleoptera) in old growth than regenerating forest in New Hampshire. A comparison of the same areas showed higher leiodid beetle abundance and richness in the old growth forest (Chandler and Peck 1992). Several species of Carabidae (Coleoptera), including one saproxylic species, found in old growth were rare or absent in younger Canadian forests (Spence et al. 1996).

By contrast, in Europe, which has undergone long-term habitat alteration and where the fauna is better known, organisms associated with dead wood are known to have been greatly affected by anthropogenic forest disturbance. At the European Union level, 14% (57 species) of saproxylic Coleoptera assessed are considered threatened and they represent the first ecological grouping specifically studied by the International Union for Conservation of Nature (Nieto and Alexander 2010). Additionally research concerning forestry practices that are better suited for conservation of saproxylic organisms (Gibb et al. 2006b) and research on specific saproxylic Coleoptera species of concern (Drag et al. 2011; Ranius et al. 2005; Siitonen and Saaristo 2000; Thomaes et al. 2008) has been conducted.

Yee et al. (2006) and Brin et al. (2010) showed that species assemblages in rotten wood differ with log diameter. Generally bigger logs accommodate more species. Old growth forests, with a higher volume of CWD, greater continuity of CWD, and greater diameter of logs are important for saproxylic species conservation (Siitonen et al. 2001; Grove 2002b). Great Smoky Mountains National Park contains large tracts of forest that have not been cut since European settlement in North America, while other areas of the park were recently logged (<100 years ago). Comparison of saproxylic species assemblages between old growth and regrowth sites are needed to determine what, if any, species are restricted to old growth forest and may be of conservation concern. Thus, the purpose of this study was to survey the Coleoptera community within CWD5 within GSMNP, compare that community with the Coleoptera found within the surrounding leaf litter, and to see how those communities differ between seasons (fall and spring) and forest types (primary and secondary).

6.2 MATERIAL AND METHODS

Study Area. Great Smoky Mountains National Park (Fig. 6.1) was established in 1934, named as an International Biosphere Reserve in 1976, and a World Heritage Site in 1983. It encompasses 211,000 ha (521,490 acres) in Tennessee and North Carolina, USA. Most of the area is topographically complex, ranging in elevation from 270–2024 m (875-6643 ft). The Great Smoky Mountains range itself extends from the northeast corner of the park to the southwest. The southeastern corner and the adjacent Cherokee Indian Reservation are part of the Balsam Mountains. Five major forest communities are recognized in the park, though 80% may be broadly classified as eastern deciduous forest (Houk and Collier 1993). Lower and intermediate elevations (1070-1525 m; 3500-5000 ft.) are dominated by northern hardwood forests and spruce-fir forests at higher elevations (above 1525 m; 5000 ft.). Cove forests are found in sheltered valleys at mid-elevations (1070-1370 m; 3500-4500 ft.). This community represents the most diverse habitat in the park with its diversity of tree species, complex understory, and deep, moist litter layer. Some of the old growth cove forest stands are among the most beautiful and best preserved examples of this forest type in existence. The eastern half of the park contains the largest remaining tract of old growth forest in the eastern U.S. (Davis et al. 1996).

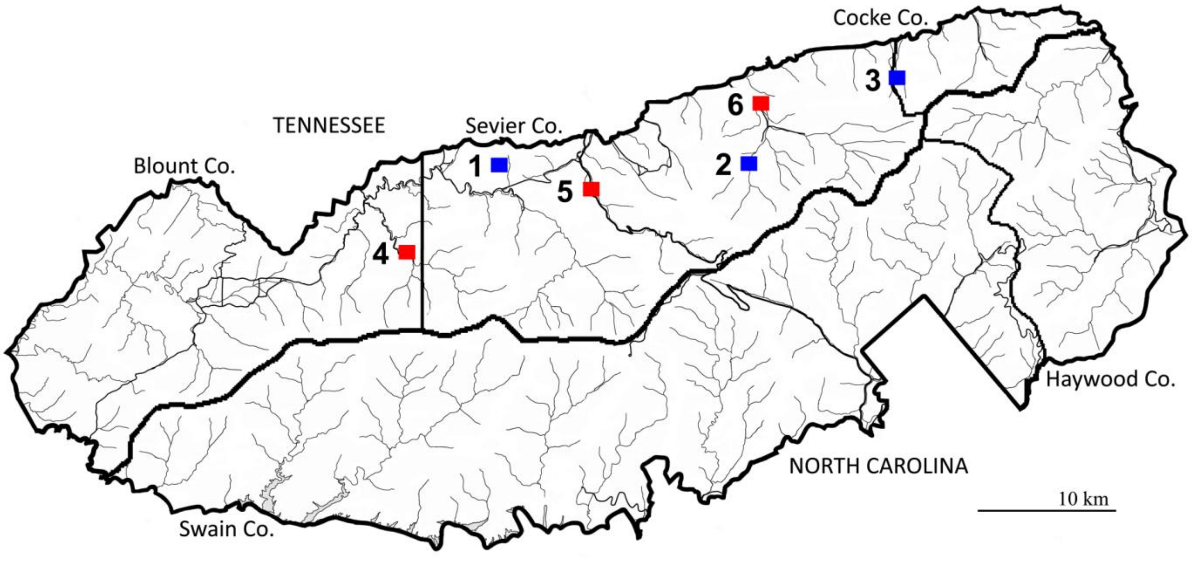

Figure 6.1. Map of collection locations in Great Smoky Mountains National Park. Primary forest sites: 1) Laurel Falls; 2) Porters Creek; 3) Albright Grove. Secondary forest sites: 4) Tremont; 5) Sugarlands Quiet Walkway; 6) Greenbrier.

Lower and more xeric parts of the western half contain large stands of pine hardwood. Cades Cove, a large area in the northwestern quarter of the park is flat and mainly covered with meadows. Access to the southwestern quarter of the park is limited by Lake Fontana, and is the largest area of roadless forest in eastern U.S. (Anonymous 2004). The park's abundant rainfall and high summer humidity provide excellent growing conditions. In the Smokies, the average annual rainfall varies from approximately 140 cm (55 inches) in the valleys to over 215 cm (85 inches) on some peaks.

The perception that U.S. national parks are protected from human-induced insults to native habitats within their boundaries is valid only in a limited way. The natural resources represented in these relatively pristine habitats are of course protected from logging, mining, and conversion to agriculture. But with this protection comes a legislative mandate to make the parks available for the enjoyment and recreation of visitors. More than 9,000,000 people visit GSMNP annually, making it the most heavily used of U.S. National Parks (Anonymous 2004).

Until the early 19th century, the American chestnut, *Castanea dentata* (Marsh.) Borkh., was a co-dominant tree in northern hardwood forests of GSMNP. The huge trunks (up to 20 ft. diameter) provided substrates for diverse communities of subcortical beetles and other insects for many years after falling. Beginning in 1904, chestnut blight rapidly spread throughout the eastern U.S., killing almost every large chestnut tree in the country (Hepting 1974).

More recently, the Fraser fir, *Abies fraseri* (Pursh) Poir., a co-dominant tree in southern Appalachian spruce-fir forests, suffered a similar fate. The balsam woolly adelgid (*Adelges piceae* (Ratzeburg), Hemiptera: Adelgidae), native to Europe, entered the southern Appalachians during the 1950s and quickly overwhelmed stands of Fraser fir in the region (Eager 1984). Many areas that once supported mature forests of red spruce (*Picea rubens* Sarg.) and Fraser fir now are in transition to diversity-impoverished rhododendron thickets. These effects can be observed in dramatic fashion on top of Clingman's Dome, where large "ghost stands" of dead fir trunks dominate patches of the landscape.

The sudden decline of these two dominant tree species has had a profound effect on the forest ecology of the region. These changes undoubtedly have had similar effects on countless small, cryptic organisms that may never be recognized due to the lack of comprehensive biodiversity information. These changes continue today. Currently, yet another insect pest, the hemlock woolly adelgid (*Adelges tsugae* (Annand), Hemiptera: Adelgidae), from Asia, has invaded the region and has decimated large stands of eastern hemlock, *Tsuga canadensis* (L.) Carrière.

Study Sites. All collections took place at six locations in GSMNP. Overstory vegetation data were obtained from Madden (Geospatial Dataset-1047498), and understory vegetation data were obtained from Madden (Geospatial Dataset-1047499); see Welch et al. (2002) and Madden et al. (2004) for a description of how data were collected. Geology data were obtained from National Park Service (2006). Vegetation disturbance history data were obtained from National Park Service (2007). Data on forest type in 1938 were obtained from National Park Service (2009). Three locations within each study site were surveyed using a point relascope sampling technique (Brissette et al. 2003; Gove et al. 1999). Findings were averaged to obtain volume of CWD per hectare at each study site.

Three study sites, hereafter referred to as "primary forest" sites, were located in least disturbed forests:

1) Laurel Falls (TN: Sevier Co.: N35˚40.808′ W83˚36.067′). The site was on Thunderhead Sandstone, has an oak-hickory forest overstory, and a light rhododendron understory. Vegetation disturbance was selective cut and during a 1938 survey this location was designated as cove hardwood. Coarse woody debris volume was 663 m^3/ha.

2) Porters Creek (TN: Sevier Co.: N35˚40.790′ W83˚23.855′). The site was on Thunderhead Sandstone, has an acid cove forest overstory, and a medium rhododendron understory. Vegetation disturbance was light cut and during a 1938 survey this location was designated as cove hardwood. Coarse woody debris volume was 290 m^3/ha.

3) Albright Grove (TN: Cocke Co.: N35˚44.173′ W83˚16.647′). The site was on Thunderhead Sandstone, has cove forest overstory, and a light rhododendron understory. Vegetation disturbance was undisturbed and during a 1938 survey this location was designated as cove hardwood. Coarse woody debris volume was 927 m^3/ha.

Three study sites, hereafter referred to as "secondary forest" sites, were located in disturbed (heavily logged) forests:

1) Greenbrier (TN: Sevier Co.: N35˚43.147′ W83˚23.349′). The site was on Roaring Fork Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designated as grassland. Coarse woody debris volume was 143 m^3/ha.

2) Tremont (TN: Blount Co.: N35˚37.308′ W83˚40.447′). The site was on Elkmont Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designated as oak/chestnut forest. Coarse woody debris volume was 139 m^3/ha.

3) Sugarlands Quiet Walkway (QW) (TN: Sevier Co.: N35˚39.826′ W83˚31.509′). The Site was on Roaring Fork Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designated as grassland. Coarse woody debris volume was 161 m^3/ha.

Substrate. Leaf litter is defined as the organic material (O soil horizon) at the soil-atmosphere boundary (largely consisting of leaves, twigs, mosses, lichens, and minor components such as fine dead animal matter and fungal matter) including 1-2 cm of the topmost portion of the A soil horizon (Coleman et al. 2004; Facelli and Picket 1991; White 2006).

Coarse woody debris is defined as dead tree trunks or branches greater than 8 cm diameter lying in contact with the ground. Decay classes follow Pyle and Brown (1999) where coarse woody debris decay class V (CWD5) represents the last stage of decay. Specifically debris of CWD5 is composed of predominantly powdery wood, easily crushed, and generally flattened.

Sampling. Sampling took place in October 2006 (hereafter referred to as the “fall” sampling period) and again April 2007 (hereafter referred to as the “spring” sampling period). Three samples were taken of leaf litter and three of CWD5 at each of the six locations during each season (72 samples total). Samples were collected using a sifting/Berlese technique as outlined in Schauff (2001). Sifters were made from one-half inch (~1.27 cm) mesh, and samples (material passed through the mesh) were approximately 6 liters in volume. Samples of CWD5 were only collected from hardwood (angiosperm) tree debris and each represents a composite of smaller samples taken from numerous pieces of CWD5. Leaf litter samples were taken at least one meter from CWD and represent a composite of numerous subsamples. All CWD5 samples were collected by MLF and all leaf litter samples were collected by MLG. Samples were labeled and transported back to Louisiana State University where specimens were extracted using a Berlese funnel. Data integrity protocols followed the recommendations of Grove (2003).

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 (primarily Arnett and Thomas (2001) and Arnett et al. (2002) and references therein, plus additional literature as needed), 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, and Great Smoky Mountains Natural History Museum (GSNP), Gatlinburg, Tennessee.

These practices are in line with the recommendations given by Gotelli (2004) and Bortolus (2008) concerning appropriate taxonomic practices when conducting community level research. Specifically: 1) specimens were identified in an appropriate manner, not through the use of "gray literature" or previous ecological publications; 2) taxonomic experts were consulted concerning the identification of various taxa and are thanked in the Acknowledgments section; 3) literature used to identify taxa is cited (see above and Discussion); 4) specimens have been deposited in scientific institutions so that further taxonomic confirmations can be made; and 5) taxonomy as a science was supported; two taxonomists were trained, more than 20 new species were described as a result of this research, and keys were provided for their identification (Ferro and Carlton 2010; Park et al. 2010; see Chapter 3).

Data analysis. Individual-based rarefaction curves were used to compare species richness among subsets (Gotelli and Colwell 2001). Curves were constructed using code developed by MLF and KEH and run in the R programming environment (R Development Core Team 2010). For each subset, 1000 rarefaction curves were created, an average curve and its 95% confidence limits were derived from the simulations, and a significant deviation from the simulated average occurred when an observed value fell outside the confidence interval. Each rarefaction curve is shown with a combination of these three lines and an average curve that lies outside the confidence interval of another curve can be considered different at the α=0.05 level.

Community similarity was assessed using Sorensen's quotient of similarity (Southwood 1978).

Chi square goodness of fit testing was performed for 59 species represented by 10 or more specimens (i.e. an expected value of five or more specimens per subset, see Crawley 2007). Tests were performed for a difference in number of specimens of a given species between different substrates, forests, and seasons. For all tests, degrees of freedom = 1 and α=0.05. A Bonferroni correction was not used (as per Gotelli and Ellison 2004: 348). With α=0.05 there is a 5% chance of reporting a significant difference even though one does not actually exist (Type I error). Therefore we should expect significance to be incorrectly reported for ~3 comparisons (5% of 59) within each group of tests.

6.3 RESULTS

Total. A total of 4261 adult beetle specimens, representing 216 lowest identifiable taxa within 159 genera and 27 families, were collected as part of this research (Appendix 2). Of the 216 lowest identifiable taxa, four were identifiable only to family or tribe, 75 were identifiable only to genus, and 137 were identified to species. Groups only identified to family, tribe, or genus may contain multiple species (see discussion). For the remainder of the results and discussion all 216 lowest identifiable taxa will be referred to as "species" in an attempt to reduce jargon and increase readability.

Staphylinidae was, by a wide margin, the most species rich family with 106 species, followed by Carabidae (25 spp.), Leiodidae (21 spp.), and Curculionidae (20 spp.). Fourteen families were represented by a single species. Seven species were represented by more than 100 specimens, and 66 species (31%) were singletons.

Table 6.1 provides a summary of the number of specimens, families, genera, and species collected for the total, each subset, and combination of subsets. The species accumulation curve (SAC) column denotes which subset had the higher species richness when normalized for number of specimens. Like letters denote curves which are not significantly different ($\alpha = 0.05$), a = highest richness, b = second highest, etc.

Substrate. Many more specimens and species were collected from leaf litter (3471 and 170, respectively) than from CWD5 (790 and 111, respectively). However, a comparison of the species accumulation curves for both subsamples (Fig. 6.3) shows species richness was not significantly different between leaf litter and CWD5 when normalized for number of specimens.

Of the 170 species from leaf litter, 105 (49% of total) were only collected in leaf litter (Fig. 6.2). Of the 111 species collected from CWD5, 46 (21%) were only collected in CWD5. The remaining 65 species (30%) were collected in both substrates. The Sorensen's quotient of similarity for these two substrates is 0.46.

Forest. Many more specimens but fewer species were collected from primary forest (2853 and 144, respectively) than from secondary forest (1408 and 146, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 6.4) shows significantly higher species richness in secondary forest when normalized for number of specimens.

Of the 144 species collected from primary forest, 70 (32% of total) were only collected in primary forest. Of the 146 species collected in secondary forest, 72 (33%) were only collected in secondary forest. The remaining 74 species (34%) were collected in both forest types. The Sorensen's quotient of similarity for these two substrates is 0.51.

Season. More specimens and more species were collected during spring (2271 and 172, respectively) than during fall (1990 and 149, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 6.5) shows significantly higher species richness during spring.

Of the 172 species collected during spring, 67 (31%) were only collected during spring. Of the 149 species collected during fall, 44 (20%) were only collected during fall. The remaining 105 species (49%) were collected during both seasons. The Sorensen's quotient of similarity for these two substrates is 0.65.

Table 6.1. Number of specimens, families, genera, and species collected for the total, each subset, and combination of subsets. SAC = Species Accumulation Curve: denotes which subset had the higher species richness when normalized for number of specimens. Like letters denote curves which are not significantly different ($\alpha = 0.05$), a = highest richness, b = second highest, etc.

		#Specimens	**#Family**	**#Genus**	**#Species**	**SAC**
1	Total	4261	27	159	216	/
2	Leaf Litter	3471	24	135	170	a
2	CWD5	790	16	82	111	a
3	Primary	2853	23	105	144	b
3	Secondary	1408	23	115	146	a
4	Spring	2271	22	128	172	a
4	Fall	1990	24	114	149	b
5	Spring, Litter	1777	20	109	136	a
5	Fall, Litter	1694	21	95	117	b
5	Spring, CWD5	494	12	64	84	a
5	Fall, CWD5	296	16	56	71	a
6	Primary, Litter	2520	20	82	107	b
6	Secondary, Litter	951	20	98	116	a
6	Secondary, CWD5	457	10	51	65	b
6	Primary, CWD5	333	16	59	77	a
7	Spring, Primary	1459	16	83	111	b
7	Fall, Primary	1394	19	75	97	c
7	Spring, Secondary	812	17	91	108	a
7	Fall, Secondary	596	15	78	97	a
8	Spring, Primary, Litter	1266	15	65	85	b
8	Fall, Primary, Litter	1254	16	59	74	c
8	Spring, Secondary, Litter	511	16	74	84	a
8	Fall, Secondary, Litter	440	15	64	76	a
8	Spring, Secondary, CWD5	301	9	41	51	b
8	Spring, Primary, CWD5	193	11	44	54	a
8	Fall, Secondary, CWD5	156	8	35	40	b
8	Fall, Primary, CWD5	140	15	38	47	a

Season x Substrate. Subsets based on a combination of season and substrate showed that the greatest number of specimens was collected in spring leaf litter (1777) and the fewest number of specimens was collected in fall CWD5 (296). Those combinations also yielded the greatest (136) and fewest (71) numbers of species collected, respectively. Species richness based on species accumulation curve comparisons was not significantly different among spring leaf litter, spring CWD5, and fall CWD5 but those were significantly higher than fall leaf litter.

Forest x Substrate. Subsets based on a combination of forest and substrate showed that the greatest number of specimens was collected in primary forest leaf litter (2520) and the fewest specimens were collected from primary forest CWD5 (333). The greatest number of species was collected in secondary forest leaf litter (116) and the fewest species were collected in secondary CWD5 (65). Species richness based on species accumulation curve comparisons (Fig. 6.6) was not significantly different between secondary forest litter and primary forest CWD5. Those two combinations were significantly higher in species richness than primary forest leaf litter and secondary CWD5.

Season x Forest. Subsets based on a combination of season and forest type showed the greatest number of specimens was collected in the spring primary forest (1459) and the fewest specimens were collected in the fall secondary forest (596). The greatest number of species was collected in spring primary forest (111). The fewest species were collected in fall primary and fall secondary forests, each of which yielded 97 species. Species richness based on species accumulation curve comparisons was not significantly different between spring and fall secondary forest. Those two were significantly higher in species richness than spring primary forest, which itself was significantly higher than fall primary forest.

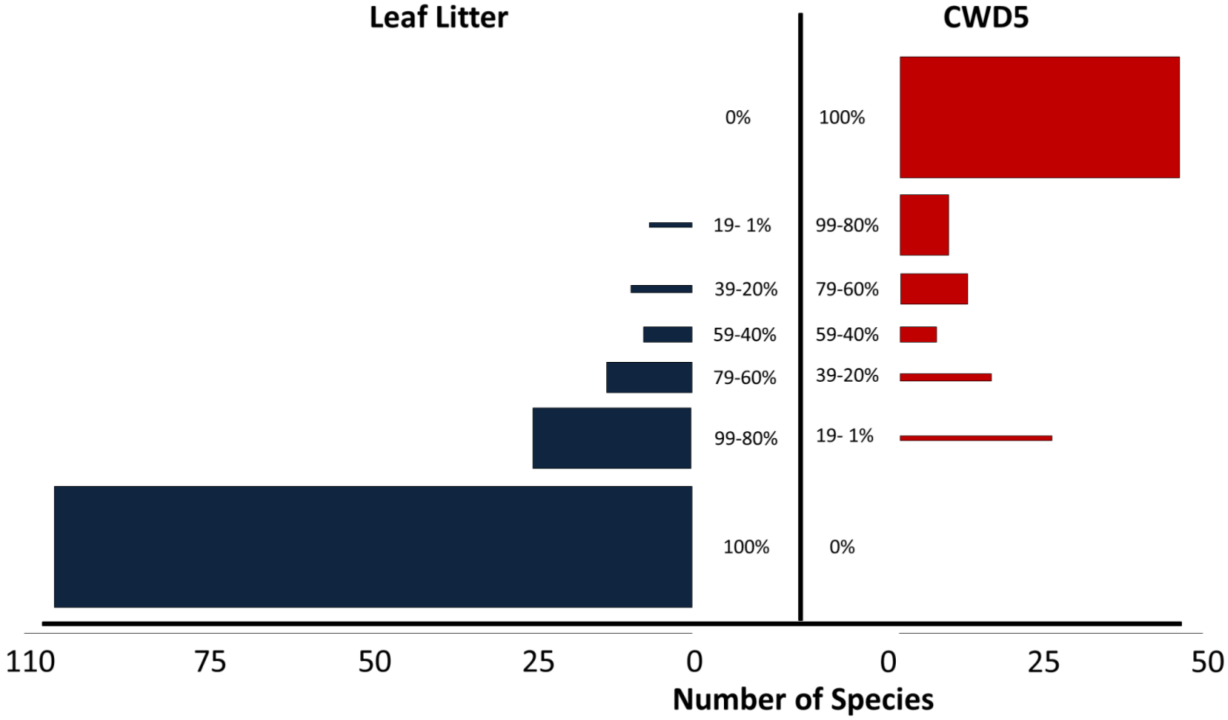

Figure 6.2. Number of species represented by proportions of specimens in leaf litter and CWD5.

Season x Forest x Substrate. A comparison of the eight possible combinations of season, forest, and substrate showed that the greatest number of specimens was collected in spring primary forest leaf litter (1266), and the fewest collected in fall primary forest CWD5 (140). The greatest number of species was collected in spring primary forest leaf litter (85) and the fewest was collected in fall secondary forest CWD5 (40). Species richness based on species accumulation curve comparisons was highest in, and not significantly different among, spring secondary forest leaf litter, fall secondary forest leaf litter, spring primary forest CWD5, and fall primary forest CWD5. Species richness among spring primary forest leaf litter, spring secondary CWD5, and fall secondary forest CWD5 was not significantly different and intermediate within all combinations. Fall primary forest leaf litter had significantly lower species richness than all other combinations.

Species Data. Of the 216 species collected, 59 (27%) were represented by 10 or more specimens (Appendix 2) and available for statistical evaluation.

Substrate. Of the 59 species available for testing, 40 species (68%) were represented by significantly more specimens in leaf litter, eight species (13%) were represented by significantly more specimens in CWD5, and 11 species (19%) showed no significant difference between the two habitats.

Forest. Of the 59 species available for testing, 28 species (48%) were represented by significantly more specimens in primary forest, 19 species (32%) were represented by significantly more specimens in secondary forest, and 12 species (20%) showed no significant difference between the two forest types.

Season. Of the 59 species available for testing, 19 species (32%) were represented by significantly more specimens in spring, nine species (15%) were represented by significantly more specimens in fall, and 31 species (53%) showed no significant difference between the two seasons.

6.4 DISCUSSION

Coarse woody debris decay class V is a unique habitat with a rich fauna equal to that of leaf litter. However, specimens in CWD5 were much less abundant. With the exception of *Mychocerus striatus* (Sen Gupta and Crowson) no species averaged more than one specimen per two samples. This apparent rarity can be explained for some species that were abundant in leaf litter (vagrants), and some species that may be holdovers from earlier decay stages (at a habitat edge). However, any species associated only with CWD5 (with the possible exception of *M. striatus*) may truly be represented by few individuals across the landscape. For example *Tohlezkus inexpectus* Vit and *Leptusa pusio* (Casey) are significantly associated with both CWD5 and primary forests. Prior to this research *T. inexpectus* was known from only a few individuals (see below), and *L. pusio* was only known from the type series of two specimens (Gusarov 2003e). *Leptusa pusio* was first collected in Ohio and is winged so it may have a wide distribution. Conversely, *T. inexpectus* is wingless and has only been collected in the Southern Appalachians, making it a possible species of interest in future conservation studies.

Physically CWD5 is usually surrounded by leaf litter on all sides. Movement from one area of CWD5 to another will often require crossing (through, over, or under) wide expanses of

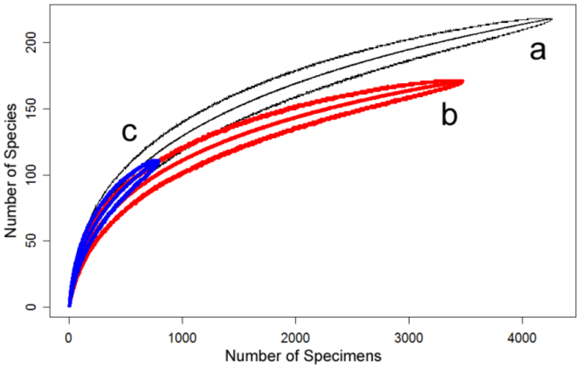

Figure 6.3. Species accumulation curves for a: total; b: leaf litter; c: CWD5.

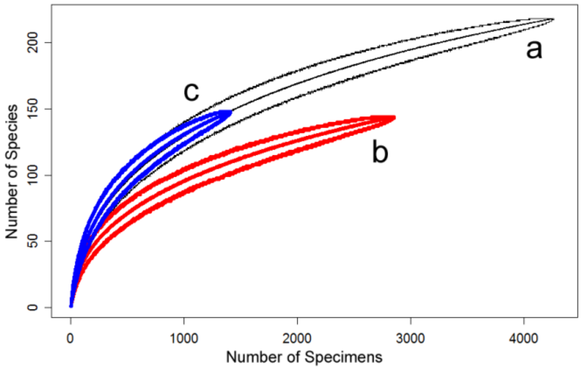

Figure 6.5. Species accumulation curves for a: total; b: fall samples; c: spring samples.

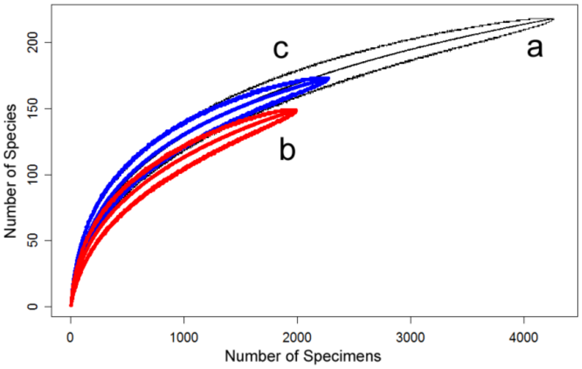

Figure 6.4. Species accumulation curves for a: total; b: primary forest; c: secondary forest.

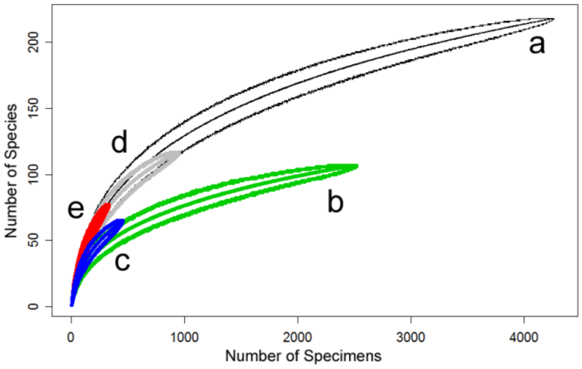

Figure 6.6. Species accumulation curves for a: total; b: leaf litter from primary forest; c: CWD5 from secondary forest; d: leaf litter from secondary forest; e: CWD5 from primary forest.

leaf litter. Any given volume of CWD5 had about 80% fewer individuals than leaf litter, but had the same overall species richness. Therefore, individuals in CWD5 have fewer encounters with other individuals than those in leaf litter. Eight species were significantly associated with CWD5 and all were also found in leaf litter except *Dryophthorus americanus* (Bedel). Twenty-six leaf litter associates were occasionally found in CWD5. Three of those, *Anillinus langdoni* Sokolov and Carlton, *Acrotrichis* spp., and *Euconnus* (*Napochus*) spp. were relatively numerous in CWD5 and are important to the habitat, even though they are not significantly associated with it. However, species associated with CWD5 did not contribute many individuals to leaf litter (maximum = 6). Eleven species were present in both habitats that showed no preference for either one.

Mychocerus striatus was by far the dominant species in CWD5, represented by an order of magnitude more individuals than any other species (246 vs. 38 for the next most numerous taxon) and was the fourth most numerous species on the forest floor. *Mychocerus striatus* is probably a fungivore (Lawrence and Stephan 1975) and is brachypterous (without fully developed flight wings). Of the other 16 species represented by 10 or more individuals collected in CWD5, six are probably fungivores or detritivores, and seven are predators, mostly of Collembola and mites. At least six species are brachypterous, including *M. striatus.* Of the eight species associated with CWD5, six are probably fungivores or detritivores and two are predators. Three of the CWD5 associates are brachypterous (*M. striatus*, *Tohlezkus inexpectus*, and some species of *Sonoma*) which seems unexpected for organisms that live in a disjunct ephemeral habitat. However, flightlessness is one outcome of habitat stability (Yee et al. 2006), indicating that CWD5 is a relatively long term, stable habitat. How the above species move from one area of CWD5 to another is unknown.

Leaf litter is ubiquitous on the forest floor and litter dwellers can move from one location to another without leaving it. Leaf litter is occasionally interrupted by islands of CWD including CWD5 which can be circumnavigated or crossed. Individuals in leaf litter encounter many more individuals compared to individuals in CWD5. Forty species were associated with leaf litter, of those 14 were not collected in CWD5, the remaining 26 were present in CWD5, three of which (see above) were numerically important in that habitat. In leaf litter 47 species were represented by 10 or more individuals. Eleven species were represented by more than 50 individuals, six of which are predators and the remaining five are probably fungivores or detritivores.

Primary forest had significantly lower species richness than secondary forest, but of species available for statistical evaluation, primary forest had more associates (28) than secondary (19). Primary CWD5 species richness was higher than primary leaf litter. It was also higher than secondary CWD5, possibly due to greater volume of habitat, an uninterrupted availability of habitat, or a combination of factors. However, only two species associated with primary forest were also associated with CWD5, but 26 were also associated with leaf litter. Low sample sizes and the resulting inability to evaluate species are probably the causes of these conflicting observations. Twelve species associated with secondary forests were also significantly associated with leaf litter, and four with CWD5. In general, both CWD5 and leaf litter harbor distinct faunas within primary and secondary forests. Subsequent researchers should be aware of these differences.

Spring had significantly higher species richness than fall, but only accounted for about 80% of the total species collected. Of the species available for statistical evaluation two were only collected in a single season. For those species associated with spring, 13 were also associated with leaf litter and five were associated with CWD5. All nine species associated with fall were also associated with leaf litter. These findings are probably biased by the inclusion of only the adult life stage in this research. In the context of this study, lack of collection from a given substrate and forest is stronger evidence for absence than lack of collection for a given season. Any non-migrant species present will be in the environment in some life stage(s) year round, so a species that overwinters as a larva or pupa and emerges as an adult in the spring was only apparently more numerous in the spring. However, since the adult stage is often the only stage that can be reliably identified, future studies would be best served sampling primarily in the spring if year round sampling is not possible.

Sorensen's quotient of similarity indicated that seasons were most similar (0.65), followed by forests (0.51), and finally substrates (0.46). However, care should be taken when comparing these variables. Season occurs frequently (several times a generation or once every few generations) and is ubiquitous across all habitats and substrates (there is no microhabitat where it's spring all year round). A consequence of the combination of these characteristics is that all autochthonous species have evolved in the presence of the inescapable pressures of season. The similarity of adult presence in season may be convergence driven by those pressures.

In contrast, forest type is not entirely ubiquitous in time or space due to forest succession and damage. Over many generations species have had the opportunity to adapt to the pressures and rewards of different forest types. These opportunities may have resulted in an increase or decrease in speciation, exploitation of microhabitats, or colonization of migrants and thus a greater divergence of species between forest types. However, the boundary between forest types is not always well defined and this may act to reduce divergence.

The boundary between CWD5 and leaf litter is very sharp. Where season is an inevitability and different forest types may only be rarely encountered, individuals may encounter a substrate boundary many times during their lives. To the extent that the habitats differ in resource availability, microclimate, and predators/parasites, the consequences of crossing that boundary may range from inconsequential to dire. Low similarity indicates that for some species individuals are cognizant of their surroundings and may have evolved specific means to recognize and avoid crossing into undesirable habitat. It may also indicate that when species do cross into another habitat they are swiftly killed, and thus not collected during this research. Jackson et al. (2009) found that when released at a boundary between forest and pasture the forest-dwelling saproxylic beetle *Odontotaenius disjunctus* was 14 times more likely to move into the forest than the pasture supporting the former hypothesis.

Minimally Collected Species. In total 157 species (73%) collected during this research were represented by fewer than 10 specimens, and 66 species (31%) were singletons, species represented by a single specimen (Appendix 2). This is a common occurrence; 32% singletons is average for tropical arthropod surveys (Coddington et al. 2009). Three general explanations for singletons have been offered: 1) undersampling bias, where an inadequate inventory was performed and more sampling would have provided an increase in the number of specimens of a particular species (Coddington et al. 2009; Scharff et al. 2003); 2) true rarity, where a species truly is represented by a few individuals with a large nearest neighbor distance (Coddington et al. 2009); and 3) edge effects, where an otherwise common species appears to be rare because sampling took place in a time or space where that species rarely occurs, or the specimen was sampled with an inappropriate method (Coddington et al. 2009; Novotný and Basset 2000). During this research, specimens were sampled in different places (substrates and forests) and times (seasons) and can be used to comment on the contribution of singletons by time and space edge effects.

Space edge effects. Of the 45 singleton species in CWD5 (species represented by a single specimen within the CWD5 samples), 19 (42%) were also collected in leaf litter. Of the 48 singleton species in leaf litter, 8 (17%) were also collected in CWD5. No singletons of the same species were collected in each substrate. Of the 49 singleton species in secondary forest, 21 (43%)

were also collected in primary forest. Of the 53 singleton species in primary forest, 15 (28%) were also collected in secondary forest. Singletons of five species were collected in both forest types.

Time edge effects. Of the 49 singleton species collected during spring, 13 (27%) were also collected during fall. Of the 53 singleton species collected during fall, 23 (43%) were also collected during spring. Singletons of five species were collected during both seasons.

Attempting to reduce the number of singletons by overcoming edge effects appears to be a double-edged sword. Sampling from a different place or time decreased the number of singletons from the original samples, but added new singletons in return. Obviously attempting to reduce edge effects by differing time and space of sampling events will not drive singletons to zero, because edges do not completely overlap. Edge effects are actually a special form of undersampling bias (Coddington et al. 2009). Increasing sampling intensity at a particular location increases the area sampled. For example, as more samples are taken in the United States the probability of collecting a rare migrant from Mexico increases. This means that surveys attempting to perform a good census of particular taxa at a particular location may actually be performing a poor census of a much larger area.

However, the “mystery of singletons” (Novotný and Basset 2000) is less of a problem when *a priori* restrictions are placed on a survey. By restricting the taxa of interest to those from initial sampling events and/or those sampled from a particular habitat, additional sampling events will not increase the overall number of singletons, but may reduce them. For example, within this research 111 species were sampled from CWD5 and 49 were singletons. Sampling from leaf litter provided additional specimens of 19 species. Sampling from additional habitats and use of additional sampling methods may have further reduced the singletons from CWD5.

This approach has an extremely important practical application. While appropriate natural history observations are difficult and impractical for many organisms, gross but meaningful statements can be made about organisms based on capture statistics, but only if those species are represented by a threshold number of specimens. A worthwhile endeavor would be to develop sampling protocols designed to reduce the number of “data deficient” species within an *a priori* restricted set.

Taxonomic Considerations. As was mentioned above not all specimens could be identified to the species level. This occurred for three primary reasons: 1) the specimen almost certainly belonged to a named species but was female and keys for the separation of females did not exist; 2) whether or not the specimen belonged to a named species or an undescribed species was unknown because descriptions of valid species were ambiguous and/or keys to separate species did not exist; and 3) the specimen was certainly an undescribed species and recognized as such by experts, but the species had not been formally described because taxonomic expertise and/or time or other resources were lacking.

Taxonomic uncertainty represents a major impediment to ecological research. An inability to identify species may result in an under- or overestimation of species richness which reduces the value of comparisons within and between studies. Additionally any new information gained about a species from an ecological study is lost if that species cannot be reliably identified. See Carlton and Robison (1998) for a good discussion on the problems of taxonomic difficulties in diversity studies.

Overcoming these difficulties is expensive and time consuming. When female specimens lack morphological characters for reliable identification, molecular techniques such as DNA barcoding may be necessary to distinguish species, but this presumes that accurate barcodes exist for those species. Where valid names exist for inadequately diagnosed species the holotype may have to be consulted and redescribed (see Gusarov 2003e). When a species is recognized as undescribed it should be designated as such in the literature (e.g. *Genus* n.sp. 1) and specimens should be clearly labeled so subsequent taxonomic workers can trace museum specimens through the literature.

An unknown number of undescribed species were collected during this study (see notes below). However, several undescribed species collected as part of this research were recognizable as such and described. Ferro and Carlton (2010) revised the eastern species of the staphylinid genus *Sonoma* and described 15 new species, three from this study: *S. chouljenkoi* Ferro and Carlton, *S. gilae* Ferro and Carlton, and *S. gimmeli* Ferro and Carlton. Additionally Park and Carlton (Park et al. 2010) described four new species of *Leptusa*, two were collected during this research: *L. gimmeli* Park and Carlton, and *L. pseudosmokyiensis* Park and Carlton. While researching *Thoracophorus*, Ferro and Gimmel (see Chapter 3) discovered that *T. longicollis* Motschulsky and *T. fletcheri* Wendeler were junior synonyms of *T. costalis* (Erichson) and synonymized the two names.

Bortolus (2008), Gotelli (2004), and Grove (2003) offered sound advice for ecologists conducting community level research. An inability to appropriately identify study organisms and track them through literature and/or voucher specimens greatly reduces the scale at which ecological questions can be addressed and devalues the potential future contributions of a given study. When conducting community level ecological research, where there is a potential to encounter many undescribed or difficult to identify species, special effort should be made to collaborate with taxonomic experts and specific funds should be requested to facilitate taxonomic and/or nomenclatural research.

Related Research. This publication represents a portion of a larger body of research, specifically the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007). This effort has resulted in a suite of publications related by collectors, localities, and even specific samples (e.g. specimens collected as part of this research were described as new species in Ferro and Carlton (2010) and Park et al. (2010)). Simultaneous research was conducted by the same authors at the same localities concerning Coleoptera in decay classes I-IV (see Chapter 7) and flight intercept traps were used to compare their effectiveness at sampling saproxylic Coleoptera with sifting and emergence (see Chapter 8).

The overall research of the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP has resulted in publications on the following taxa: Cantharidae: *Atalantycha* Kazantsev (Kazantsev 2005); Carabidae: *Anillinus* Casey (Sokolov 2011, Sokolov et al. 2004, 2007; Sokolov and Carlton 2008, 2010); Cerylonidae: *Philothermus* Aubé (Gimmel and Slipinski 2007); Chrysomelidae: *Psylliodes* Latreille (Konstantinov and Tishechkin 2004); Leiodidae: *Ptomaphagus* (*Appadelopsis* Gnaspini) (Tishechkin 2007); Mycetophagidae: *Pseudotriphyllus* Reitter (Carlton and Leschen 2009); Staphylinidae: Aleocharinae: *Leptusa* Kraatz (Park et al. 2010); Pselaphinae: *Arianops* Brendel (Carlton 2008); *Reichenbachia* Leach (Carlton 2010); *Sonoma* Casey (Ferro and Carlton 2010).

Conclusion. This represents the first systematic survey of the Coleoptera within extremely decayed downed coarse woody debris. Results indicate that the Coleoptera community within CWD5 is distinct from leaf litter and may harbor numerous undescribed or rarely collected species. Sampling CWD5 and leaf litter in the spring yields the highest species richness but sampling in the fall is also profitable. The CWD5 and leaf litter communities in primary and secondary forests are different and this should be recognized when conducting biotic surveys and developing land management policies. Taxonomic expertise and funding are desperately needed to overcome taxonomic difficulties that greatly hinder our ability to describe and understand forest communities. As an overlooked habitat much more collecting should be done in CWD5 to better understand its importance to the landscape.

6.5 SPECIES ACCOUNTS

Beetle species are generally poorly known and information about their habits often comes from anecdotal evidence or is based on a generalization of the habits of their family, subfamily, tribe, or genus. For example, within the list below specific natural history observations have only been made for two species, *Adranes lecontei* Brendel (Staphylinidae) and *Stelidota octomaculata* (Say) (Nitidulidae), but neither are complete. In this research 59 species were represented by 10 or more individuals and their prevalence between substrates, forests, and seasons is available to statistical interpretation. While not a substitute for proper natural history observations, this does provide gross natural history information and represents a jumping off point for future researchers hoping to study particular species or higher taxa.

When available, information on range, habitat, collection methods, and basic biology of most insects is usually scattered throughout the literature. Below is a summary of the habits of the 59 species represented by 10 or more individuals in this research. Basic biological information is provided for each taxon and important resources with descriptions, keys, distributional data, and biological/life history data are referenced.

CARABIDAE

Rhysodinae

Clinidium valentinei Bell (Fig. 6.7)
Range: three regions: north-central Alabama; mountainous Georgia, North Carolina, South Carolina, Tennessee; southwestern Pennsylvania. **Habitat:** humid ravines at low elevations in the southern Appalachians. **Collection Method:** sifting/Berlese forest litter and CWD5 (this study). **Biology:** possibly feeds on slime molds, otherwise unknown. **Present Study:** indifferent to substrate, forest, and season. **References:** Bell 1970; Bell and Bell 1985; Bousquet and Larochelle 1993; Ciegler 2000; Downie and Arnett 1996.

Trechinae

Anillinus cherokee Sokolov and Carlton (Fig. 6.8)
Range: Blount Co., Tennessee; Graham Co., North Carolina. **Habitat:** deciduous hardwood forests at middle altitudes (600 – 1510 m). **Collection Method:** sifting/Berlese forest litter. **Biology:** blind, flightless, presumed predatory, otherwise unknown. **Present Study:** **s**ignificantly higher abundance in leaf litter, primary forest, and spring. **References:** Sokolov and Carlton 2008.

Anillinus langdoni Sokolov and Carlton (Fig. 6.9)
Range: northwest ranges of Great Smoky Mountains: Cocke, Monroe, and Sevier Counties, Tennessee. **Habitat:** litter of hardwood forests at low to middle altitudes (700 – 1300 m). **Collection Method:** sifting/Berlese forest litter and rotten logs. **Biology:** blind, flightless, presumed predatory, otherwise unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Sokolov et al. 2004, 2007.

Polyderis laevis (Say) (Fig. 6.10)
Range: eastern North America: Quebec, south to Texas, west to Iowa. **Habitat:** lowlands, pastures, open ground, leaf litter. **Collection Method:** inspecting ant nests, under stones, sifting/Berlese wood chips, light trapping. **Biology:** overwinters as an adult, predacious, frequent flyer. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Ciegler 2000; Downie and Arnett 1996; Larochelle and Larivière 2003 (and references therein); Lindroth 1966 (as *Tachys laevis* Say).

Trechus (Microtrechus) pisgahensis Barr (Fig. 6.11)
Range: North Carolina, high altitudes (1400 – 1600 m). **Habitat:** mountains, coniferous forests, moist areas including leaf litter and moss. **Collection Method:** collection from leaf litter, searching under moss. **Biology:** overwinters as an adult, flightless, presumably predatory. **Present Study:** indifferent to substrate and season, all specimens taken in primary forest. **References:** Barr 1979 (as *Trechus* (*Microtrechus*) *vandykei pisgahensis* Barr); Bousquet and Larochelle 1993; Larochelle and Larivière 2003.

CERYLONIDAE
Ceryloninae

Mychocerus striatus (Sen Gupta and Crowson) (Fig. 6.12)
Range: North Carolina, Tennessee. **Habitat:** forests, under and in rotten logs, rarely leaf litter. **Collection Method:** sifting/Berlese litter, rotten wood. **Biology:** larvae and adults possess piercing mouthparts, probably a fungivore, brachypterous. **Present Study:** significantly more abundant in CWD5, secondary forest, in the spring. **References:** Lawrence and Stephan 1975 (as *Lapethus striatus* (Sen Guta and Crowson)); Sen Gupta and Crowson 1973 (as *Lapecautomus striatus* (Sen Gupata and Crowson)).

CORYLOPHIDAE

Peltinodinae

***Holopsis* spp.** (Fig. 6.13)
Accurate species identifications cannot be performed until a species level revision is completed. Important higher level work on this family can be found in Bowestead 1999, Leschen and Bowestead 2001, and Slipinski et al. 2009.
Range: Pennsylvania to Florida, West to Texas and Southern California. **Habitat:** members of the family have been collected on leaves, flowers, in leaf litter, and under bark. **Collection Method:** sifting/Berlese litter, sweep netting. **Biology:** both adults and larvae feed on fungal spores. **Present Study:** significantly more abundant in leaf litter and secondary forest, indifferent to season. **References:** Bowestead 1999; Downie and Arnett 1996 (as *Bathona* Casey and *Corylophodes* Matthews); Lawrence 1991; Leschen and Bowestead 2001; Slipinski et al. 2009.

CURCULIONIDAE

Cossoninae

Caulophilus dubius (Horn) (Fig. 6.14)
Range: throughout eastern United States: New York to Florida, west to Michigan and Texas. **Habitat:** under bark of dead trees and *Vitus* vine, in leaf litter and tree holes. **Collection Method:** searching under bark and sifting/Berlese leaf litter and rotten wood. **Biology:** unknown. **Present Study:** significantly more abundant in leaf litter and spring, indifferent to forest. **References:** Blatchley and Leng 1916 (as *Allomimus dubius* Horn); Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998.

Cryptorhynchinae

Eurhoptus pyriformis LeConte (Fig. 6.15)
Range: eastern and central United States, North Carolina to Florida, west to Texas, Colorado, and Wisconsin. **Habitat:** in moss, pine litter, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Anderson 2002; Blatchley and Leng 1916; Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998.

Eurhoptus n. sp. (R. S. Anderson pers. com.) (Fig. 6.16)
This genus contains numerous undescribed species and is in need of revision.
Range: unknown. **Habitat:** unknown. **Collection Method:** sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Anderson 2002 (key to genus).

Dryophthorinae

Dryophthorus americanus (Bedel) (Fig. 6.17)
Range: throughout eastern North America. **Habitat:** "very old logs", dead pine, forest litter. **Collection Method:** sifting/Berlese litter, collecting under bark, flight intercept trap, UV light. **Biology:** breeds under bark of dead pines, winged. **Present Study:** significantly higher abundance in CWD5, secondary forest, and spring. **References:** Anderson 2002; Blatchley and Leng 1916; Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998.

Entiminae

Panscopus impressus Pierce (Fig. 6.18)
This genus is in need of revision (Anderson 2002). Buchanan (1936) designated a subspecies, Panscopus impressus thoracicus, *but in light of the uncertainty of its validity specimens from this study are only identified to the species level.*
Range: central eastern United States, Indiana, North Carolina, South Carolina, Tennessee, Virginia. **Habitat:** swept from weeds in low damp woods, leaf litter. **Collection Method:** sweep netting, sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Anderson 2002; Blatchley and Leng 1916; Buchanan 1936; Ciegler 2010.

EUCINETIDAE

Tohlezkus inexpectus Vit (Fig. 6.19)
Range: Sevier Co., Tennessee, and Macon Co., North Carolina. **Habitat:** rotten wood, very rarely in leaf litter. **Collection Method:** dung trap, sifting/Berlese litter and CWD5. **Biology:** adults have unique suctorial mouthparts, possibly feed on slime molds. **Present Study:** significantly higher abundance in CWD5, primary forest, and spring. **References:** Vit 1995.

LEIODIDAE

Catopocerinae

***Catopocerus* spp.** (female) (Fig. 6.20)
Males of Catopocerus appalachianus *Peck and possibly an undescribed species were collected; however, none were represented by more than 10 specimens. Information provided below applies to the genus in general.*
Range: unglaciated mountain ranges in eastern and western North America. **Habitat:** moist forest litter, soil, well rotten logs, under rocks, in caves. **Collection Method:** sifting/Berlese litter, rotten pig liver bait, carrion pitfall traps. **Biology:** eyeless, wingless, probably feeds on organic debris and fungi, larvae and teneral adults collected in the spring. **Present Study:**

significantly higher abundance in leaf litter, indifferent to forest and season. **References:** Downie and Arnett 1996; Peck 1974, 2001.

Cholevinae

Ptomaphagus appalachianus (Peck) (Fig. 6.21)
Range: northern Georgia and Alabama, eastern Tennessee. **Habitat:** caves, forest floor debris, tree hole, rotten tree roots. **Collection Method:** sifting/Berlese litter, carrion bait traps. **Biology:** probably a scavenger on decaying organic matter, collected from January through September. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Peck 1978 (as *Adelopsis appalachiana* Peck).

***Ptomaphagus* spp.** (female) (Fig. 6.22)
The only other member of this genus we collected was Ptomaphagus appalachianus *(Peck) and many of these specimens are probably females of that species; however, Tishechkin 2007 reported several undescribed species within GSMNP.*
Range: this genus is found eastern North America. **Habitat:** caves, forest floor debris, tree hole, rotten tree roots. **Collection Method:** sifting/Berlese litter, carrion bait traps. **Biology:** probably a scavenger on decaying organic matter. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Blatchley 1910; Peck 1978 (as *Adelopsis*), 2001; Peck and Thomas 1998; Tishechkin 2007.

Leiodinae

***Agathidium* spp.** (female) (Fig. 6.23)
This genus was represented in this research by males of six identifiable species and one possibly undescribed species; however, none of the males were represented by more than 10 specimens. Information provided below applies to the genus in general.
Range: throughout eastern United States and worldwide. **Habitat:** high humidity locations, forests, leaf litter, dead wood. **Collection Method:** collection and dissection of slime molds (warming a slime mold in the laboratory will cause adults to move and become visible), sifting/Berlese leaf litter and dead wood, flight intercept traps. **Biology:** winged and wingless species, strongly associated with slime molds (Myxomycetes), Wheeler and Miller (2005) provide a list of host associations for numerous species. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Blatchley 1910; Downie and Arnett 1996 (key out of date); Peck 2001; Peck and Thomas 1998; Miller and Wheeler 2005; Wheeler and Miller 2005.

NITIDULIDAE

Nitidulinae

Stelidota octomaculata (Say) (Fig. 6.24)
Range: eastern North America, west to Ontario and Arizona. **Habitat:** sap in spring, fungi, rotten fruit, acorns and seeds of numerous tree species (see Galford et al. 1991). **Collection Method:** hand collection, under bark, sifting/Berlese forest litter, pitfall traps. **Biology:** feeds on acorns in winter, overwinters as an adult, begins breeding March to May, Galford et al. (1991) reared this species from seeds of 40 plant species. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Blatchley 1910; Downie and Arnett 1996; Galford et al. 1991 (life history); Parsons 1943; Peck and Thomas 1998; Peng et al. 1990 (key to immatures).

PTILIIDAE

Ptiliidae is one of the least known families of Coleoptera. Most genera are in need of revision and many genera and species remain to be described. Until genera are revised identification to species will remain difficult or impossible.

Acrotrichinae

***Acrotrichis* spp.** (Fig. 6.25)
Range: throughout North America. **Habitat:** leaf litter, decaying logs, tree holes, fungi, animal dung, under bark, moist decaying organic matter. **Collection Method:** sifting/Berlese organic material, flight intercept trap. **Biology:** De Coninck and Coessens (1981) studied *Acrotrichis intermedia* (Gillmeister): probably general detritivore, adults live about 150 days and produce ~10 eggs each, probably reproduction takes place throughout the year with overlap of generations. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Blatchley 1910 (as *Trichopteryx* Kirby and Spence); De Coninck and Coessens 1981; Downie and Arnett 1996; Dybas 1990; Hall 2001; Peck and Thomas 1998.

Ptiliinae

***Pteryx* spp.** (Fig. 6.26)
Range: throughout North America. **Habitat:** forest floor debris, tree holes, logs, sphagnum bogs. **Collection Method:** sifting/Berlese organic material. **Biology:** probably general detritivore. **Present Study:** significantly higher abundance in CWD5, indifferent to forest type or season. **References:** Blatchley 1910; Downie and Arnett 1996; Dybas 1990; Hall 2001.

SCARABAEIDAE
Aphodiinae

Dialytellus tragicus (Schmidt) (Fig. 6.27)
Range: southeastern Canada and northeastern United States, south to North Carolina and Tennessee. **Habitat:** found near deer dung in forested habitats and leaf litter, rarely in CWD5. **Collection Method:** sifting/Berlese leaf litter and rotten wood, presumably this species could also be collected with deer dung baited traps. **Biology:** feeds on deer and sheep dung in shaded locations, cold adapted species, generally active in winter. **Present Study:** significantly higher abundance in leaf litter, primary forests, and spring. **References:** Downie and Arnett 1996 (as *Aphodius humeralis* (LeConte)); Gordon and Skelley 2007; Ratcliffe et al. 2002 (as *A. humeralis*).

STAPHYLINIDAE
Aleocharinae

Aleocharinae gen. spp. (Fig. 6.28)
These specimens could not be reliably identified to genus. Aleocharinae is the largest subfamily of the Staphylinidae with 21 tribes, 183 genera, and 1385 described species known from North America and is badly in need of a comprehensive revision. See Newton et al. (2001), and references therein, for further information about this subfamily.
Range: throughout North America. **Habitat:** ubiquitous in terrestrial habitats. **Collection Method:** sifting/Berlese leaf litter, pitfall traps, bait traps, UV light, etc. **Biology:** virtually every mode of life (many very specialized) is known in this subfamily: free living, parasitic, herbivore, carnivore, fungivore, flier, walker, runner, swimmer, gregarious, solitary, etc., but life history is almost unknown at the species level. **Present Study:** indifferent to substrate, forest type, and season. **References:** Downie and Arnett 1996; Newton et al. 2001.

Aleodorus bilobatus (Say) (Fig. 6.29)
Range: eastern North America: Ontario to southern New England, south to Georgia, west to Illinois and Iowa. **Habitat:** moist habitats, under bark, sifted vegetable debris, dead grass, moss, and duff. **Collection Method:** sifting/Berlese leaf litter, hand collection. **Biology:** unknown, specimens have been collected from March to November. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Downie and Arnett 1996; Gouix and Klimaszewski 2007; Hoebeke 1985.

Athetini gen. spp. Casey (Fig. 6.30)
These specimens could only be reliably identified to Athetini, a large difficult tribe. Seevers (1978) characterization of the tribe and genera is inadequate. Currently 64 genera are recognized within the tribe in North America (Newton et al. 2001) but a complete revision is needed. Gusarov (2002a-e, 2003a-e, 2004a-b) has greatly contributed to our knowledge of many genera and Elven et al (2010) provided the first molecular phylogeny of the tribe, but more work needs to be done.

Range: throughout North America. **Habitat:** ubiquitous; decaying plants and animals, dung, bird and mammal nests, riparian areas, ant nests, under bark and logs. **Collection Method:** sifting/Berlese leaf litter. **Biology:** unknown; predators. **Present Study:** significantly higher abundance in leaf litter and spring, indifferent to forest type. **References:** Downie and Arnett 1996; Elven et al. 2010; Gusarov 2002a-e, 2003a-e, 2004a-b; Newton et al. 2001; Seevers 1978.

Leptusa gimmeli Park and Carlton (Fig. 6.31)
Range: Tennessee. **Habitat:** known only from Albright Grove, GSMNP, old growth forest. **Collection Method:** sifting/Berlese leaf litter, one specimen collected from dead wood with emergence chamber. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Park et al. 2010.

Leptusa pusio (Casey) (Fig. 6.32)
Range: Ohio, Tennessee. **Habitat:** forest leaf litter. **Collection Method:** sifting/Berlese leaf litter, and collected from dead wood with emergence chamber. **Biology:** unknown.
Present Study: significantly higher abundance in CWD5, primary forest, and spring.
References: Downie and Arnett 1996; Gusarov 2003e; Park et al. 2010.

***Leptusa* spp.** (Fig. 6.33)
Ten species of Leptusa *are known from GSMNP. Despite the revision by Park et al. (2010) some specimens could only be reliably identified to genus.*
Range: eastern United States. **Habitat:** forest leaf litter, rotten wood. **Collection Method:** sifting/Berlese leaf litter, and collected from dead wood with emergence chamber. **Biology:** unknown. **Present Study:** indifferent to substrate, forest type and season. This is almost certainly a reflection of the habits of multiple species represented by these specimens.
References: Blatchley 1910; Downie and Arnett 1996; Newton et al. 2001; Park et al 2010.

***Myllaena* spp.** (Fig. 6.34)
There are 22 species known from North America. Klimaszewski (1982, 1986, 1992) provided a key to species and distributional data for this genus. Our specimens could not be identified due to time constraints.
Range: throughout North America. **Habitat:** riparian habitats. **Collection Method:** sifting/Berlese leaf litter and rotten wood. **Biology:** unknown, adults have been collected year round. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate and season. **References:** Blatchley 1910; Downie and Arnett 1996; Gouix and Klimaszewski 2007; Klimaszewski 1982, 1986, 1992; Newton et al. 2001.

Dasycerinae

***Dasycerus* spp.** (Fig. 6.35)
This species contains three species known from the Appalachian Mountains. Löbl and Calame (1996) provided a key to species. Our specimens could not be identified due to time constraints and uncertainty about the presence of undescribed species.

Range: southern Appalachian: Virginia to Georgia. **Habitat:** moist broadleaf forest litter. **Collection Method:** sifting/Berlese forest litter. **Biology:** eastern species are wingless with small eyes, dissected females have only been found with a single egg, known to occur on fruiting fungi, but may not specifically feed on them. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Löbl and Calame 1996; Newton et al. 2001, Wheeler and McHugh 1994.

Osoriinae

Thoracophorus costalis (Erichson) (Fig. 6.36)
Range: throughout eastern North America: New Jersey to Florida, west to Louisiana and Illinois. **Habitat:** under bark, in dead wood, forest litter. **Collection Method:** sifting/Berlese litter, debris, and dead wood. **Biology:** unknown. **Present Study:** significantly higher abundance in CWD5, secondary forest, and spring. **References:** Blatchley 1910; Downie and Arnett 1996 (figure is not *T. costalis*); Horn 1871 (as *Glyptoma costale* Erichson, figure and key to common species in North America); Irmler 1985; Notman 1920; Peck and Thomas 1998; see Chapter 3.

Oxytelinae

***Anotylus* spp.** (Fig. 6.37)
This genus is in need of revision. Newton et al. (2001) report 18 species, at least 5 of them adventive in North America. Keys may be found in Casey 1893 (as Oxytelus *Gravenhorst in part), Downie and Arnett 1996, and Hatch 1957, but the accuracy of these keys is unknown.*
Range: throughout North America. **Habitat:** dung, rotting plant and animal matter, forest litter, some reported from mammal and ant nests. **Collection Method:** sifting/Berlese leaf litter. **Biology:** basically unknown at the species level, in general species probably feed on dung or decaying vegetation, see Hammond (1976) for more information. **Present Study:** significantly higher abundance in litter, primary forest, and spring. **References:** Casey 1893 (as *Oxytelus* Gravenhorst in part); Downie and Arnett 1996; Hammond 1976; Hatch 1957; Newton et al. 2001.

***Carpelimus* spp.** (Fig. 6.38)
This genus was redefined by Herman (1970) but is badly in need of revision. About 79 species are known in North America North of Mexico. Casey (1889), Downie and Arnett (1996), and Hatch (1957) provide keys to some species, but the accuracy of these keys is unknown.
Range: throughout North America. **Habitat:** moist habitats such as wet debris near streams and ponds, others in leaf litter. **Collection Method:** sifting/Berlese forest litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Casey 1889 (as *Trogophloeus* Mannerheim); Downie and Arnett 1996; Hatch 1957; Herman 1970; Newton et al. 2001.

Paederinae

Sunius rufipes (Casey) (Fig. 6.39)
Range: North Carolina, Tennessee, Virginia. **Habitat:** damp litter, under bark. **Collection Method:** sifting/Berlese litter, UV light. **Biology:** unknown, Paederinae are considered predators. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Casey 1905 (as *Hemimedon rufipes* Casey).

Pselaphinae

Actiastes fundatum Grigarick and Schuster (Fig. 6.40)
Range: Tennessee. **Habitat:** sycamore tree hole, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predatory. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Grigarick and Schuster 1971.

***Actiastes* spp.** (female) (Fig. 6.41)
Female Actiastes *Casey cannot be identified to species. These specimens probably represent* Actiastes fundatum *Grigarick and Schuster and/or* Actiastes suteri *(Park), both of which are known from GSMNP.*
Range: Alabama, Georgia, North Carolina, Tennessee. **Habitat:** rhododendron duff, tree holes, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predatory. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Chandler 1990b; Grigarick and Schuster 1971.

Adranes lecontei Brendel (Fig. 6.42)
Range: Kentucky, Mississippi, New York, Pennsylvania, Tennessee. **Habitat:** lives in nests of *Lasius* spp. ants (Hymenoptera: Formicidae); nests have been found in beech logs in advanced stages of decay. **Collection Method:** sifting *Lasius* spp. ant nests, rarely sifting/Berlese forest litter. **Biology:** obligate myrmecophile on *Lasius* spp. ants; adults feed on fluids obtained from their adult and immature hosts; possibly feed on dead immature ants; see Park (1932a) and Akre and Hill (1973) for interesting behavioral observations of the genus. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate or season, probably heavily influenced by their host. **References:** Akre and Hill 1973; Blatchley 1910; Downie and Arnett 1996; Hill et al. 1976; Newton et al. 2001; Park 1932a (with notes on life history), 1935, 1964; Wickham 1901.

Batrisodes beyeri Schaeffer (Fig. 6.43)
Range: North Carolina. **Habitat:** forest leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown; some members of this genus are associated with ants, others are litter dwellers, members of this subfamily are predatory, see Park (1932b) about feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte). **Present Study:** significantly higher

abundance in leaf litter and primary forest, indifferent to season. **References:** Park 1932b (as *B. globosus* LeConte), 1947, 1948; Schaeffer 1906.

***Batrisodes* spp.** (female) (Fig. 6.44)
Female Batrisodes *Reitter cannot be reliably identified. These female specimens are probably representative of the twelve described and five known but undescribed species that have been collected in GSMNP.*
Range: Eastern North America. **Habitat:** within this genus some members are found in leaf litter, mosses, and rotten wood, others are associated with ants or caves. **Collection Method:** sifting/Berlese litter. **Biology:** poorly known, but see Park (1932b) about feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte). **Present Study:** indifferent to substrate, forest type, and season. **References:** Blatchley 1910; Chandler 1990b; Downie and Arnett 1996; Park 1932b, 1947, 1948; Newton et al. 2001.

Conoplectus canaliculatus (LeConte) (Fig. 6.45)
Range: eastern United States, NewYork to Florida, west to Texas and Ohio. **Habitat:** moist habitats (sphagnum bogs, swamps), hardwood duff, rotten logs, pine floor duff, tree holes. **Collection Method:** sifting/Berlese litter. **Biology:** one of the most abundant pselaphines in eastern North America, predacious, occasionally collected with ants. **Present Study:** significantly higher abundance in CWD5 and secondary forest, indifferent to season. **References:** Carlton 1983; Downie and Arnett 1996 (as *Rhexidius canaliculatus* (LeConte)); Park et al. 1950 (as *R. canaliculatus*); Reichle 1966 (as *R. canaliculatus*).

***Ctenisodes* spp.** (female) (Fig. 6.46)
This genus was last treated by Casey (1897) (as Pilopius *Casey) and is in need of revision.*
Range: throughout North America. **Habitat:** western species are known from arid habitats, one species associated with ants, eastern species are found in leaf litter and rotten wood. **Collection Method:** sifting/Berlese litter. **Biology:** predacious, overwinters as adults in Illinois prairie. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and fall. **References:** Newton et al. 2001; Casey 1897 (as *Pilopius*); Chandler 1990b (as *Pilopius*); Downie and Arnett 1996 (as *Pilopius*); Mickey and Park 1956 (as *Pilopius*); Newton et al. 2001 (as *Pilopius*); Park 1964 (as *Pilopius*); Park et al. 1949, 1953 (as *Pilopius*).

Euboarhexius perscitus (Fletcher) (Fig. 6.47)
Range: southern Appalachian: Georgia, North Carolina, Tennessee. **Habitat:** leaf litter, rhododendron litter, under rock. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Carlton and Allen 1986; Fletcher 1932 (as *Rhexidius perscitus* Fletcher).

Eutyphlus dybasi Park (Fig. 6.48)
Range: southern Appalachian: Tennessee. **Habitat:** leaf litter, rhododendron litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious.

Present Study: significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Park 1956.

***Eutyphlus* spp.** (female) (Fig. 6.49)
Eutyphlus *females cannot be reliably identified. These female specimens are probably representative of the four species that have been collected in GSMNP. The vast majority are probably* Eutyphlus similis *LeConte.*
Range: eastern North America, particularity southern Appalachians. **Habitat:** leaf litter, rhododendron litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Chandler 1990b; Downie and Arnett 1996; Newton et al. 2001; Park 1956.

Machaerodes carinatus (Brendel) (Fig. 6.50)
Range: eastern North America: Pennsylvania to Georgia, west to Ohio. **Habitat:** pine, oak, rhododendron, and beech leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Chandler 1990b, 1994; Downie and Arnett 1996; Newton et al. 2001; Park 1953.

Mipseltyrus nicolayi Park (Fig. 6.51)
Range: North Carolina, Tennessee. **Habitat:** deep leaf mold in rhododendron thickets. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, wingless, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Park 1953.

Pseudactium arcuatum (LeConte) (Fig. 6.52)
Range: Alabama, Florida, Georgia, South Carolina, Tennessee. **Habitat:** forest floor debris, hardwood litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, wingless, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and fall. **References:** Carlton and Chandler 1994.

Rhexius schmitti Brendel (Fig. 6.53)
Range: eastern North America west to Oklahoma. **Habitat:** rotten wood, leaf litter. **Collection Method:** sifting/Berlese litter, UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Chandler 1990a; Downie and Arnett 1996.

***Rhexius* spp.** (female) (Fig. 6.54)
Female Rhexius *LeConte cannot be reliably identified. These female specimens are probably representative of the two described and two undescribed species that have been collected in GSMNP.*
Range: eastern North America west to Oklahoma. **Habitat:** rotten wood, leaf litter, flood debris. **Collection Method:** sifting/Berlese litter, grass roots, flight intercept trap, UV light. **Biology:**

unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Blatchley 1910, Chandler 1990a, b; Downie and Arnett 1996; Newton et al. 2001.

***Sonoma* spp.** (female) (Fig. 6.55)
Female Sonoma *Casey cannot be reliably identified. These female specimens are probably representative of the eight described species that have been collected in GSMNP.*
Range: central eastern and western United States. **Habitat:** leaf litter, rhododendron litter, rotten wood. **Collection Method:** sifting/Berlese litter and rotten wood, Lindgren funnel, Malaise trap, flight intercept trap, rarely at UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in CWD5, indifferent to forest type and season. **References:** Ferro and Carlton 2010; Chandler 1990b; Downie and Arnett 1996; Newton et al. 2001.

Trimiomelba dubia (LeConte) (Fig. 6.56)
Range: eastern United States west to Texas. **Habitat:** leaf litter, rotten logs. **Collection Method:** sifting/Berlese litter and rotten wood, at UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Blatchley 1910; Chandler 1990b, 1999; Downie and Arnett 1996 (as *T. laevis* Casey, and *T. convexula* (LeConte)); Newton et al. 2001.

Scaphidiinae

Baeocera pallida Casey (Fig. 6.57)
Range: eastern North America west to Ontario and Texas. **Habitat:** forest litter, on spring edge, sifted chestnut oak litter, humus, rotten wood. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, some species in this genus feed on slime molds (see Lawrence and Newton 1980), adults collected April to October. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate and season. **References:** Lawrence and Newton 1980; Löbl and Stephan 1993.

Scydmaeninae

Nearly all the genera in the subfamily Scydmaeninae are in need of revision. Many have numerous undescribed species and/or have not been treated in the last 50-100 years. Until genera are revised identification to species will remain difficult or impossible. See O'Keefe (2001) (and references therein) and Grebennikov and Newton (2009) for up-to-date literature on the subfamily.

***Euconnus* spp.** (Fig. 6.58)
***Euconnus* (*Napochus*) spp.** (Fig. 6.59)
***Euconnus* (*Scopophus*) spp.** (Fig. 6.60)
Range: mostly Midwest, Northeast, and Southeastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter,

pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** only *Euconnus* (*Napochus*) sp. was found in significantly higher abundance in leaf litter and secondary forest. **References:** Blatchley 1910; Downie and Arnett 1996 (usefulness of keys uncertain); Grebennikov and Newton 2009; O'Keefe 2001; Peck and Thomas 1998.

***Parascydmus* spp.** (Fig. 6.61)
Range: Eastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** significantly higher abundance in primary forest in spring, indifferent to substrate. **References:** O'Keefe 2001.

***Scydmaenus* spp.** (Fig. 6.62)
Range: Southwestern, Central, and Eastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** significantly higher abundance in leaf litter, indifferent to forest type and season. **References:** Blatchley 1910; Downie and Arnett 1996 (usefulness of keys uncertain); O'Keefe 2001; Peck and Thomas 1998.

Steninae

***Stenus* spp.** (Fig. 6.63)
Stenus *is one of the largest beetle genera with 167 species known from North America and over 1800 species worldwide. No comprehensive key to the species of North America exists. See Newton et al. (2001) and references therein for a list of partial keys to the North American fauna.*
Range: throughout North America. **Habitat:** diverse habitats including rocks and plants near streams, on vegetation in general, in forest leaf litter and debris. **Collection Method:** sifting/Berlese litter and debris. **Biology:** specialized predators of Collembola and other small arthropods, adults have a unique protrusible labium used in prey capture and some have pygidial glands that allow them to skim across water. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Blatchley 1910; Brunke et al. 2011; Casey 1884; Hatch 1957; Newton et al. 2001; Puthz 1967, 1971, 1972, 1973, 1974a-b, 1975a-b, 1984, 1988, 1994; Sanderson 1946, 1957.

Tachyporinae

Ischnosoma lecontei Campbell (Fig. 6.64)
Range: Appalachian Mountains from Virginia to Georgia at 600 – 2020 m elevation, one questionable record from Ohio. **Habitat:** leaf litter of various hardwoods, edge of streams, rotting logs and stumps, tree holes. **Collection Method:** sifting/Berlese litter and debris.

Biology: unknown, adults have been collected year round. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Campbell 1991.

TENEBRIONIDAE

Lagriinae

Anaedus brunneus (Ziegler) (Fig. 6.65)
Range: eastern United States: New York to Florida, west to Indiana. **Habitat:** sandy localities beneath bark and stones, forest litter. **Collection Method:** sifting/Berlese litter, searching under bark. **Biology:** overwinters as an adult, otherwise unknown. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Blatchley 1910; Downie and Arnett 1996.

Figure 6.7-6.12. Habitus images. 6.7) *Clinidium valentinei* Bell (Carabidae: Rhysodinae). 6.8) *Anillinus cherokee* Sokolov & Carlton (Carabidae: Trechinae). 6.9) *Anillinus langdoni* Sokolov & Carlton (Carabidae: Trechinae). 6.10) *Polyderis laevis* (Say) (Carabidae: Trechinae). 6.11) *Trechus* (*Microtrechus*) *pisgahensis* Barr (Carabidae: Trechinae). 6.12) *Mychocerus striatus* (Sen Gupta & Crowson) (Cerylonidae: Ceryloninae).

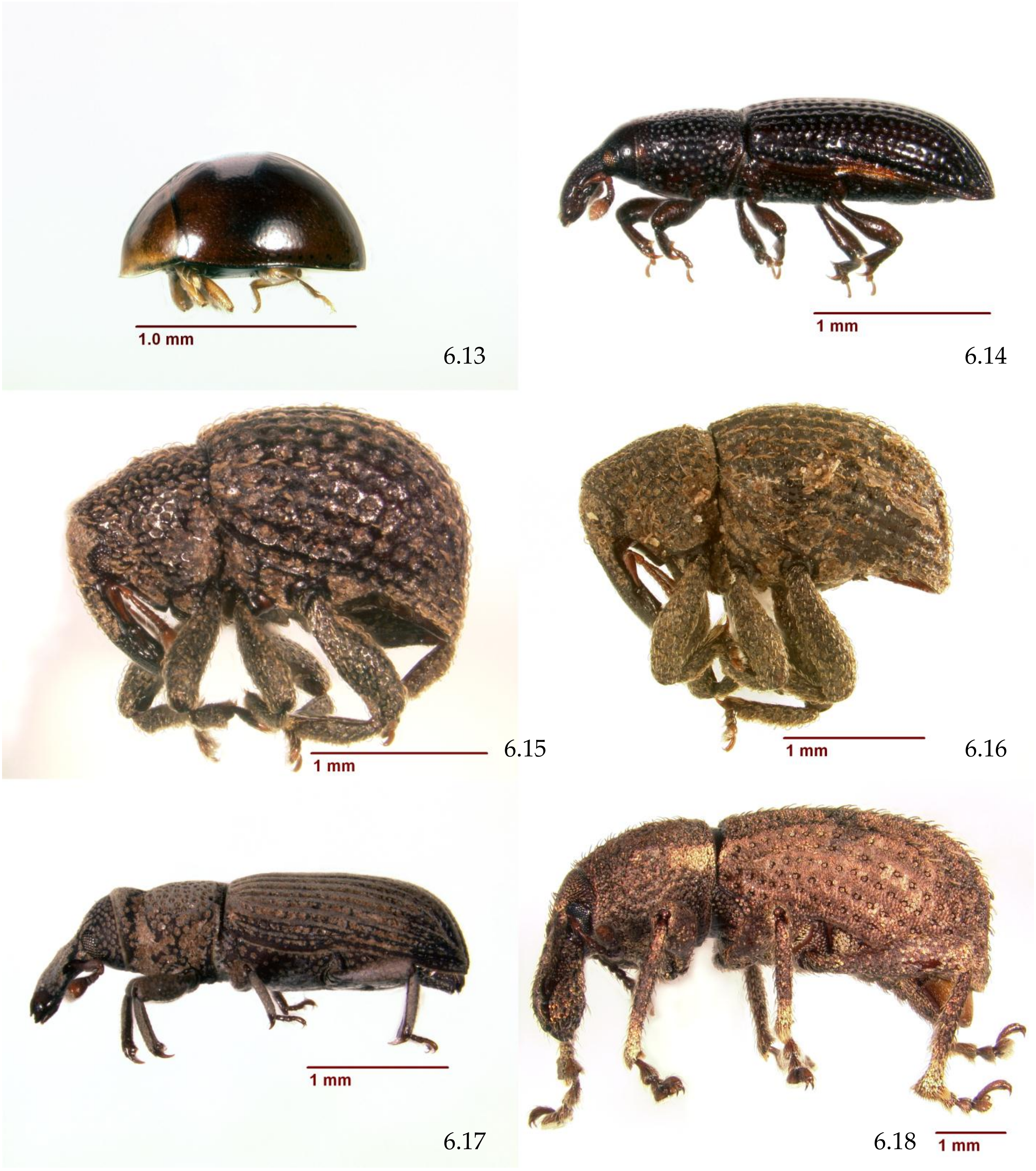

Figure 6.13-6.18. Habitus images. 6.13) *Holopsis* sp. (Corylophidae: Peltinodinae). 6.14) *Caulophilus dubius* (Horn) (Curculionidae: Cossoninae). 6.15) *Eurhoptus pyriformis* LeConte (Curculionidae: Cryptorhynchinae). 6.16) *Eurhoptus* n. sp. (Curculionidae: Cryptorhynchinae). 6.17) *Dryophthorus americanus* (Bedel) (Curculionidae: Dryophthorinae). 6.18) *Panscopus impressus* Pierce (Curculionidae: Entiminae).

Figure 6.19-6.24. Habitus images. 6.19) *Tohlezkus inexpectus* Vit (Eucinetidae). 6.20) *Catopocerus* sp. (female) (Leiodidae: Catopocerinae). 6.21) *Ptomaphagus appalachianus* (Peck) (Leiodidae: Cholevinae). 6.22) *Ptomaphagus* sp. (female) (Leiodidae: Cholevinae). 6.23) *Agathidium* sp. (female) (Leiodidae: Leiodinae). 6.24) *Stelidota octomaculata* (Say) (Nitidulidae: Nitidulinae).

Figure 6.25-6.30. Habitus images. 6.25) *Acrotrichis* sp. (Ptiliidae: Acrotrichinae). 6.26) *Pteryx* sp. (Ptiliidae: Ptiliinae). 6.27) *Dialytellus tragicus* (Schmidt) (Scarabaeidae: Aphodiinae). 6.28) Aleocharinae gen. sp. (Staphylinidae), representative of the specimens that could not be identified to genus. 6.29) *Aleodorus bilobatus* (Say) (Staphylinidae: Aleocharinae). 6.30) Athetini gen. sp. (Staphylinidae: Aleocharinae) representative of the specimens that could not be identified to genus.

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Figure 6.31-6.36. Habitus images. 6.31) *Leptusa gimmeli* Park & Carlton (Staphylinidae: Aleocharinae). 6.32) *Leptusa pusio* (Casey) (Staphylinidae: Aleocharinae). 6.33) *Leptusa* sp. (Casey) (Staphylinidae: Aleocharinae). 6.34) *Myllaena* sp. (Staphylinidae: Aleocharinae). 6.35) *Dasycerus* sp. (Staphylinidae: Dasycerinae). 6.36) *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae).

Figure 6.37-6.42. Habitus images. 6.37) *Anotylus* sp. (Staphylinidae: Oxytelinae). 6.38) *Carpelimus* sp. (Staphylinidae: Oxytelinae). 6.39) *Sunius rufipes* (Casey) (Staphylinidae: Paederinae). 6.40) *Actiastes fundatum* Grigarick & Schuster (Staphylinidae: Pselaphinae). 6.41) *Actiastes* sp. (female) (Staphylinidae: Pselaphinae). 6.42) *Adranes lecontei* Brendel (Staphylinidae: Pselaphinae).

Figure 6.43-6.48. Habitus images. 6.43) *Batrisodes beyeri* Schaeffer (Staphylinidae: Pselaphinae). 6.44) *Batrisodes* sp. (Staphylinidae: Pselaphinae). 6.45) *Conoplectus canaliculatus* (LeConte) (Staphylinidae: Pselaphinae). 6.46) *Ctenisodes* sp. (Staphylinidae: Pselaphinae). 6.47) *Euboarhexius perscitus* (Fletcher) (Staphylinidae: Pselaphinae). 6.48) *Eutyphlus dybasi* Park (Staphylinidae: Pselaphinae).

Figure 6.49-6.54. Habitus images. 6.49) *Eutyphlus* sp. (female) (Staphylinidae: Pselaphinae). 6.50) *Machaerodes carinatus* (Brendel) (Staphylinidae: Pselaphinae). 6.51) *Mipseltyrus nicolayi* Park (Staphylinidae: Pselaphinae). 6.52) *Pseudactium arcuatum* (LeConte) (Staphylinidae: Pselaphinae). 6.53) *Rhexius schmitti* Brendel (Staphylinidae: Pselaphinae). 6.54) *Rhexius* sp. (female) (Staphylinidae: Pselaphinae).

Figure 6.55-6.60. Habitus images. 6.55) *Sonoma* sp. (female) (Staphylinidae: Pselaphinae). 6.56) *Trimiomelba dubia* (LeConte) (Staphylinidae: Pselaphinae). 6.57) *Baeocera pallida* Casey (Staphylinidae: Scaphidiinae). 6.58) *Euconnus* sp. (Staphylinidae: Scydmaeninae). 6.59) *Euconnus* (*Napochus*) sp. (Staphylinidae: Scydmaeninae). 6.60) *Euconnus* (*Scopophus*) sp. (Staphylinidae: Scydmaeninae).

Figure 6.61-6.65. Habitus images. 6.61) *Parascydmus* sp. (Staphylinidae: Scydmaeninae). 6.62) *Scydmaenus* sp. (Staphylinidae: Scydmaeninae). 6.63) *Stenus* sp. (Staphylinidae: Steninae). 6.64) *Ischnosoma lecontei* Campbell (Staphylinidae: Tachyporinae). 6.65) *Anaedus brunneus* (Ziegler) (Tenebrionidae: Lagriinae).

CHAPTER 7: COMPARISON OF COLEOPTERA EMERGENT FROM VARIOUS DECAY CLASSES OF DOWNED COARSE WOODY DEBRIS IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

"I try all things, I achieve what I can."
— Herman Melville, *Moby-Dick*

7.1 INTRODUCTION

Dead trees are unique habitats. No other habitat is 1) a contiguous patch of biological material that is 2) not actively defended metabolically; 3) is in the presence of plenty of available oxygen; and 4) is persistent for years, decades, or centuries. For the organisms that interact with woody debris, the habitat 1) offers a long term (one to many generations) source of matter and energy; 2) provides mechanical protection from competitors, predators, and parasites; 3) offers patches of reduced environmental variability; and is 4) evolutionarily passive (lineages do not evolve in response to the actions of the organisms that inhabit their carcasses).

Hamilton (1978) recognized the unique qualities of this habitat and commented on four examples of convergence within the "arbonecrophilic" insect fauna: wing polymorphism; male haploidy; social organization, including subsocial and eusocial; and sexual dimorphism. He postulated that dead wood may have played an important role in the reinvasion of water by terrestrial insects, and may have been the ancestral habitat of progenitors of major insect groups. For example, the evolution of elytra (and therefore Coleoptera) is thought to have resulted from utilization of the numerous tight spaces provided by dead and dying trees. Support for this is provided by data from the oldest fossil beetles, their wood borings, and the habits of the members of the suborder Archostemata, the most plesiotypic extant beetles (Crowson 1960, 1981; Grimaldi and Engel 2005; Hunt et al. 2007).

Attitudes toward dead wood concerning its use as fuel, role in the carbon cycle, and the role it plays in a healthy ecosystem changed greatly at the end of the 1970s and beginning of the 1980s (Speight 1989; Thomas 2002). Studies of dead wood, in particular its role as a reservoir for biodiversity, have recently increased largely due to a desire to use invertebrates as indicators of high quality forests and because many species of conservation concern are also dead wood dependent (Speight 1989; Grove 2002b). Numerous studies of saproxylic organisms, particularly beetles, have been performed in Europe where taxa are relatively well known (see below). At the European Union level, 14% (57 species) of saproxylic Coleoptera assessed are considered threatened and they represent the first ecological grouping specifically studied by the International Union for Conservation of Nature (Nieto and Alexander 2010). Australia, Canada, and the United States have proactive programs to study the effects of anthropogenic forest change on saproxylic organisms as well (see below).

Works important to the current culture of woody debris research include: Elton (1966) who described the ecology of dead and dying wood in Wytham Woods, England, and provided the now famous quote:

> When one walks through the rather dull and tidy woodlands - say in the managed portions of the New Forest in Hampshire - that result from modern forestry practices, it

> is difficult to believe that dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna.

Fager (1967) expanded on Elton's findings and provided a more precise survey of the dead wood fauna of Wytham Woods. Maser et al. (1979) and Maser and Trappe (1984) revisited the relationship of forest managers to woody debris and helped to overturn long held guesses about the role of woody debris in managed forests. Harmon et al. (1986) reviewed and synthesized the ecology of coarse woody debris (CWD) in temperate ecosystems. Speight (1989) provided an overview of the use of saproxylic invertebrates to identify European forests of international importance for nature conservation, reviewed dead wood as habitat for saproxylic species, and highlighted important species of conservation concern. Grove (2002b) reviewed saproxylic insect ecology within a framework of sustainable forest management. These authors highlighted the importance of dead woody material as a structural and functional component of the ecosystem, and emphasized its importance as habitat for wildlife.

Ideally a program of study on maintenance of biodiversity in dead wood would begin with 1) descriptions of the dead wood (substrate), its physical and chemical properties, how it begins, the forms it takes, and its variation through space and time. These descriptions would be followed by 2) surveys of organisms that interact with dead wood and elucidation of their natural history in relation to substrates. Armed with this knowledge 3) management plans would be enacted to reduce the impact of human caused perturbations on those species most affected by human interactions. Finally 4) a monitoring program would be put in place to judge the efficacy of the management programs.

While conceptually simple, the action plan outlined above is in practice quite complex. For example the variety of substrates is often dependent on the actions of organisms. Yee et al. (2006) provided a good example. In Tasmania the interaction of large logs (1 above) with a brown rot fungus (2 above) creates a substrate in the inner heartwood of the log (1 again) that supports a unique community of beetles (2 again). Thus to know the substrates you need to know the organisms, and to know the organisms you need to know the substrates.

The enormous number of complex interactions in dead wood provides for a full and fertile field of study. The literature reviewed below represents fascicles of a global thesis on maintenance of biodiversity associated with dead wood. Studies are grouped by region for ease of reference.

Europe. In Europe efforts to identify and protect dwindling high quality forest habitats and the organisms that reside within them (Speight 1989) have resulted in a throng of descriptive research on the ecology of dead wood (Gibb et al. 2006a; Martikainen and Kaila 2004; Okland et al. 1996). Siitonen (2001) estimated that 20-25% of all forest dwelling species in Finland were dependent on dead wood. Comparisons of fauna associated with CWD and fine woody debris (FWD) have shown that fungi have highest species richness (per unit wood volume) on FWD (Heilmann-Clausen and Christensen 2004; Kruys and Jonsson 1999; Norden et al. 2004) and that both FWD and CWD are important for maintaining beetle and fly species richness (Brin et al. 2010; Jonsell et al. 2007; Lindhe et al. 2005; Schiegg 2001). Studies of faunal succession within decaying wood and stumps show a general increase in species richness with an increase in wood age (Hovemeyer and Schauermann 2003; Irmler et al. 1996; Wallace 1953). Fayt et al. (2006) showed that habitat around dead wood resources was important for some species. For example, saproxylic Syrphidae (Diptera) required dead wood in open stands surrounded by a well-developed herb layer that provided the floral resources required for reproduction. Not so for Cerambycidae observed in the same study. Sverdrup-Thygeson et al. (2010) studied landscape effects on saproxylic beetles of conservation concern in hollow oaks (*Quercus* spp.). Species assemblages differed between oaks in open landscapes and forests, indicating that the two habitats cannot be substituted. Saproxylic Coleoptera associated with polypore fungi were studied, showing that different fungi species harbor different beetle communities (Kaila et al. 1994) and that species associated with fungi were affected by forest management (Jonsell and Nordlander 2002). Bouget et al. (2011a, b) showed differences in vertical stratification of saproxylic beetles in forests and that specialist taxa resided within the canopy. Comparisons between managed and old growth forests showed higher abundance of saproxylic Coleoptera (Martikainen et al. 2000), higher proportion of rare Coleoptera (Vaisanen et al. 1993), greater number of red-listed species of polypore fungi and saproxylic Coleoptera (Siitonen et al. 2001), and a higher proportion of specialist slugs (Gastropoda) (Kappes 2006) in old growth forests.

Many European studies explored forest management practices that promote the retention of saproxylic species in a managed landscape (Jonsson et al. 2005). Refugia such as high stumps created by cutting a tree at a height of 4-5 m and leaving the stump (Abrahamsson and Lindbladh 2006; Gibb et al. 2006b; Hedgren 2007; Jonsell et al. 2004; Lindhe and Lindelow 2004), and snags (Bouget et al. 2011b; Kaila et al. 1997; Schroeder et al. 2011) are important habitats for saproxylic beetles in logged forests. Dead wood produced by wind events (windthrow) is important for saproxylic species, especially clearing specialists (Wermelinger et al. 2002). In their review of the effects of windthrow on insect communities, Bouget and Duelli (2004) recommend a half-salvaging method to meet the needs of managers and biodiversity. The effect on biodiversity by extraction of logging residues for bioenergy was studied by Jonsell (2007; 2008) who cataloged beetle species associated with logging residues and recommended the retention of residues from deciduous trees.

Research specific to European saproxylic species of conservation concern, particularly beetles, is quite extensive. Most species require old growth structures. For example, immature *Osmoderma eremita* (Scopoli) (Scarabaeidae) require trunk hollows with wood mould, generally found in trees 100-400 years old (Ranius et al. 2005). Immature *Lucanus cervus* L. (Lucanidae) take 3-7 years to develop and require decaying wood, stumps, or roots generally only readily available in old growth habitat (Harvey et al. 2011a,b). *Rosalia alpina* (L.) (Cerambycidae) requires old sun-exposed trees in beech forests to complete its life cycle. Interestingly, a complex of flightless saproxylic weevils (Curculionidae) are restricted to, and indicators of, ancient woodland not because of dependence on old growth structures (they develop in small and medium sized twigs) but because of poor dispersal ability (Buse 2011). Jonsell et al. (1998) reviewed substrate requirements for saproxylic invertebrates of conservation concern in Sweden. Research on life history and conservation of other species has been performed (Horak et al. 2011; Rotheray and MacGowan 2000; Siitonen and Saaristo 2000) and several conferences on conservation of European saproxylic beetles have been held (Barclay and Telnov 2005; Bowen 2003; Buse et al. 2009).

The extensive research of dead wood ecology within Europe and greater understanding of the needs of species of conservation concern have allowed for initial recommendations for changes in forest management (Ehnstrom 2001). While nuanced, recommendations call for an overall increase in dead wood in forests that often can be achieved through "benign neglect," or simply allowing an accumulation of dead wood through natural processes such as windthrow and bark beetle outbreaks (Muller et al. 2010). In an extreme example of a proactive increase in saproxylic habitat live nonnative trees in an Italian forest were turned into snags using explosives, drug over with tractors to produce leaning dead trees, and made into habitat trees by removing sections to create rot holes and bird nest holes (Cavalli and Mason 2003). However, changes in European forest management have occurred only recently and long term effectiveness cannot yet be assessed (Davies et al. 2008).

Australia. In Australia, where the amount of managed forest is quickly increasing, research mainly centers on preemptive strategies to reduce impacts of management on sensitive forest species (Baker 2006; Grove 2002a,c; Michaels and Bornemisszza 1999; Yee et al. 2006). The Warra Long Term Ecological Research site, established in a Tasmanian *Eucalyptus obliqua* L.Her. forest, is host to more than 20 "deadwoodology" research projects that explore the biotic and abiotic aspects of wood decay (Grove 2009). The hallmark study at Warra involves a comparison of saproxylic beetles collected from freshly killed regrowth (80 years old) and old growth (300+ years old) *E. obliqua* logs. The first decade of sampling has shown that older (larger) logs host more species, more unique species, and more obligately saproxylic species than smaller logs (Grove and Foster 2011a, b). Leschen (2006) examined the phylogenetic assemblage of saproxylic beetles in New Zealand.

Tropics. Few studies of tropical and subtropical saproxylic insects have been conducted. Mecke et al. (2001) surveyed Coleoptera and Hymenoptera emergent from dead *Araucaria* sp. (Araucariaceae) limbs in Brazil. Tavakilian et al. (1997) associated Cerambycidae with host plants on a grand scale by collecting beetles emergent from 200 species of trees in French Guiana. Touroult et al. (2010) assessed seven collection methods of Cerambycidae in French Guiana and concluded that, time permitting, collection using emergence and flight intercept traps yielded the best results. In Guadeloupe, Touroult (2004) used emergence traps to collect 15 species of Cerambycidae associated with twigs girdled by *Oncideres amputator* (F.) (Cerambycidae). Wu et al. (2008) studied Coleoptera emergent from dead wood in China and found distinct beetle assemblages between broad-leafed and coniferous tree genera. Lachat et al. (2006) found higher saproxylic beetle richness in natural forests than in teak and fuelwood plantations in Benin, West Africa. At the same site Lachat et al. (2007) found higher richness of saproxylic beetles on snags of native trees that on exotic tree snags.

North America. Studies of North American dead wood ecology can be loosely divided into three major groups based on region; western, Canadian (boreal), and eastern forests.

Western North America. Descriptions of western CWD dynamics and management for the Rocky Mountain and intermountain regions, especially in relation to fire ecology, are given by Graham et al. (1994) and Brown et al. (2003).

Western coastal forests were one of the important birthplaces of the modern view of dead wood ecology (Maser et al. 1979; Maser and Trappe 1984). These studies have continued, especially in the Pacific Northwest, where descriptive research has been performed on mortality type and rate, dead wood composition, spatial distribution, influence on soils, influence in aquatic systems, and management for wildlife and timber production (Maser et al. 1998; Laudenslayer et al. 2002). Deyrup (1975, 1976) performed a species level inventory of Diptera, Coleoptera, Neuroptera, and Hymenoptera associated with dead and dying Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in western Washington state. Koenigs et al. (2002) surveyed insects from CWD in Klamath National Forest, California and provided a list of insect orders and Coleoptera families collected. A comparison of ant communities in harvested and non-harvested stands in British Columbia, Canada found fewer large ant species in harvested stands due to lack of large pieces of CWD (Higgins and Lindgren 2006). Lattin (1993) provided an overview of arthropod conservation in old growth forests and a list of arthropods most likely to be impacted by forest fragmentation. Harmon (1992) provided an overview of a long-term decomposition experiment that is underway in the H. J. Andrews Experimental Forest, Oregon. An annotated list of insects and other arthropods resultant from studies at Andrews Experimental Forest was compiled by Parsons et al. (1991) and represents the most important compilation of saproxylic species from that region.

Canada. Research on CWD ecology within Canada's boreal forests is often centered on descriptive studies and/or prevention of environmental impacts from management (similar to Australian research), but draws from, and makes comparisons with research from boreal forests in Europe (Dollin et al. 2008). Langor et al. (2006, 2008) provided a review of the state of saproxylic insect conservation in Canada and called for an increase in basic taxonomy, studies of natural history, and more studies capturing range of natural variation within forest systems. They concluded that this baseline work was essential for the creation of good forest management policies.

Research on the effect of management schemes has been conducted in Canada. Klimaszewski et al. (2008) studied the effectiveness of Natural Disturbance Management, specifically the effect of gap size, on the rove beetle (Staphylinidae) community in a yellow-birch (*Betula alleghaniensis* Britt.) dominated boreal forest. They found that smaller, more numerous gaps had less of an effect on rove beetle community than fewer larger gaps when compared to uncut controls. They also recommended the use of Staphylinidae as bioindicators due to their high species richness and numerous trophic and functional roles and provided a list of species collected. Work and Hibbert (2011) used Diptera to explore the effects of additional biomass removal (limbs, stumps, etc.) after tree harvest and found that the number of pieces of CWD was more important to saproxylic fly diversity than total volume. Webb et al. (2008) studied the effect of remnant habitats left after clearcutting on saproxylic beetles but received inconclusive results possibly due to inadequacies in the study design. Jacobs et al. (2007) failed to find evidence of short term effects on saproxylic Coleoptera in variably harvested white spruce (*Picea glauca* (Moench) Voss) stands, but did find differences between Coleoptera attracted to snags that had recently been killed versus those that had been dead for several years.

Descriptive and comparative studies of species interactions and succession have been performed in Canadian forests. Paquin and Duperre (2001) compared the beetle fauna in seven forest habitats in northern and southern boreal zones in Quebec. They listed 757 species collected (not including 20,000 unidentified specimens of the subfamily Aleocharinae (Staphylinidae)), and found that more Canadian beetle species are associated with decaying processes than with living plants. Importance of tree species composition was investigated by Janssen et al. (2011), who found that black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) and balsam fir (*Abies balsamea* (L.) Mill.) CWD were inhabited by different saproxylic beetle communities. Vanderwel et al. (2006) found differences in Coleoptera, Diptera, and Hymenoptera family composition among different pine (*Pinus* spp.) CWD decay classes, but found that overall species abundance was not influenced by volume of surrounding CWD. Boulanger and Sirois (2007) found two distinct waves in postfire succession of Coleoptera in black spruce (*Picea mariana* (Mill.) B.S.P.)) in Quebec. The first wave immediately followed the fire and consisted of subcortical predators, xylophages, and ascomycete fungus feeders. The second wave consisted of micro- and saprophagous species, but only occurred after the snag fell and greater moisture content of the log allowed for an increase in fungal growth. Kebli et al. (2011) assessed the fungal community in CWD in Quebec and found that fungal richness was influenced by log species and independent of log decay. Dechene and Buddle (2010) found that oribatid mite diversity was highest in samples taken directly on downed aspen CWD than samples taken adjacent to, or 1 m away from CWD.

Saproxylic beetles specific to CWD of quaking aspen (*Populus tremuloides* Michx.) in Canada have been the subject of several studies. Hammond (1997) collected more than 39,000 arthropod specimens, including 257 saproxylic Coleoptera species, emergent from aspen bolts or from flight intercept traps attached to snags in Alberta. Later sampling resulted in collection of 49 early colonizing saproxylic Coleoptera species from fresh cut aspen stumps, bolts, and simulated snags (Hammond et al. 2001). In a third study saproxylic beetle communities differed between two different aged aspen stands and many species favored old stands and/or large diameter snags (Hammond et al. 2004).

Several studies specific to Nova Scotia and the Maritime Provinces of Canada have been performed. Kehler et al. (2004) found higher beetle richness in hardwood stands than soft wood stands. They also found that volume of intermediate sized CWD was the best indicator of species richness in hardwood stands, but volume of well decayed wood was the best indicator in softwood stands. Majka and Pollock (2006) reviewed individual and institutional collections and published new records for four families of saproxylic beetles from the Maritime Provinces of Canada. Majka (2007b) updated records for Eucnemidae (Coleoptera) and provided a list of possibly rare saproxylic beetles for the Maritime Provinces of Canada. Bishop et al. (2009) compared saproxylic beetle assemblages among forest habitats that had been disturbed naturally (windthrow, fire) or through human intervention (clearcutting) and found that the managed forest supported a different faunal assemblage than naturally disturbed forest. Dollin et al. (2008) found that stand age and harvest treatment affected saproxylic beetle richness and provided a list of species potentially indicative of old growth forest in Nova Scotia. Brunke et al. (2011) provide a key and ecological information on rove beetles (Staphylinidae), including many saproxylic species, from eastern Canada and the adjacent United States.

Eastern North America. In eastern North America succession of wood decay and the insects inhabiting dead wood were the subject of numerous early works. Townsend (1886) provided a list of beetles collected from dead basswood (*Tilia americana* L.) in Michigan. Packard (1890) compiled and summarized much of what was known about insects injurious to forest trees, many of which would now be considered saproxylic. Harrington (1896) listed beetles associated with beech (*Fagus grandifolia* Ehrhart) in Canada. Felt (1906) reported on insects associated with dead and dying park and woodland trees in New York. Shelford (1913) described four decay stages of beech (*F. grandifolia*) in Illinois and listed insects associated with each stage. Adams (1915) provided a successional list of insects associated with decaying wood in Illinois forests. Blackman and Stage (1918, 1924) collected beetles emergent from dead wood of American larch (*Larix laricina* (Du Roi) K. Koch) and Hickory (*Carya glabra* (Mill.) Sweet) in New York. In Minnesota Graham (1925) studied movement and succession of insects within dead wood in relation to the varying temperature and humidity microclimate. Brues (1927) compiled a list of insects emergent from seasoned firewood housed in a storeroom in his Massachusetts home. Doane et al. (1936) published a textbook on forest insects, including numerous saproxylic species, of the United States. Savely (1939) studied the ecology and succession of invertebrates and vertebrates in dead oak (*Quercus* spp.) and pine (*Pinus* spp.) in a North Carolina forest. Beer (1949) reported on Buprestidae emergent from dead wood. Howden and Vogt (1951) studied the community of arthropods associated with various decay stages of standing dead pine (*Pinus virginiana* Mill.) in Maryland.

More recent studies of CWD in eastern North America include descriptive studies and inventories of CWD amount, type, and recruitment for the entire region (Chojnacky et al. 2004) and for the forests of the southern U.S. (McMinn and Hardt 1996; Van Lear 1996; Waldrop 1996). Webster and Jenkins (2005) studied the effect of historic land use (prior to 1940) on contemporary distributions of CWD in the western portion of Great Smoky Mountains National Park, Tennessee. They found that primary forest had significantly more down dead wood than areas of previous concentrated settlement (2.4 times more) or diffuse disturbance (1.6 times more) suggesting that it may take more than a century for CWD to recover to primary forest levels in disturbed areas.

The use of CWD by fungi, invertebrates, and vertebrates in eastern forests has been the subject of numerous studies (see McMinn and Crossley 1996). Deyrup and Mosley (2004) reported congregations of *Aradus gracilicornis* Stal (Aradidae) under the bark of fire-killed south Florida slash pine (*Pinus elliottii densa* Little and Dorman) in Florida. Hanula (1996) provided a partial list of wood feeding insects, their hosts, and habits (where known) from the southeastern U.S. (including 439 species of Coleoptera). Ferro et al. (2009) surveyed beetles emergent from twig bundles of southern red oak (*Quercus falcata* Michaux) in Louisiana and reviewed the literature on Coleoptera from fine woody debris. They also found that species richness varied based on twig position; bundles hung above the ground had the highest species richness, propped bundles were intermediate, and bundles lying directly on the ground had the least. Stephenson et al. (2008) compared myxomycete (plasmodial slime molds or myxogastrids) on fine woody debris in forests in Argentina, Australia, Costa Rica, New Zealand, and the United States. They found higher richness in twigs from temperate forests and their findings suggest differences in assemblages between myxomycetes on twigs and in leaf litter. Braccia and Batzer

(2001) surveyed invertebrates found in woody debris in a South Carolina flood plain during dry and wet periods. During wet periods they collected both floating and submerged CWD. Submerged and dry CWD contained mostly "perennial inhabitants" and "seasonal colonizers" whereas floating CWD supported those groups and many "seasonal refugees." Ulyshen and Hanula (2010) surveyed the succession of saproxylic beetles emergent from logs of loblolly pine (*Pinus taeda* L.) that had been aged between 1 month and 9 years. They found that species richness peaked within the first year and beetle communities were significantly different among decay classes. They also provided a list of the 209 beetle species collected. Ferro (Chapter 6) compared the beetle fauna of leaf litter and the final decay stage of downed coarse woody debris (CWD5) in Tennessee. Both substrates harbored unique communities, 110 species were collected from CWD5, and eight species were significantly associated with it.

Several studies have directly or indirectly examined differences in vertical stratification of arthropods associated with CWD in eastern North America. Ulyshen (2011) provided a general review of arthropod vertical stratification in temperate forests including a section on use of "aerial" dead wood (snags, dead branches and twigs, and rotting heartwood) by arthropods. Ulyshen and Hanula (2007) sampled beetles at two different heights (0.5 m and 15 m) in a Georgian forest. They found no difference in abundance or species richness between the two trapping heights. Twenty-nine percent of species collected were exclusive to ground layer collections whereas 31% were exclusive to canopy collections. Ulyshen and Hanula (2009a) compared emergent, early successional saproxylic beetles among two forest types, three tree species, and two wood postures in South Carolina. They found higher species richness in the upland pine-dominated stands, no richness differences among tree species, and higher species richness in logs. However, snags were found to contain a distinct fauna and may be important for species conservation. Hymenoptera collected from the same study, but reported on by Ulyshen et al. (2011), did not show differences in species richness between forest types, among tree species, or between wood postures. However, communities within the upper and lower portions of snags were distinct and community composition differed among tree species.

A comparison of the dead wood dependent beetle fauna of an old-growth and a 40-year-old regrowth forest in New Hampshire has been the subject of several studies. Chandler (1987) found differences in Pselaphinae (Staphylinidae) species composition between the two forests. Later Chandler (1991) revisited the sites and surveyed 21 slime-mold and fungus feeding saproxylic beetle families. He grouped species based on host type and found that species composition differed between the two forests; old growth sites contained higher richness of species that feed beneath bark, while basidiomycete-feeding species were richer in regrowth forests. A survey of Leiodidae at the same locations (Chandler and Peck 1992) showed no difference in species richness between the two forests, but greater abundance in the old-growth forest.

Responses of arthropods to current management schemes involving fire have been investigated in eastern forests. Early successional saproxylic beetle richness and abundance did not differ among control, mechanical reduction of understory (thinning), prescribed burn, and thinning plus burn treatments in a North Carolina forest (Campbell et al. 2008b). However, several families and some particular species did show significant differences in abundance among the treatments. A similar study, with an additional treatment of herbicide plus burn, was conducted in a long leaf pine (*Pinus palustris* Mill.) forest in Alabama (Campbell et al. 2008a). Abundance of all Coleoptera was not different among treatments; however, richness of all Coleoptera, some complexes, and families differed among treatments. Total species richness and abundance of Scolytinae (Curculionidae) and Trogossitidae were all highest on thinned plus burn treatments. Hanula et al. (2009) found that in general ground dwelling arthropods did not vary use of CWD in response to burn frequency in a long-leaf pine (*P. palustris*) forest in Florida. Ulyshen et al. (2010) studied the effects of fire on early successional beetles in loblolly pine (*P. palustris*) CWD in Georgia. Twice as many specimens emerged from unburned logs than burned logs. However, both treatments had similar species richness and community composition indicating saproxylic beetles in loblolly pine CWD were tolerant of low level fires.

Additional manipulations of habitat and dead wood have been performed to study the responses of saproxylic beetles in eastern forests. Warriner et al. (2002) studied the response of ground beetles (Carabidae) and longhorn beetles (Cerambycidae) to partial cutting (thinning) in a Mississippi forest. Collections were made two years after thinning took place and both families showed higher diversity in thinned than uncut controls. Ulyshen et al. (2004) sampled saproxylic beetle diversity in gaps of different sizes and ages in a South Carolina forest. They found no difference in abundance based on gap size, but found higher abundance and diversity in young gaps than old gaps. Ulyshen and Hanula (2009c) studied the effects of removal of CWD, addition of CWD (logs), and addition of CWD (snags) on ground dwelling arthropods and early successional saproxylic beetles in South Carolina. They found no difference in richness or abundance of saproxylic beetles among the treatment sites. However, ground beetle richness increased at sites with increased CWD.

Despite previous studies on the ecology of dead wood in eastern North America, basic knowledge needed to make good management decisions is still lacking. Most important are comprehensive lists of species (e.g. Coleoptera, Diptera) that require dead wood, an understanding of their natural history, and an understanding of how they have been impacted by past and current human endeavors. Diameter of woody debris, decay class, and land use history (specifically continuity of substrates) have all been shown to influence saproxylic beetle distributions (see above). Old growth forests, with a higher volume of CWD, greater continuity of CWD, and greater diameter of logs are important for saproxylic species conservation (Siitonen et al. 2001; Grove 2002b). Large tracts of forest that have not been cut since European settlement in North America are found in Great Smoky Mountains National Park (GSMNP), whereas other areas of the park were recently logged (<100 years ago). Comparison of saproxylic species assemblages between old growth and regrowth sites are needed to determine what, if any, species are restricted to old growth forest and may be of conservation concern. The purpose of this study was to survey and compare the saproxylic Coleoptera communities within woody debris of different size classes (fine and coarse), different decay stages (defined below), and forest types (primary and secondary).

7.2 MATERIAL AND METHODS

Study Area. Great Smoky Mountains National Park (GSMNP, Fig. 7.1) was established in 1934, named as an International Biosphere Reserve in 1976, and a World Heritage Site in 1983. It encompasses 211,000 ha (521,490 acres) in Tennessee and North Carolina, USA. The area

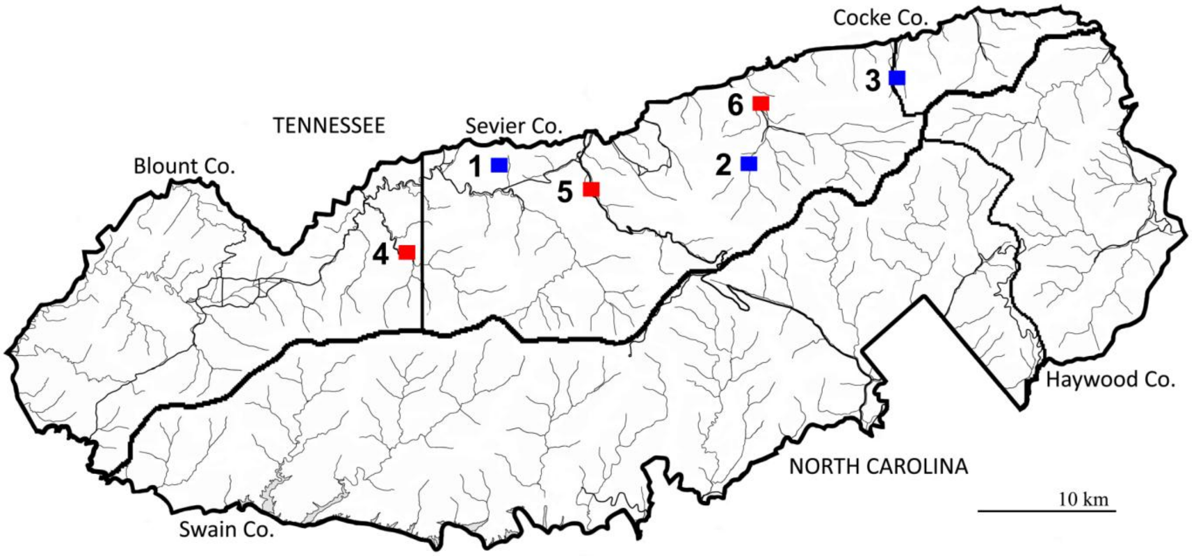

Figure 7.1. Map of collection locations in Great Smoky Mountains National Park. Primary forest sites: 1) Laurel Falls; 2) Porters Creek; 3) Albright Grove. Secondary forest sites: 4) Tremont; 5) Sugarlands Quiet Walkway; 6) Greenbrier.

is topographically complex, ranging in elevation from 270–2024 m (875-6643 ft). The Great Smoky Mountains range itself extends from the northeast corner of the park to the southwest. The southeastern corner and the adjacent Cherokee Indian Reservation are part of the Balsam Mountains. Five major forest communities are recognized in the park, though 80% may be broadly classified as eastern deciduous forest (Houk and Collier 1993). Lower and intermediate elevations (1070-1525 m; 3500-5000 ft.) are dominated by northern hardwood forests and spruce-fir forests at higher elevations (above 1525 m; 5000 ft.). Cove forests are found in sheltered valleys at mid-elevations (1070-1370 m; 3500-4500 ft.). This community represents the most diverse habitat in the park with its diversity of tree species, complex understory, and deep, moist litter layer. Some of the old growth cove forest stands are among the most beautiful and best preserved examples of this forest type in existence. The eastern half of the park contains the largest remaining tract of old growth forest in the eastern U.S. (Davis 1996). Lower and more xeric parts of the western half contain large stands of pine hardwood. Cades Cove, a large area in the northwestern quarter of the park is flat and mainly covered with meadows. Access to the southwestern quarter of the park is limited by Lake Fontana, and is the largest area of roadless forest in eastern U.S. (Anonymous 2004). The park's abundant rainfall and high summer humidity provide excellent growing conditions. In the Smokies, the average annual rainfall varies from approximately 140 cm (55 inches) in the valleys to over 215 cm (85 inches) on some peaks.

The perception that U.S. national parks are protected from human-induced insults to native habitats within their boundaries is valid only in a limited way. The natural resources represented in these relatively pristine habitats are of course protected from logging, mining, and conversion to agriculture. But with this protection comes a legislative mandate to make the parks available for the enjoyment and recreation of visitors. More than 9,000,000 people visit GSMNP annually, making it the most heavily used of U.S. National Parks (Anonymous 2004).

Until the early 19th century the American chestnut, *Castanea dentata* (Marsh.) Borkh., was a co-dominant tree in northern hardwood forests of GSMNP. The huge trunks (up to 20 ft. diameter) provided substrates for diverse communities of subcortical beetles and other insects for many years after falling. Beginning in 1904, chestnut blight rapidly spread throughout the eastern U.S., killing almost every large chestnut tree in the country (Hepting 1974).

More recently, the Fraser fir, *Abies fraseri* (Pursh) Poir., a co-dominant tree in southern Appalachian spruce-fir forests, suffered a similar fate. The balsam woolly adelgid (*Adelges piceae* (Ratzeburg), Hemiptera: Adelgidae), native to Europe, entered the southern Appalachians during the 1950s and quickly overwhelmed stands of Fraser fir in the region (Eagar 1984). Many areas that once supported mature forests of red spruce (*Picea rubens* Sarg.) and Fraser fir now are in transition to diversity-impoverished rhododendron thickets. These effects can be observed in dramatic fashion on top of Clingman's Dome, where large "ghost stands" of dead fir trunks dominate patches of the landscape.

The sudden decline of these two dominant tree species has had a profound effect on the forest ecology of the region. These changes undoubtedly have had similar effects on countless small, cryptic organisms that may never be recognized due to the lack of comprehensive biodiversity information. These changes continue today. Currently, yet another insect pest, the hemlock woolly adelgid (*Adelges tsugae* (Annand), Hemiptera: Adelgidae), from Asia, has invaded the region and has decimated large stands of eastern hemlock, *Tsuga canadensis* (L.) Carrière.

Study Sites. All collections took place at six locations in GSMNP. Overstory vegetation data were obtained from Madden (Geospatial Dataset-1047498), and understory vegetation data were obtained from Madden (Geospatial Dataset-1047499); see Welch et al. (2002) and Madden et al. (2004) for a description of how data were collected. Geology data were obtained from National Park Service (2006). Vegetation disturbance history data were obtained from National Park Service (2007). Data on forest type in 1938 were obtained from National Park Service (2009). Three locations within each study site were surveyed using a point relascope sampling technique (Brissette et al. 2003; Gove et al. 1999). Findings were averaged to obtain volume of CWD per hectare at each study site.

Three study sites, hereafter referred to as "primary forest" sites, were located in least disturbed forests:

1) Laurel Falls (TN: Sevier Co.: N35˚40.808′ W83˚36.067′). The site was on Thunderhead Standstone, has an oak-hickory forest overstory, and a light rhododendron understory. Vegetation disturbance was selective cut and during a 1938 survey this location was designed as cove hardwood. Coarse woody debris volume was 663 m^3/ha.

2) Porters Creek (TN: Sevier Co.: N35˚40.790′ W83˚23.855′). The site was on Thunderhead Standstone, has an acid cove forest overstory, and a medium rhododendron understory. Vegetation disturbance was light cut and during a 1938 survey this location was designed as cove hardwood. Coarse woody debris volume was 290 m^3/ha.

3) Albright Grove (TN: Cocke Co.: N35˚44.173′ W83˚16.647′). The site was on Thunderhead Standstone, has cove forest overstory, and a light rhododendron understory. Vegetation disturbance was undisturbed and during a 1938 survey this location was designed as cove hardwood. Coarse woody debris volume was 927 m^3/ha.

Three study sites, hereafter referred to as "secondary forest" sites, were located in disturbed (heavily logged) forests:

1) Greenbrier (TN: Sevier Co.: N35˚43.147′ W83˚23.349′). The site was on Roaring Fork Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designed as grassland. Coarse woody debris volume was 143 m^3/ha.

2) Tremont (TN: Blount Co.: N35˚37.308′ W83˚40.447′). The site was on Elkmont Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designed as oak/chestnut forest. Coarse woody debris volume was 139 m^3/ha.

3) Sugarlands Quite Walkway (QW) (TN: Sevier Co.: N35˚39.826′ W83˚31.509′). The site was on Roaring Fork Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designed as grassland. Coarse woody debris volume was 161 m^3/ha.

Substrate. For this study fine woody debris was defined as woody debris 2.5-7 cm diameter originating from trees. No prior decay classification could be found for fine woody debris therefore one is introduced here. The classification is based on visible external characteristics and structural quality of the wood and contains two states, fresh and weathered. Fresh fine woody debris (FWD1) possessed firm bark with intact twigs, showed no visible signs of weathering or fungal intrusion, and was structurally sound. Weathered fine woody debris (FWD2) had loose bark or lacked bark, had lost all small twigs, showed signs of weathering and/or fungal intrusion, and was spongy to the touch, easily broken, or otherwise structurally compromised. This classification is not intended to encompass all fine woody debris decay possibilities but applied well within the context of this study.

For this study coarse woody debris was defined as dead wood greater than 8 cm diameter but only pieces 8-20 cm diameter were collected. The decay classification of coarse woody debris used for this research is taken from Pyle and Brown (1999). Decay class I (CWD1) is a solid piece of wood with firmly attached bark and small twigs but without weathering stains. Decay class II (CWD2) is a solid piece but shows noticeable decay and lacks firmly attached bark. Decay class III (CWD3) is still solid but shows noticeable signs of decay, possesses little to no bark, and the outer wood surface will flake or shred if thudded perpendicularly. Decay class IV (CWD4) still contains hard chunks of wood, may be oval, and can be easily cleaved into large pieces if kicked. Decay class V (CWD5) is generally flattened, can be easily crushed, and is composed of predominantly powdery wood or separated fibers of cellulosic material.

Sampling. Woody debris samples were collected during April 2006 at each of the six study sites. Only samples from hardwood (angiosperm) tree debris were collected and each represented a composite of subsamples taken from numerous pieces of debris available at the site. For this research CWD5 was not collected (but see Chapter 6) and CWD3 and CWD4 were combined (CWD3-4). Three samples of each of the following were taken at each study site: FWD1, FWD2, CWD1, CWD2, CWD3-4 (15 samples at each site) resulting in a grand total of 90 samples. Each sample consisted of enough substrate to fill a 68 L emergence chamber three-fourths of its capacity. Emergence chambers consisted of a sealable plastic tote box with ventilation holes and a bottom collection cup. See Ferro and Carlton (2011) for a detailed description of the emergence chamber design and a review of emergence chambers used to collect saproxylic insects. Chambers were removed to a shady, forested location near the Twin Creeks Science and Education Center in GSMNP. This approximated the environment from which the wood was collected and reduced the risk of overheating. The array was surrounded by a battery-powered electrified fence to protect against bears and feral hogs.

Chambers were serviced six times during the spring, summer, and early fall of 2006, and three more times during spring, summer, and fall of 2007, otherwise the chambers were left unattended. Servicing consisted of removal of specimens and old preservative, then addition of new preservative.

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 (primarily Arnett and Thomas (2001) and Arnett et al. (2002) and references therein, plus additional literature as needed), and/or comparison with authoritatively identified reference specimens. All immature Coleoptera and 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, and Great Smoky Mountains Natural History Museum (GSNP), Gatlinburg, Tennessee.

These practices are in line with the recommendations given by Gotelli (2004) and Bortolus (2008) concerning appropriate taxonomic practices when conducting community level research. Specifically: 1) specimens were identified in an appropriate manner, not through the use of "gray literature" or previous ecological publications; 2) taxonomic experts were consulted concerning the identification of various taxa and are thanked in the Acknowledgments section; 3) literature used to identify taxa is cited (see above and Discussion); 4) specimens have been deposited in scientific institutions so that further taxonomic confirmations can be made; and 5) taxonomy as a science was supported; two taxonomists were trained, more than 20 new species were described as a result of this research, and keys were provided for their identification (Ferro and Carlton 2010; Park et al. 2010; see Chapter 3).

Data analysis. Individual-based rarefaction curves were used to compare species richness among subsets (Gotelli and Colwell 2001). Curves were constructed using code developed by MLF and KEH and run in the R programming environment (R Development Core Team 2010). For each subset, 1000 rarefaction curves were created, an average curve and its 95% confidence limits were derived from the simulations, and a significant deviation from the simulated average occurred when an observed value fell outside the confidence interval. Each rarefaction curve is shown with a combination of these three lines and an average curve that lies outside the confidence interval of another curve can be considered different at the α=0.05 level.

Community similarity was assessed using Sorensen's quotient of similarity (Southwood 1978). A null Sorensen's quotient of similarity was produced taking the average of 10 comparisons of two datasets consisting of 100 randomly selected specimens each.

Chi square goodness of fit testing was performed for 27 species represented by 10 or more specimens (i.e. an expected value of five or more specimens per subset, see Crawley 2007) emergent from FWD (degrees of freedom = 1 and α=0.05). Chi square goodness of fit testing was performed for 35 species represented by 15 or more specimens emergent from CWD (degrees of freedom = 2 and α=0.05). Chi square goodness of fit testing was performed for 71 species represented by 10 or more specimens total (degrees of freedom = 1 and α=0.05). Tests were performed for a difference in number of specimens of a given species between different decay classes of FWD, decay classes of CWD, and forest types, respectively. A Bonferroni correction was not used (as per Gotelli and Ellison 2004: 348). With α=0.05 there is a 5% chance of reporting a significant difference even though one does not actually exist (Type I error). Therefore we should expect significance to be incorrectly reported for ~1-4 comparisons within each group of tests.

7.3 RESULTS

Total. A total of 5673 adult beetle specimens, representing 305 lowest identifiable taxa within 227 genera and 50 families, were collected as part of this research (Appendix 3). Of the 305 lowest identifiable taxa, 8 were identifiable only to family or tribe, 63 were identifiable only to genus, and 234 were identified to species. Groups only identified to family, tribe, or genus may contain multiple species (see discussion). For the remainder of the results and discussion all 305 lowest identifiable taxa will be referred to as "species" in an attempt to reduce jargon and increase readability.

Staphylinidae was, by a wide margin, the most species rich family with 83 species, followed by Curculionidae (30 spp.), Cerambycidae (29 spp.), Tenebrionidae (15 spp.), and Carabidae (12 spp.). Nineteen families were represented by a single species. Ten species were represented by more than 100 specimens, and 115 species (38%) were singletons.

Table 7.1 provides a summary of the number of specimens, families, genera, and species collected for the total, each subset, and combination of subsets. The species accumulation curve (SAC) column denotes which subset had the higher species richness when normalized for number of specimens. Like letters denote curves which are not significantly different (α = 0.05), a = highest richness, b = second highest, etc.

Substrate. Many more specimens and species were collected from CWD (4129 and 247, respectively) than from FWD (1544 and 162, respectively) partially because more samples of CWD were taken than FWD. However, a comparison of the species accumulation curves for both subsamples (Fig. 7.2) shows species richness was not significantly different between CWD and FWD when normalized for number of specimens.

Forest. Many more specimens but an equal number of species were collected from primary forest (3347 and 207, respectively) than from secondary forest (2326 and 207, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 7.3) shows significantly higher species richness in secondary forest when normalized for number of specimens.

Table 7.1. Number of specimens, families, genera, and species collected for the total, each subset, and combination of subsets. SAC = Species Accumulation Curve: denotes which subset had the higher species richness when normalized for number of specimens. Like letters denote curves which are not significantly different ($\alpha = 0.05$), a = highest richness, b = second highest, etc.

		#Specimens	#Family	#Genus	#Species	SAC
1	Total	5673	50	227	305	/
2	FWD	1544	36	138	162	a
2	CWD	4129	45	192	247	a
3	Primary	3347	41	165	207	b
3	Secondary	2326	40	171	207	a
4	2006	1575	44	180	225	a
4	2007	4098	37	163	205	b
5	FWD1	803	24	78	91	b
5	FWD2	741	32	104	118	a
5	CWD1	1003	32	95	110	b
5	CWD2	1719	38	127	156	a
5	CWD3-4	1407	28	102	127	b
6	FWD1 - Primary	458	19	53	60	c
6	FWD2 - Primary	467	26	71	76	b
6	FWD1 - Secondary	345	17	47	51	c
6	FWD2 - Secondary	274	24	70	77	a
7	CWD1 - Primary	526	24	61	70	a
7	CWD2 - Primary	1091	31	88	107	a
7	CWD3-4 - Primary	477	25	65	84	a
7	CWD1 - Secondary	628	25	72	72	a
7	CWD2 - Secondary	805	23	67	86	a
7	CWD3-4 - Secondary	602	22	72	85	a

Table 7.2. Sorensen's quotient of similarity values for substrate x decay class combinations.

	FWD1	FWD2	CWD1	CWD2	CWD3-4
FWD1	x	0.46	0.50	0.48	0.38
FWD2		x	0.44	0.49	0.47
CWD1			x	0.50	0.45
CWD2				x	0.50
CWD3-4					x

Year. Fewer specimens but more species were collected during 2006 (1575 and 225, respectively) than 2007 (4098 and 205, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 7.4) shows significantly higher species richness during 2006 when normalized for number of specimens. Ninety-five species (35%) were only collected during 2006, and 77 species (28%) were only collected during 2007.

Substrate x Decay Class. Subsets based on a combination of substrate and decay class showed that the greatest number of specimens was collected from CWD2 (1719) and the fewest number of specimens was collected from FWD2 (741). The greatest number of species was collected from CWD2 (156) and the fewest species were collected from FWD1 (98). Species richness based on species accumulation curve comparisons (Fig. 7.5) was higher in, and not significantly different among, FWD2 and CWD2. Species richness was lower in, and not significantly different among, FWD1, CWD1, and CWD3-4.

Sorensen's quotient of similarity for these substrates (Table 7.2) showed the least similarity between FWD1 and CWD3-4 (0.38) and the greatest similarity (0.50) between the following combinations: FWD1 and CWD1; CWD1 and CWD2; and CWD2 and CWD 3-4. The null Sorensen's quotient of similarity was 0.37 (range 0.29–0.43).

Forest x FWD Substrate x Decay Class. Subsets based on a combination of forest type, FWD substrate, and decay class showed that the greatest number of specimens was collected from primary forest FWD2 (467) and the fewest number of specimens was collected from secondary FWD2 (274). The greatest number of species was collected from secondary FWD2 (77) and the fewest species were collected from secondary FWD1 (47). Species richness based on species accumulation curve comparisons (Fig. 7.6) was highest for secondary FWD2, intermediate for primary FWD2, and lowest for primary FWD1 and secondary FWD1 which were not significantly different from one another.

Forest x CWD Substrate x Decay Class. Subsets based on a combination of forest type, CWD substrate, and decay class showed that the greatest number of specimens was collected from primary CWD2 (1091) and the fewest number of specimens was collected from primary CWD3-4 (477). The greatest number of species was collected from primary CWD2 (107) and the fewest species were collected from primary CWD1 (70). Species richness based on species accumulation curve comparisons (Fig. 7.7) was nearly indistinguishable for all subsets. Species richness of all subsets was not significantly different from the richness of primary CWD2. However, species richness of secondary CWD3-4 and secondary CWD2 (not significantly different from one another) were higher than species richness of primary CWD1 and primary CWD3-4 (not significantly different from one another).

Species Data. Of the 306 species collected, 71 were represented by 10 or more specimens (Appendix 3) and available for statistical evaluation in one or more of the tests below.

Fine Woody Debris. Of the 27 species available for testing, 10 species (37%) were represented by significantly more specimens in FWD1, 11 species (41%) were represented by significantly more specimens in FWD2, and six species (29%) showed no significant difference between the two habitats.

Coarse Woody Debris. Of the 35 species available for testing, four species (11%) were represented by significantly more specimens in CWD1, 14 species (40%) were represented by significantly more specimens in CWD2, eight species (23%) were represented by significantly

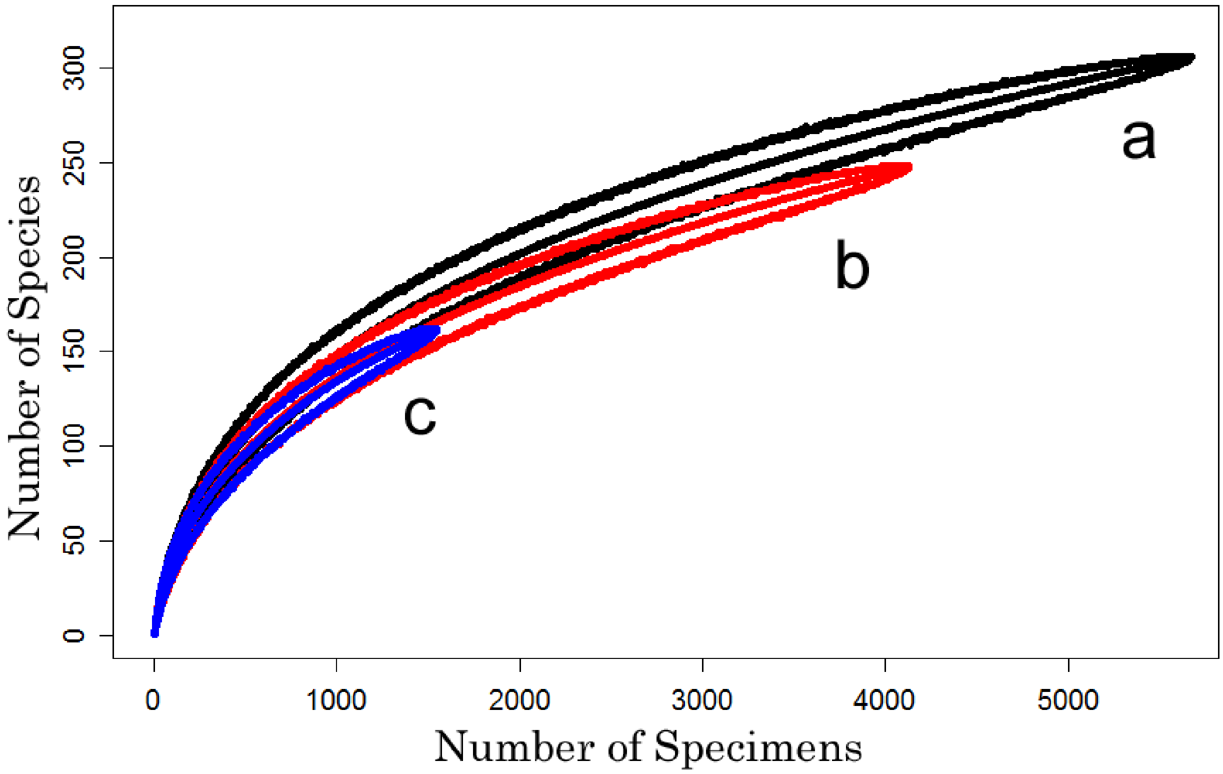

Figure 7.2. Species accumulation curves for a: total; b: CWD; c: FWD.

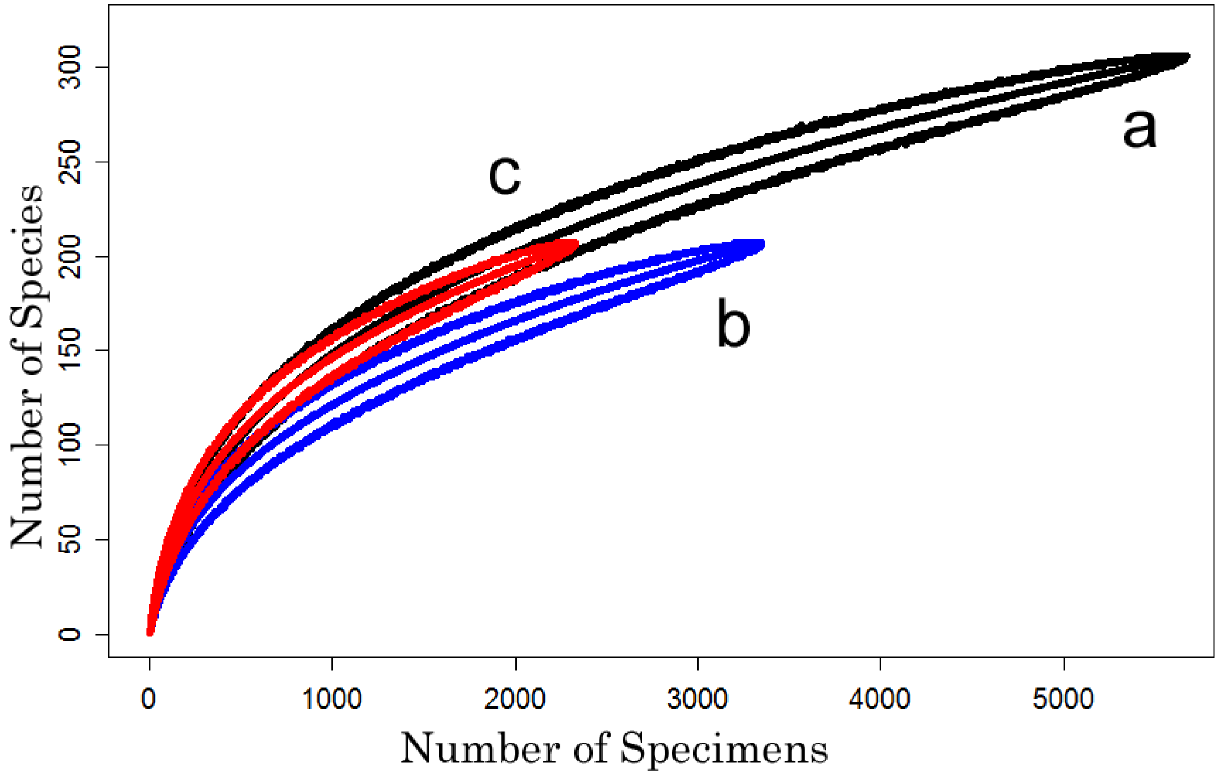

Figure 7.3. Species accumulation curves for a: total; b: primary forest; c: secondary forest

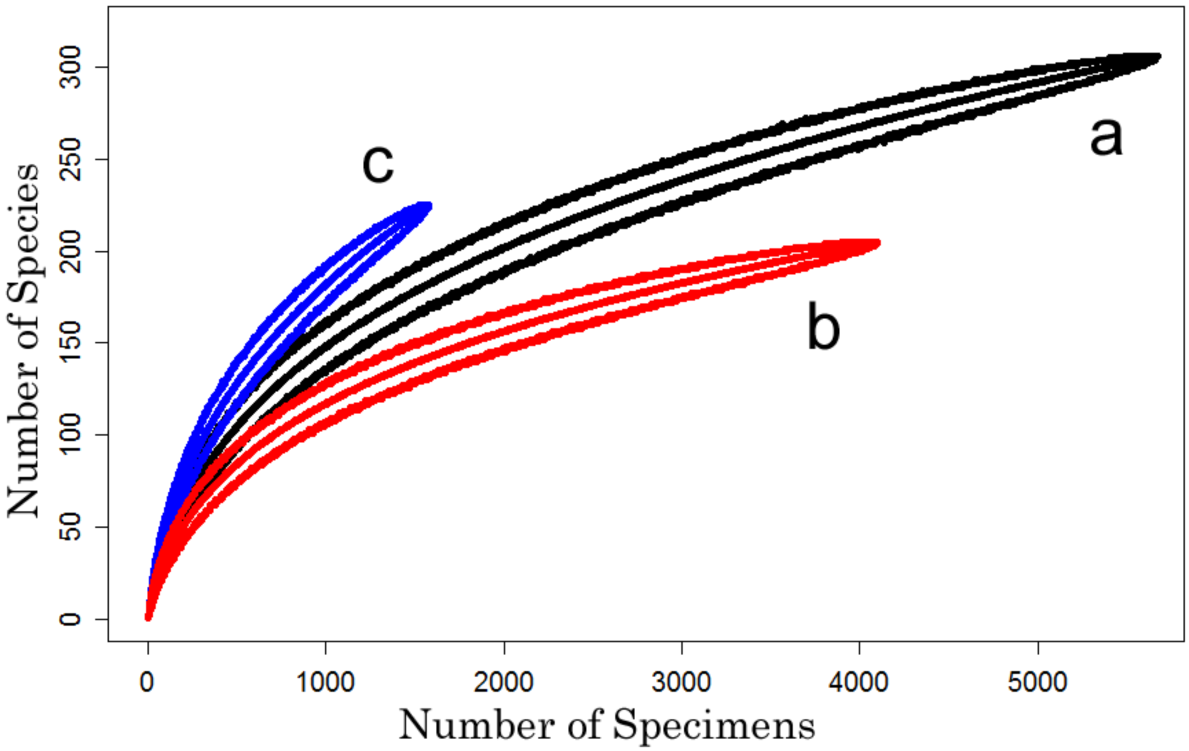

Figure 7.4. Species accumulation curves for a: total; b: 2007; c: 2006

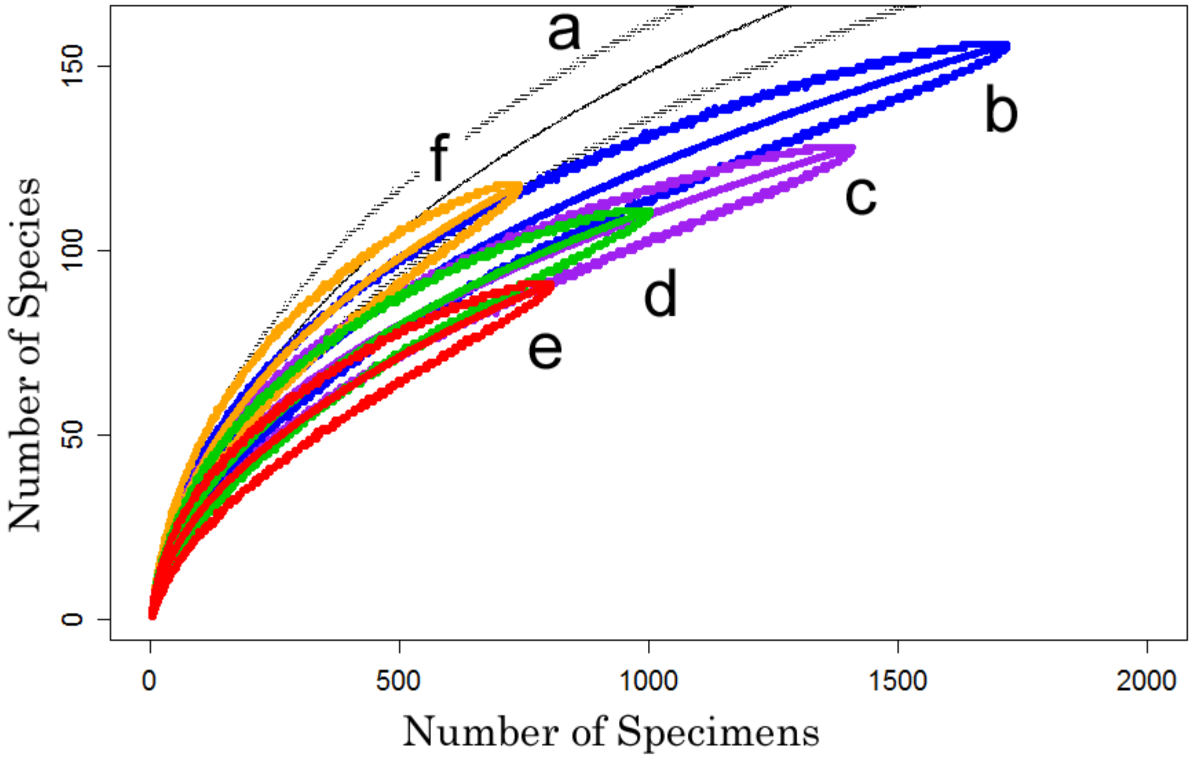

Figure 7.5. Species accumulation curves for a: total; b: CWD2; c: CWD3-4; d: CWD1; e: FWD1; f: FWD2

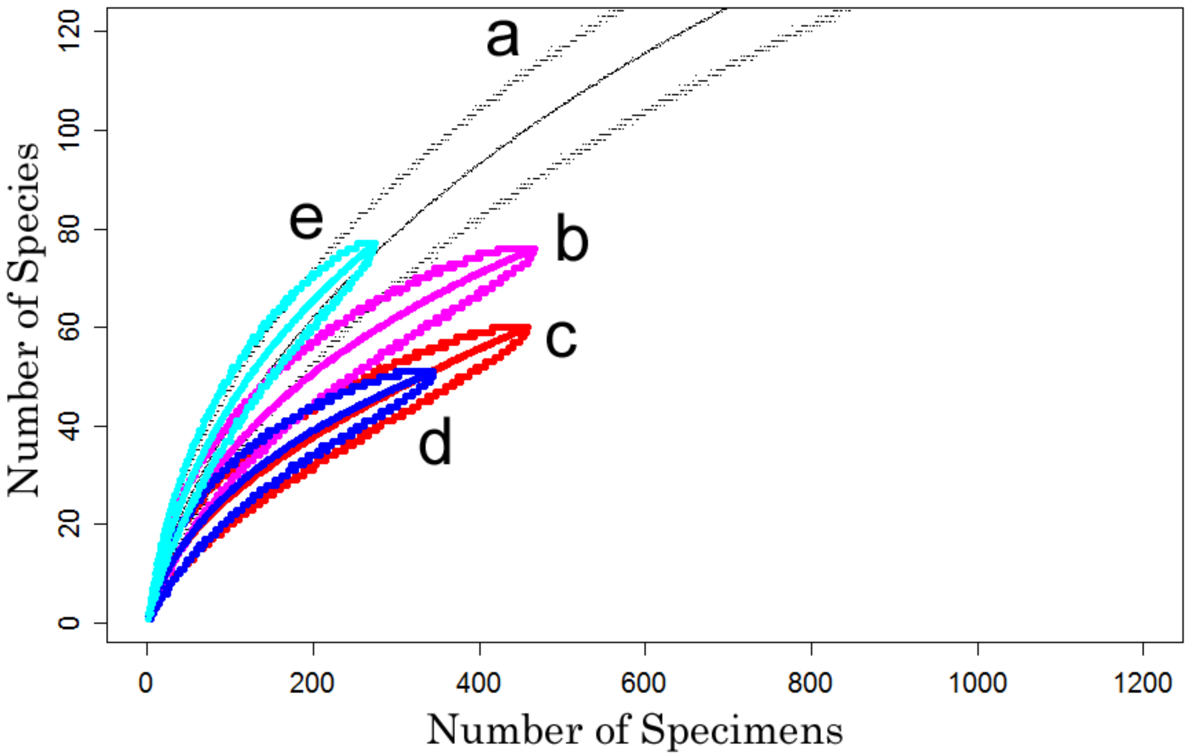

Figure 7.6. Species accumulation curves for a: total; b: primary FWD2; c: primary FWD1; d: secondary FWD1; e: secondary FWD2

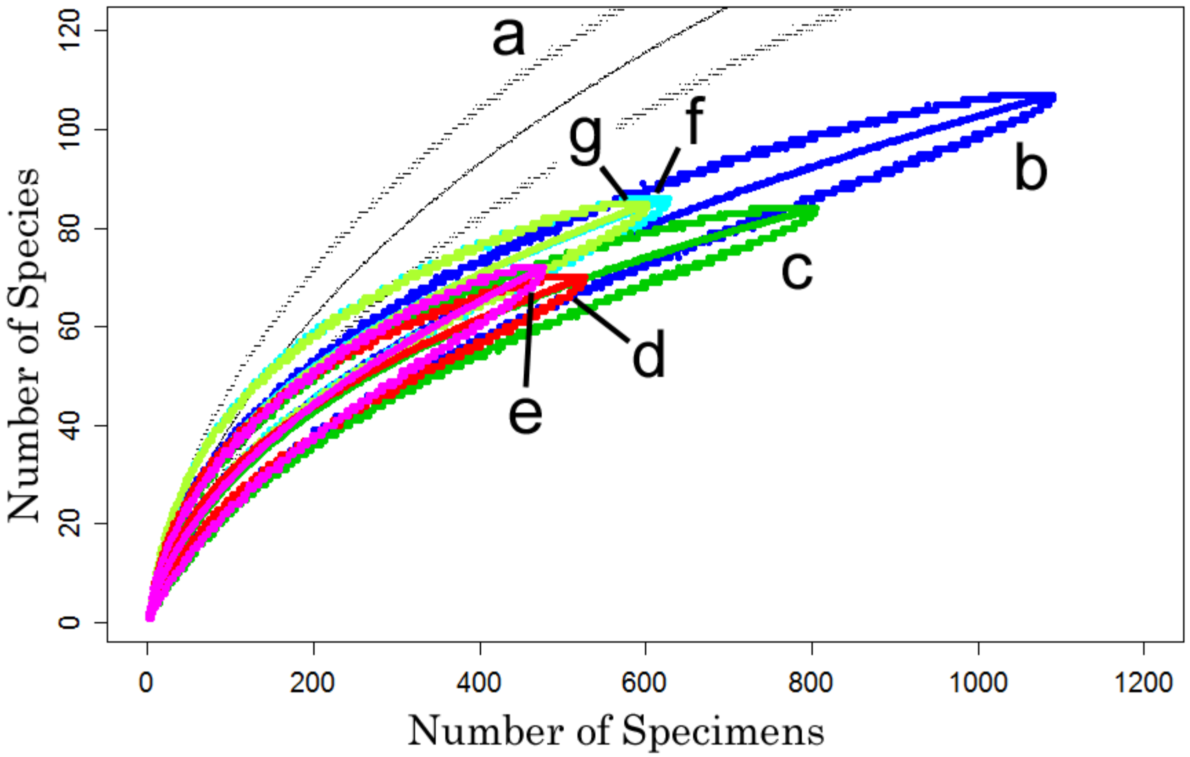

Figure 7.7. Species accumulation curves for a: total; b: primary CWD2; c: primary CWD3-4; d: primary CWD1; e: secondary CWD1; f: secondary CWD2; g: secondary CWD3-4

more specimens in CWD3-4, and nine species (26%) showed no significant difference among the three habitats.

Forest. Of the 71 species available for testing, 16 (23%) were represented by significantly more specimens in secondary forests, 27 (38%) were represented by significantly more specimens in primary forests, and 28 (39%) showed no significant difference between the two forest types.

7.4 DISCUSSION

Henry David Thoreau listed 70 items one should take on a 12 day hike in the Maine woods (Thoreau 1988). However, he neglected to include the item he used to write the list: a pencil. Pencils are easily overlooked and much taken for granted, but vitally important and surprisingly complicated to make (see Petroski 1989). Dead wood is much the same way; it can be found in abundance, costs nothing, is seemingly inert, easily overlooked, and until recently often taken for granted (some collectors report specimens from "wood trash"). Much about dead wood sits outside of the human experience; it is an opaque habitat, the organisms that reside within are difficult to collect and enumerate, and in many cases decay is so slow a career or even a lifetime are not enough to follow a decent sized tree from death to dissolution.

In this study we used emergence chambers to overcome the difficulty of collecting specimens, and sampled wood of various decay classes to overcome the sluggishness of decomposition. While the latter allowed us to look at the effects of perhaps a decade or more of decay in only two years, it didn't allow for substrate standardization (wood species, time since death, etc.). Even with this limitation the results were very promising.

Substrate x Decay Class. Comparisons of similarity (Table 7.2) implied that the size, decay class, and size x decay class combinations used to designate microhabitats were meaningful in circumscribing Coleoptera communities. If there were no differences in beetle communities in different types of dead wood (including size and decay class), then Sorensen's quotient of similarity would have been near 1.00 for each comparison. If no real differences in Coleoptera community existed between size classes of woody debris, but did exist among decay classes, Sorensen's quotient of similarity would be near 1.00 for FWD1 x CWD1. If the designated decay classes were not meaningful, then CWD1 x CWD2 or CWD2 x CWD3-4 would be near 1.00. If size x decay class designations had been random in relation to a real aspect of dead wood that better defined beetle communities, then Sorensen's quotient of similarity would have been near the null value (0.37) for each comparison. Additionally Sorensen's quotient of similarity values imply that none of the size x decay class designations are redundant (value near 1.00), nor are any neighboring combinations incorrectly designated (value near 0.37), which has important implications for future research.

Fine Woody Debris. The difference in species emergent from FWD1 and FWD2 (Appendix 3) suggests that FWD undergoes faunal succession. More species were collected from FWD2 than FWD1 (118 versus 91), but FWD1 had more unique species (71) than FWD2 (44). A total of 162 species were collected from FWD and of the species that were available for statistical evaluation, about equal numbers were associated with both substrates (10 and 11 in FWD1 and FWD2, respectively). *Aulonothroscus distans* Blanchard (Throscidae) was the most numerous species from FWD1, represented by 371 specimens, but only 111 specimens were collected from FWD2. *Thoracophorus costalis* (Erichson) (Staphylinidae) was the most numerous species from FWD2, represented by 127 specimens, but only 18 specimens from FWD1. The biology of both of these species is poorly known (see below).

To our knowledge succession of Coleoptera in FWD has only been addressed in two other studies, both conducted over 80 years ago. Blackman and Stage (1918) recorded 11 species of Coleoptera emergent from limbs of American larch. Specimens were collected from limbs of their "Tree No. 1" over two years, yielding three beetle species the first year and eight species the next year.

Later, Blackman and Stage (1924) surveyed beetles emergent from dead hickory over six summers following tree death. They collected 16, 28, 20, and two beetle species from FWD during the first four summers following death, respectively. No FWD remained after the fourth year. The community in the second year twigs contained all but two of the first year species and an additional 14 species. Third year twigs lost 15 species that had been present in second year twigs, but gained an additional seven species, one of which had been present in first year twigs. Fourth year twigs contained only two species, one that had not been collected before, and another that was present in all previous years. Their findings imply three successional stages within hickory FWD. However, if the second year bloom results from species that require two years to develop, e.g. immatures of those species were already in the limbs the first year, then perhaps there are only two true successional stages.

Beetle communities within fine woody debris are also influenced by position of the substrate. Ferro et al. (2009) found that twigs resting on the ground had significantly lower richness than expected from a null distribution, whereas twigs hung 1.5 m above the ground had significantly higher richness than expected. Propped twigs were intermediate. What effect greater heights have on beetle communities in FWD is unknown (but see Ulyshen (2011) for a review of arthropod vertical stratification in temperate forests).

Many more species associated with FWD should be expected. The species accumulation curve for FWD (Fig. 7.2) did not reach an asymptote and was not significantly different from that of CWD (from which 247 species were obtained). In Switzerland Schiegg (2001) collected more beetle species from beech limbs (5-10 cm diameter) than from trunks. Ferro et al. (2009) reviewed community level surveys of Coleoptera in FWD in North America and listed 98 species from prior research and an additional 35 species from their own research, with four species overlapping. The 162 species collected from FWD during this research overlap their list by 10, bringing the total number to 281. Although conducted in different U.S. states, the small overlap of species among these studies indicates that FWD harbors a highly diverse, but largely uncataloged, beetle fauna.

Fine woody debris is an unexplored habitat that contains a rich fauna including important indicators of habitat continuity (Buse 2011), undergoes succession, and is influenced by vertical position. Despite having been largely overlooked, FWD possesses numerous attributes that make it ideal for study even at the masters or undergraduate level. The substrate can be easily standardized and obtained in large quantities to provide numerous replicates. Fine woody debris can be easily collected, transported, quantified, and stored. Collection of animal specimens from FWD using passive traps, such as emergence chambers, provides an accurate quantification of fauna within the substrate (Ferro et al. 2009), and allows for associations of parasites and hosts. Time required to set up a study is minimal, and substrate decay is swift enough that a single study may encompass the entire process.

Coarse Woody Debris. A total of 247 species were collected from CWD, and of those more than half (143) were not collected from FWD (Appendix 3) indicating that the size distinctions used have biological meaning for some species. Blackman and Stage (1924) and Schiegg (2001) both found large differences in insect fauna between FWD (<6-10 cm diameter) and CWD (>6-20 cm diameter) but did not find differences within CWD up to 35 cm diameter. However, Yee et al. (2006) found differences in beetle fauna between logs 30-60 cm diameter and those greater than 100 cm diameter. Limitations within this research prohibited surveying material greater than 20 cm diameter. Possibly, species collected during this research are also representative of those found in larger wood up to some size threshold. A third assemblage of beetles is likely associated with large diameter CWD (>100 cm), including species that occur in no other habitat; whether this is the case will remain a mystery until appropriate studies (*sensu* Grove 2009) are conducted.

The relationship between species richness and decay class was unexpected. The highest species richness was found in CWD2, whereas richness was not significantly different between CWD1 and CWD3-4, implying that richness peaks at an intermediate stage of decay. Hammond et al. (2004) reported a gradual increase in species richness in more advanced stages of decay in quaking aspen, but their most decayed state was not as decayed as CWD3-4 (however, use of different decay stage classifications makes comparisons difficult). Conversely Ulyshen and Hanula (2010) found highest species richness within the first year of death for loblolly pine followed by a large drop in species. In the present study the time since death was not known, so the possibility exists that an initial pulse of species richness was lost or diluted because substrate classified as CWD1 was collected before or after that initial pulse. However, comparisons of saproxylic fauna between hard and softwood may not be appropriate. Savely (1939) reported that oak retained a higher species richness than pine as decay increased.

Species assemblage changed with decay class (Fig. 7.8). Of species present in only two decay classes, 22 species were shared between CWD1 and CWD2, 26 were shared between CWD2 and CWD3-4, but only eight were shared between CWD1 and CWD3-4. The overlap in species decreased with greater difference in decay. Sorensen's quotient of similarity (Table 7.2) also supports this trend; CWD2 is equally similar to CWD1 and CWD3-4 (0.50) but CWD1 is less similar to CWD3-4 (0.45). The high species richness found in CWD2 may be an artifact of an overlap between early and late colonizing species, but may also result from species that are specifically associated with that stage. Of the species available for statistical evaluation (Appendix 3), 14 were associated with CWD2, whereas only four were associated with CWD1 and eight were associated with CWD3-4.

The final decay stage of rotten wood (CWD5) was also sampled for beetles at these locations and was reported in Ferro (see Chapter 6). For that research specimens were collected using a sifting/Berlese technique rather than emergence; therefore, direct comparisons between the two studies may be inappropriate. Ferro (see Chapter 6) collected a total of 111 species from CWD5, of those 54 were only collected in CWD5, and 57 were collected from other classes of CWD (Appendix 3). Despite differences in collection technique, those findings fit well with the patterns already seen among CWD decay classes. Species richness among decay classes peaks at

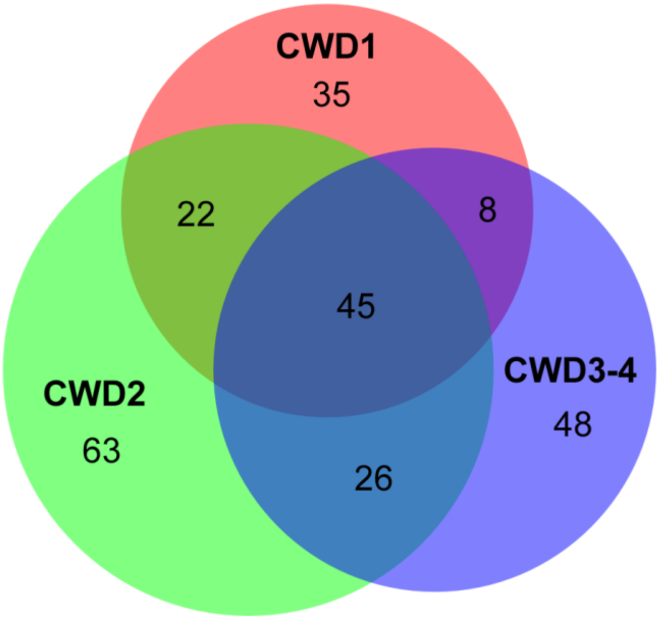

Figure 7.8. Species overlap among CWD decay stages.

CWD2 and decreases with increased decay: 110, 156, 127, and 111, from least- to most-decayed, respectively. Additionally, species overlap decreases with increased difference in decay, e.g. CWD1 shared 67 species with CWD2, 53 species with CWD3-4, and 28 species with CWD5.

The greatest limitation of research on CWD succession is time. As was mentioned above, this research traded substrate standardization for the opportunity to survey substrate that had been dead for a period of time much longer than the length of the study. During succession there is a shift from host plant specificity to habitat specificity (Harmon et al. 1986), so substrate standardization may be more important during the initial stages of decay than at the end, but this is speculative until proper studies are carried out.

Accurate knowledge of dead wood habitat is becoming more important as habitat loss, global climate change, and invasive species alter landscapes. Standardized long-term research experiments such as those at Warra, Tasmania (Grove 2009) and H. J. Andrews Experimental Forest, Oregon (Harmon 1992) are incredibly important. However, they require enormous resources, generally only look at a few tree species, and are only representative of one or a few locations. These limitations and the conflict between substrate standardization and time may seem insurmountable, but could easily be overcome in the following manner. As newly dead trees of interest (because of size, species, mode of death, location, etc.) are encountered they are recorded, tagged, and publicized. Recorded information would include tree species, time of death, mode of death, general dimensions, state of decay (wounded, hollow), and other information as was deemed important. Tagging would involve one or several heavy chains or cables placed around the main trunk and/or large limbs of the tree, each with an attached identification tag. Each tree's information, including location and photographs, would then be made public, either through a central repository on the internet, or through lists maintained by the organizations that manage the land on which the tree grew.

The suggested system would be relatively inexpensive and simple to initiate. Over time parks and preserves would have a growing list of legacy trees that future researchers could request to study, either in an active or passive manner. In actuality the proposed system is already in place in many parks and reserves throughout the world, but at the level of habitat, landscape, quadrat, etc. where rainfall, land use, fire history, etc. are recorded and publicized. Legacy CWD would represent another, finer, layer.

Year. Substrate was quarantined in emergence chambers in spring 2006 and remained so until the end of the study in fall 2007, thus specimens collected the second year are a result of continued emergence. Differences in catch between the first and second years of collection were surprising. Overall species richness (Fig. 7.4) was highest during the first year of emergence (2006) and 95 species were unique to that year. However an additional 77 species were unique to the second year and additional collecting beyond the second year may have yielded more species.

The number of specimens tripled from the first to second year (1575 to 4098). Nine species accounted for 2843 specimens in the 2007 catch, an increase of 2292 specimens from the previous year (Table 7.3). Conditions within emergence chambers may have been favorable for reproduction and some increase may represent a second generation. De Coninck and Coessens (1981) found that *Acrotrichis intermedia* (Gillmeister) (Ptiliidae) reproduced throughout the year with overlap of generations.

However, reproduction is a poor explanation for the occurrence of members of other taxa, such as the genus *Cryptophagus* (Cryptophagidae). It was represented by a single specimen in 2006, but in 2007 specimens were collected from all size and decay classes and totaled 124 specimens. Substrate collection in the spring may provide an appropriate explanation. Individuals of species that overwinter as pupae in the soil would have left the substrate during fall 2005 and be poorly represented in 2006 emergence samples. Those same species present as

Table 7.3. Species represented by an increase of greater than 50 specimens from 2006 to 2007.

Family	Species	2006	2007	Increase
Throscidae	*Aulonothroscus distans* Blanchard	171	959	788
Staphylinidae	*Thoracophorus costalis* (Erichson)	85	771	686
Ptiliidae	*Pteryx* spp.	113	291	178
Curculionidae	*Dryophthorus americanus* Bedel	67	239	172
Eucinetidae	*Tohlezkus inexpectus* Vit	19	144	125
Cryptophagidae	*Cryptophagus* spp.	1	124	123
Ptiliidae	Ptiliidae gen. spp.	26	109	83
Staphylinidae	*Hesperus apicialis* (Say)	60	134	74
Curculionidae	*Caulophilus dubius* Horn	9	72	63

larvae when the substrate was collected would not reach adulthood until the following spring 2007. Variation in the time of substrate collection in future studies may help elucidate the natural history of some species.

Forest. Overall species richness was higher in secondary forest despite collection of an equal number of species between forest types (Fig. 7.3). However, primary forest had more statistically associated species than secondary forest (Appendix 3). Of the 27 species associated with primary forest six were also associated with FWD1, eight with FWD2, three with CWD1, eight with CWD2, and three with CWD3-4. Ferro (see chapter 6) also found more species associated with primary than secondary forest during a survey of the beetle fauna in leaf litter and CWD5 at these same locations. Higher number of associates in primary forests is possibly due to greater volume of habitat, an uninterrupted availability of habitat, or a combination of factors. Of the 16 species associated with secondary forest, three were also associated with FWD1, one with FWD2, one with CWD1, five with CWD2, and two with CWD3-4. In general size and decay classes of woody debris harbor distinct faunas within primary and secondary forests. Subsequent research should be planned with these differences in mind.

Minimally Collected Species. In total 234 species (77%) collected during this research were represented by fewer than 10 specimens, and 115 species (38%) were singletons, species represented by a single specimen (Appendix 3). This is a common occurrence; 32% singletons is average for tropical arthropod surveys (Coddington et al. 2009). Generally these findings are explained as undersampling bias (Coddington et al. 2009) and increased sampling intensity is recommended. Ferro (see Chapter 6) argued that increased sampling will reduce initial singletons at the cost of adding more, and recommended an *a priori* restriction of taxa of interest.

This approach has an extremely important practical application. While appropriate natural history observations are difficult and impractical for many organisms, gross but meaningful statements can be made about organisms based on capture statistics, but only if those species are represented by a threshold number of specimens. A worthwhile endeavor would be to develop sampling protocols designed to reduce the number of "data deficient" species within an *a priori* restricted set.

Taxonomic Considerations. As was mentioned above not all specimens could be identified to the species level. This occurred for three primary reasons: 1) the specimen almost certainly belonged to a named species but was female and keys for the separation of females did not exist; 2) whether the specimen belonged to a named species or an undescribed species was unknown because descriptions of valid species were ambiguous and/or keys to separate species did not exist; and 3) the specimen certainly belonged to an undescribed species and recognized as such by experts, but the species had not been formally described because taxonomic expertise and/or time or other resources were lacking.

Taxonomic uncertainty represents a major impediment to ecological research. An inability to identify species may result in an under- or overestimation of species richness which reduces the value of comparisons within and between studies. Additionally any new information gained about a species from an ecological study is lost if that species cannot be reliably identified. See Carlton and Robison (1998) for a good discussion on the problems of taxonomic difficulties in diversity studies.

Overcoming these difficulties is expensive and time consuming. When female specimens lack morphological characters for reliable identification, molecular techniques such as DNA barcoding may be necessary to distinguish species, but this presumes that accurate barcodes exist for those species. Where valid names exist for inadequately diagnosed species the holotype may have to be consulted and redescribed (see Gusarov 2003e). When a species is recognized as undescribed it should be designated as such in the literature (e.g. *Genus* n.sp. 1) and specimens should be clearly labeled so subsequent taxonomic workers can trace museum specimens through the literature.

An unknown number of undescribed species were collected during this study (see notes below). However, several undescribed species collected as part of this research were recognizable as such and described. Ferro and Carlton (2010) revised the eastern species of the staphylinid genus *Sonoma* and described 15 new species, including three from this study: *S. chouljenkoi* Ferro and Carlton, *S. gilae* Ferro and Carlton, and *S. gimmeli* Ferro and Carlton. Additionally, Park and Carlton (in Park et al. 2010) described four new species of *Leptusa*, including two collected during this research: *L. ferroi* Park and Carlton, and *L. gimmeli* Park and Carlton. While researching *Thoracophorus*, Ferro and Gimmel (see Chapter 3) discovered that *T. longicollis* Motschulsky and *T. fletcheri* Wendeler were junior synonyms of *T. costalis* (Erichson) and synonymized the two names.

Bortolus (2008), Gotelli (2004), and Grove (2003) offered sound advice for ecologists conducting community level research. An inability to appropriately identify study organisms and track them through literature and/or voucher specimens greatly reduces the scale at which ecological questions can be addressed and devalues the potential future contributions of a given study. When conducting community level ecological research, especially where there is a potential to encounter many undescribed or difficult to identify species, special effort should be made to collaborate with taxonomic experts and specific funds should be requested to facilitate taxonomic and/or nomenclatural research.

Related Research. This publication represents a portion of a larger body of research, specifically the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007). This effort has resulted in a suite of publications related by collectors, localities and even specific samples. Simultaneous research was conducted by the same authors at the same localities comparing Coleoptera in CWD5 and leaf litter (see Chapter 8) and flight intercept traps were used to compare their effectiveness at sampling saproxylic Coleoptera with sifting and emergence (see Chapter 6).

The overall research of the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP has resulted in publications on the following taxa: Cantharidae: *Atalantycha* Kazantsev (Kazantsez 2005); Carabidae: *Anillinus* Casey (Sokolov 2011; Sokolov et al. 2004, 2007; Sokolov and Carlton 2008, 2010); Cerylonidae: *Philothermus* Aubé (Gimmel and Slipinski 2007); Chrysomelidae: *Psylliodes* Latreille (Konstantinov and Tishechkin 2004); Leiodidae: *Ptomaphagus* (*Appadelopsis* Gnaspini) (Tishechkin 2007); Mycetophagidae: *Pseudotriphyllus* Reitter (Carlton and Leschen 2009); Staphylinidae: Aleocharinae: *Leptusa* Kraatz (Park et al. 2010); Pselaphinae: *Arianops* Brendel (Carlton 2008); *Reichenbachia* Leach (Carlton 2010); *Sonoma* Casey (Ferro and Carlton 2010).

Conclusion. Woody debris is an important but difficult habitat to study. Use of emergence chambers allowed for collection and association of 305 species with different sizes and decay classes of woody debris. Results indicate that the Coleoptera communities within the five size and decay classes studied are distinct and may harbor numerous undescribed or rarely collected species. Additionally, communities in woody debris differ between primary and secondary forests and this should be recognized when conducting biotic surveys and developing land management policies. Taxonomic expertise and funding are desperately needed to overcome taxonomic difficulties that greatly hinder our ability to describe and understand forest communities. Fine woody debris represents a dynamic but largely overlooked habitat that is ideal for short term ecological studies. Management agencies should recognize large dead trees as long-term high-quality habitat and actively work to capture data on legacy trees that can be studied by future researchers.

7.5 SPECIES ACCOUNTS

Beetle species are generally poorly known and information about their habits often comes from anecdotal evidence or is based on a generalization of the habits of their family, subfamily, tribe, or genus. For example, within the list below specific natural history observations have only been made for two species, *Adranes lecontei* Brendel (Staphylinidae) and *Rhinosimus viridiaeneus* (Randall) (Salpingidae). In this research 71 species were represented by 10 or more individuals and their prevalence between substrates and/or forests is available to statistical interpretation. While not a substitute for proper natural history observations, this does provide gross natural history information and represents a jumping off point for future researchers hoping to study particular species or higher taxa.

When available, information on range, habitat, collection methods, and basic biology of most insects is usually scattered throughout the literature. Below is a summary of the habits of the 71 species represented by 10 or more individuals in this research. Basic biological information is provided for each taxon and important resources with descriptions, keys, distributional data, and biological/life history data are referenced.

ANOBIIDAE

Anobiinae

Oligomerus obtusus LeConte (Fig. 7.9)
Range: northeastern Canada and United States, south to Tennessee, west to Michigan. **Habitat:** reared from beech. **Collection Method:** emergence. **Biology:** unknown other than host plant. **Present Study:** significantly higher abundance in FWD2 and secondary forest. **References:** Blatchley 1910; Champlain and Knull 1922; Downie and Arnett 1996; White 1962, 1976, 1982.

Priobium sericeum (Say) (Fig. 7.10)
Range: northeastern United States, south to Florida, west to Texas, and north to Minnesota. **Habitat:** dead branches of oak, cherry, and hickory, emergent from dry mountain laurel (*Kalmia latifolia* L.), occasionally in flooring and furniture. **Collection Method:** emergence. **Biology:**

unknown other than host plants. **Present Study:** significantly higher abundance in FWD1, CWD1, and primary forest. **References:** Champlain and Knull 1922 (as *Trypopitys sericeus* (Say)); Downie and Arnett 1996; Majka 2007a; Majka et al. 2011; Peck and Thomas 1998; White 1962 (as *T. sericeus*), 1982.

BUPRESTIDAE

Chrysochroinae

Dicerca divaricata (Say) (Fig. 7.11)
Range: northeastern Canada and United States, south to Georgia, west to Texas and North Dakota. **Habitat:** emergent or collected from many trees including maple, American elm, ash, oak, and eastern redbud; collected on but not reared from gymnospermous plant genera. **Collection Method:** emergence. **Biology:** infests heartwood, collected from stumps, polyphagous. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Downie and Arnett 1996; Majka et al. 2011; MacRae 2006; Nelson 1975; Nelson et al. 2008; Packard 1890.

CARABIDAE

Harpalinae

Gastrellarius honestus (Say) (Fig. 7.12)
Range: northeastern Canada and United States, south to South Carolina, west to Michigan. **Habitat:** lowlands and mountains, mixed forests and thickets, in leaf litter, under bark. **Collection Method:** searching under loose bark, pitfall trapping, night searching with a head lamp, emergence. **Biology:** nocturnal, brachypterous, predacious, adults found overwintering in logs, larval habitat in decaying wood. **Present Study:** significantly higher abundance in CWD3-4. **References:** Ball and Bousquet 2001; Blatchley 1910 (as *Pterostichus honestus* Say); Bousquet and Larochelle 1993; Ciegler 2000; Downie and Arnett 1996; Lindroth 1961-1969 (as *P. honestus*); Majka et al. 2011.

Rhysodinae

Clinidium baldufi Bell (Fig. 7.13)
Range: Pennsylvania south to Florida and west to Missouri. **Habitat:** Collected from American chestnut and white oak. **Collection Method:** emergence chamber. **Biology:** under bark of moist rotting wood of logs or stumps, brachypterous. **Present Study:** not significantly associated with any substrate or forest type. **References:** Bell 1970; Bell and Bell 1985; Bousquet and Larochelle 1993; Ciegler 2000; Downie and Arnett 1996; Peck and Thomas 1998.

Trechinae

Mioptachys flavicauda (Say) (Fig. 7.14)
Range: northeastern Canada and United States, south to Florida and west to California. **Habitat:** lowlands, forested areas, under bark, in decaying logs and woodchips. **Collection Method:** searching under loose bark, sifting/Berlese wood chips, carrion traps, emergence. **Biology:** nocturnal, associated with dead and dying hardwood trees, probably capable of flight, predatory, adults overwinter, feeds on mites and springtails. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910 (as *Tachys flavicauda* Say); Bousquet and Larochelle 1993; Ciegler 2000; Downie and Arnett 1996; Lindroth 1961-1969 (as *T. flavicauda*); Majka et al. 2011; Nelson 1991; Peck and Thomas 1998; Ulke 1903 (as *T. flavicauda*).

CERAMBYCIDAE

A taxonomic treatment of all species of Cerambycidae known to occur in North American north of Mexico including keys, descriptions, synonymies, references, parasites, and ecological data was prepared by E. G. Linsley and J. A. Chemsak (Chemsak 1963; Linsley 1961, 1962a,b, 1963, 1964; Linsley and Chemsak 1972, 1976, 1984, 1995, 1997). A host plant index for Cerambycidae is found in Linsley and Chemsak (1997). Keys to species and photographs of all Cerambycidae known from the eastern United States may be found in Lingafelter (2007).

Lamiinae

Eupogonius pauper LeConte (Fig. 7.15)
Range: eastern North America, south to Florida, west to Texas and Kansas. **Habitat:** recorded from 19+ trees, shrubs, and vines including maple, hickory, oak, walnut, ash, cherry, and mulberry. **Collection Method:** emergence. **Biology:** flight period March to August. **Present Study:** significantly higher abundance in FWD1 and secondary forest. **References:** Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1984, 1997; Majka et al. 2011; Peck and Thomas 1998.

Leptostylus transversus (Gyllenhal) (Fig. 7.16)
Range: eastern North America, south to Florida and northeast Mexico, west to Arizona, Kansas, and South Dakota. **Habitat:** recorded from 23+ species of mostly hardwoods including maple, hickory, oak, walnut, ash, cherry, and pine. **Collection Method:** emergence. **Biology:** flight period year round, spring to summer in northern range. **Present Study:** significantly higher abundance in secondary forest. **References:** Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1995, 1997; Peck and Thomas 1998.

Microgoes oculatus (LeConte) (Fig. 7.17)
Range: eastern North America, south to Alabama, west to Illinois. **Habitat:** recorded from many plants including dogwood, beech, oak, cottonwood, hickory, maple, and pine. **Collection Method:** emergence. **Biology:** flight period June to August, feeds under bark and enters wood to pupate. **Present Study:** significantly higher abundance in primary forest. **References:** Turnbow and Thomas 2002; Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1984, 1997; Majka et al. 2011.

Urographis fasciatus (DeGeer) (Fig. 7.18)
Range: eastern North America, south to Florida, west to Texas and Wisconsin. **Habitat:** recorded from 15+ trees including maple, hichory, walnut, oak, elm, and pine. **Collection Method:** emergence. **Biology:** flight period April to September. **Present Study:** significantly higher abundance in primary forest. **References:** Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1995, 1997; Packard 1890; Peck and Thomas 1998.

Lepturinae

Analeptura lineola Say (Fig. 7.19)
Range: eastern North America, south to Florida, west to Ontario. **Habitat:** recorded from birch, hornbeam, *Ostrya virginiana* (Mill.) K.Koch, and pine. **Collection Method:** emergence. **Biology:** flight period May to August, attracted to flowers including goatsbeard, hydrangea, grape, false Solomon's seal. **Present Study:** significantly higher abundance in FWD2. **References:** Turnbow and Thomas 2002; Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1976, 1997; Majka et al. 2011; Peck and Thomas 1998.

Trachysida mutabilis (Newman) (Fig. 7.20)
Range: eastern North America, west to Georgia and Alberta. **Habitat:** recorded from 17+ hardwoods including oak, maple, beech, and elm. **Collection Method:** emergence. **Biology:** flight period April to July, females deposit pink scaly eggs under bark of decaying wood, larvae mine the wood and adults emerge through circular holes. **Present Study:** significantly higher abundance in FWD2, CWD1, and primary forest. **References:** Downie and Arnett 1996; Lingafelter 2007; Linsley and Chemsak 1976, 1997; Majka et al. 2011.

CERYLONIDAE

Cerylon castaneum Say (Fig. 7.21)
Range: northern and eastern North America, British Columbia east to Maine, south to Texas. **Habitat:** under bark of maple, beech, and spruce. **Collection Method:** emergence, searching under bark of dead logs. **Biology:** collected from numerous fungi, larvae collected in July under bark. **Present Study:** significantly higher abundance in primary forest. **References:** Blatchley 1910; Downie and Arnett 1996; Lawrence 1982a; Lawrence and Stephan 1975; Majka et al. 2011.

Mychocerus striatus (Sen Gupta and Crowson) (Fig. 7.22)
Range: North Carolina, Tennessee. **Habitat:** forests, under and in rotten logs, rarely leaf litter. **Collection Method:** sifting/Berlese litter, rotten wood, emergence chamber. **Biology:** larvae and adults possess piercing mouthparts, probably a fungivore, brachypterous. **Ferro et al. (Chap. 6):** significantly more abundant in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in CWD3-4 and secondary forest. **References:** Lawrence 1982a; Lawrence and Stephan 1975 (as *Lapethus striatus* (Sen Gupta and Crowson)); Sen Gupta and Crowson 1973 (as *Lapecautomus striatus* (Sen Gupta and Crowson)).

Philothermus glabriculus (LeConte) (Fig. 7.23)
Range: eastern North America, Ontario and Main south to Florida and west to Texas. **Habitat:** rotten logs, sawdust piles, leaf litter, tree holes, and forest debris. **Collection Method:** searching under bark of dead logs, malt traps, emergence, sifting/Berlese. **Biology:** found under bark of maple, hickory, beech, pine, oak, hemlock, and elm. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Downie and Arnett 1996; Gimmel and Slipinski 2007; Lawrence 1982a; Lawrence and Stephan 1975; Majka et al. 2011; Peck and Thomas 1998.

CIIDAE

Ceracis singularis (Dury) (Fig. 7.24)
Range: eastern North America, south to Florida, west to Texas and Ontario. **Habitat:** collected from fruiting bodies of 18+ fungi, including *Polyporus gilvus* (Schw.) Fries and *Fomes robiniae* (Murrill) Sacc. & D. Sacc. **Collection Method:** emergence. **Biology:** breeds in polypore fungi. **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Downie and Arnett 1996; Lawrence 1967, 1971, 1982b; Peck and Thomas 1998.

Octotemnus laevis Casey (Fig. 7.25)
Range: widespread throughout northern North America from Alaska to Nova Scotia, south into California, Kansas, and Alabama. **Habitat:** recorded from 14+ fungi, especially associated with *Coriolus* spp. **Collection Method:** emergence. **Biology:** breeds in polypore fungi. **Present Study:** significantly higher abundance in FWD1 and primary forest. **References:** Blatchley 1910; Downie and Arnett 1996; Lawrence 1971, 1973, 1982; Majka et al. 2011; Thayer and Lawrence 2002.

CRYPTOPHAGIDAE

Atomaria, Cryptophagus, *and at least four other genera in this family contain undescribed species and need to be revised. Existing literature was inadequate for confident species-level identification.*

***Atomaria* spp.** (Fig. 7.26)
The genus is in need of revision. Between 10 and 70 species are reported from North America (see Majka et al. 2010).
Range: throughout North America. **Habitat:** rotting vegetation, dead wood, mammal dung, mammal nests. **Collection Method:** emergence. **Biology:** feed on fungal spores and hyphae, some species phytophagous. **Present Study:** significantly higher abundance in FWD2. **References:** Blatchley 1910; Bousquet 1990; Downie and Arnett 1996 (usefulness of keys unknown); Leschen 1996; Leschen and Skelley 2002; Majka et al. 2010, 2011.

***Cryptophagus* spp.** (Fig. 7.27)
Between 30 and 40 species are reported from North America. The key provided by Woodroffe and Coombs (1961) is based on limited specimens and may not be reliable.
Range: throughout North America. **Habitat:** leaf litter, rotting wood, mammal nests, with social insects, fungal fruiting bodies. **Collection Method:** emergence, sifting/Berlese. **Biology:** feed on fungal spores and hyphae. **Present Study:** significantly higher abundance in FWD1 and CWD2. **References:** Blatchley 1910; Bousquet 1989, 1990; Downie and Arnett 1996 (usefulness of keys unknown); Leschen 1996; Leschen and Skelley 2002; Majka and Langor 2010; Majka et al. 2011; Peck and Thomas 1998; Woodroffe and Coombs 1961.

CURCULIONIDAE
Cossoninae

Caulophilus dubius (Horn) (Fig. 7.28)
Range: throughout eastern United States: New York to Florida, west to Michigan and Texas. **Habitat:** under bark of dead trees and *Vitus* (grape) vine, in leaf litter and tree holes. **Collection Method:** searching under bark and sifting/Berlese leaf litter and rotten wood, emergence. **Biology:** unknown. **Ferro et al. (Chap. 6):** significantly more abundant in leaf litter and spring, indifferent to forest. **Present Study:** significantly more abundant in FWD1 and primary forest. **References:** Blatchley and Leng 1916 (as *Allomimus dubius* Horn); Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998.

Stenoscelis brevis (Boheman) (Fig. 7.29)
Range: eastern North America, south to Florida, west to Kansas. **Habitat:** under bark, hollow tree, emergent from apple wood. **Collection Method:** sifting/Berlese, emergence. **Biology:** associated with dead hardwood trees. **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Blatchley and Leng 1916; Ciegler 2010; Downie and Arnett 1996; Majka et al. 2011; Packard 1890; Peck and Thomas 1998.

Cryptorhynchinae

Apteromechus ferratus (Say) (Fig. 7.30)
Range: eastern North America south to Florida, west to Michigan and Missouri. **Habitat:** collected from chestnut, sassafras, in branches of red bay, under bark of beech, possibly from oak. **Collection Method:** at lights, emergence. **Biology:** unknown other than host plants. **Present Study:** significantly higher abundance in secondary forest. **References:** Anderson 2002; Blatchley and Leng 1916; Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998; Whitehead 1979.

Cophes fallax (LeConte) (Fig. 7.31)
Cophes *Champion needs to be revised and redefined. The last treatment (Sleeper 1955) does not cover all species in North America.*
Range: eastern North America, south to Florida and west to Texas. **Habitat:** emergent from hickory limbs dead two years and *Cassia* sp., collected from maple, woods trash, hollow tree. **Collection Method:** at lights, sifting, emergence. **Biology:** unknown other than host plants. **Present Study:** significantly higher abundance in FWD1 and primary forest. **References:** Anderson 2002; Blatchley and Leng 1916 (as *Cryptorhynchus fallax* LeConte); Ciegler 2010; Downie and Arnett 1996; Peck and Thomas 1998.

Dryophthorinae

Dryophthorus americanus (Bedel) (Fig. 7.32)
Range: throughout eastern North America. **Habitat:** "very old logs", dead pine, forest litter. **Collection Method:** sifting/Berlese litter, collecting under bark, flight intercept trap, UV light, emergence chamber. **Biology:** breeds under bark of dead pines, winged. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in FWD1, CWD2, and primary forest. **References:** Anderson 2002; Blatchley and Leng 1916; Ciegler 2010; Downie and Arnett 1996; Majka et al. 2011; Peck and Thomas 1998.

Scolytinae

Xyleborus atratus Eichhoff (Fig. 7.33)
Range: eastern North America, south to Florida and west to Texas. **Habitat:** reported from 27+ tree species including hardwoods and softwoods (see Atkinson et al. 1990 for a complete list). **Collection Method:** Lindgren funnel trap with ethanol, MV and UV lights, emergence. **Biology:** introduced species from Asia, first collected in North America in 1988. **Present Study:** not significantly associated with any substrate or forest type. **References:** Atkinson et al. 1990; Downie and Arnett 1996; Majka et al. 2011; Peck and Thomas 1998; Vandenberg et al. 2000.

Xylosandrus crassiusculus (Motschulsky) (Fig. 7.34)
Range: northeastern United States, west to Texas. **Habitat:** attacks landscape and nursery stock. **Collection Method:** emergence, Frontalin-baited trap. **Biology:** introduced species from Asia, reported to attack cut or injured trees 1.5 cm diameter to large logs. **Present Study:** significantly higher abundance in secondary forest. **References:** Peck and Thomas 1998; Rabaglia 2003; Wood 1982 (and references therein).

Xylosandrus germanus (Blandford) (Fig. 7.35)
Range: northeastern United States, west to Illinois, south to Tennessee. **Habitat:** inhabits unthrifty branches, boles, and stumps of a wide variety of hosts. **Collection Method:** emergence, traps. **Biology:** introduced species from Asia, generally attacks injured or dying trees, but will attack seemingly healthy trees as well, Hoffmann (1941) provides data on life history within the United States. **Present Study:** significantly higher abundance in FWD1 and primary forest. **References:** Downie and Arnett 1996; Hoffmann 1941; Majka et al. 2011; Peck and Thomas 1998; Rabaglia 2003; Wood 1982.

Xyloterinus politus (Say) (Fig. 7.36)
Range: eastern North America, south to Florida, west to Minnesota. **Habitat:** numerous hardwoods including maple, hickory, beech, oak, elm, occasionally pine. **Collection Method:** emergence, traps. **Biology:** monogamous. **Present Study:** significantly higher abundance in CWD1 and primary forest. **References:** Anderson 2002; Downie and Arnett 1996; Majka et al. 2011; Wood 1982.

ELATERIDAE

Elateridae is the ninth most diverse family of beetles in the world but is poorly known and most North American genera are in need of revision (see Johnson 2002b). Three species of Ampedus *Dejean are highlighted below. No comprehensive key exists to separate the 71 species of* Ampedus *known from North America. Partial keys may be found in the following: LeConte (1853, 1884) (as* Elater *L.); Van Dyke (1932) (as* Elater *"cordifer group"); Blatchley(1910) (Indiana and surrounding states); Dietrich (1945) (northeastern United States); Brooks (1960) (central Canada); Lane 1971 (Pacific Northwest); and Downie and Arnett 1996 (northeastern North America).An unpublished thesis (Ramberg 1979) may be helpful to anyone wishing to revise this genus.*

Ampedus areolatus (Say) (Fig. 7.37)
Range: northeastern United States, south to Tennessee, west to Wyoming. **Habitat:** poorly known. **Collection Method:** collected at lights, emergence, beaten from vegetation at the margins of low woods. **Biology:** poorly known. **Present Study:** significantly higher abundance in CWD2 and primary forest. **References:** Blatchley 1910 (as *Elater areolatus* Say); Dietrich 1945; Downie and Arnett 1996; LeConte 1853 (as *E. areolatus*); Majka and Johnson 2008; Majka et al. 2011; Peck and Thomas 1998.

Ampedus luteolus (LeConte) (Fig. 7.38)
Range: northeastern United States, south to Tennessee, west to Indiana. **Habitat:** poorly known. **Collection Method:** beating foliage, emergence. **Biology:** poorly known. **Present Study:** not significantly associated with any substrate or forest type. **References:** Dietrich 1945; Downie and Arnett 1996; LeConte 1853 (as *Elater luteolus* LeConte).

Ampedus semicinctus (Randall) (Fig. 7.39)
Range: northeastern United States, south to Tennessee, west to Indiana. **Habitat:** collected in spruce, pine, hemlock, and fir forests. **Collection Method:** emergence. **Biology:** collected under loose pine bark and beating oak. **Present Study:** not significantly associated with any substrate or forest type. **References:** Dietrich 1945; Downie and Arnett 1996; LeConte 1853 (as *Elater semicinctus* Randall); Majka and Johnson 2008; Majka et al. 2011.

ENDOMYCHIDAE

Bystus ulkei (Crotch) (Fig. 7.40)
Range: eastern United States, Pennsylvania south to Florida, west to Missouri. **Habitat:** collected from old fungus-covered logs. **Collection Method:** emergence. **Biology:** poorly known. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910 (as *Rhymbus ulkei* (Crotch)); Boving and Craighead 1930 (as *R. ulkei);* Crotch 1873 (as *Alexia ulkei* Crotch); Peck and Thomas 1998; Shockley et al. 2009; Strohecker 1986.

EUCINETIDAE

Tohlezkus inexpectus Vit (Fig. 7.41)
Range: Sevier Co., Tennessee, and Macon Co., North Carolina. **Habitat:** rotten wood, very rarely in leaf litter. **Collection Method:** dung trap, sifting/Berlese litter and CWD5, emergence chamber. **Biology:** adults have unique suctorial mouthparts, possibly feed on slime molds. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, primary forest, and spring; previously known from five specimens (Vit 1995 and C. E. Carlton collection). **Present Study:** significantly higher abundance in FWD2, CWD3-4, and primary forest. **References:** Vit 1995.

EUCNEMIDAE

Isarthrus rufipes (Melsheimer) (Fig. 7.42)
Range: northeastern North America, south to Georgia, west to Oklahoma. **Habitat:** emergent from badly decayed beech and caught running on beech. **Collection Method:** emergence, malaise trap. **Biology:** overwinter as larvae. **Present Study:** significantly higher abundance in

primary forest. **References:** Downie and Arnett 1996 (as *Dromaeolus rufipes* (Melsheimer)); Dury 1888 (as *Deltometopus rufipes* (Melsheimer)); Knull 1947 (as *Del. rufipes*); Muona 2000.

Isorhipis obliqua (Say) (Fig. 7.43)
Range: northeastern North America, south to Georgia, west to Texas and Wyoming. **Habitat:** in deciduous and spruce forests, emergent from beech, elm, birch, and heartwood of decayed maple. **Collection Method:** emergence, flight intercept trap. **Biology:** larvae bore from sapwood to heartwood and return to surface to pupate, adults and immatures overwinter, pupal stage is very short, may produce mating swarms. **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Downie and Arnett 1996; Knull 1946; Majka 2007b; Majka et al. 2011; Muona 2000; Peck and Thomas 1998; Peterson 1960 (illustrated larva).

Melasis pectinicornis Melsheimer (Fig. 7.44)
Range: northeastern North America, south to Florida, west to Louisiana. **Habitat:** reported from maple, blackgum, oak, elm, birch, and beech. **Collection Method:** emergence. **Biology:** under bark of fallen maple and blackgum, emergent from dead birch and beech. **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Blatchley 1910; Downie and Arnett 1996; Dury 1888; Hopping 1926; Kirk 1922; Muona 2000; Peck and Thomas 1998; Peterson 1960 (illustrated larva).

Microrhagus subsinuatus LeConte (Fig. 7.45)
Range: northeastern North America, south to North Carolina, west to Wisconsin. **Habitat:** emergence from dead decayed beech, collected from alder, swept from milkweed. **Collection Method:** emergence, flight intercept trap, on vegetation. **Biology:** reported to be active on dead beech in daytime in June. **Present Study:** not significantly associated with any substrate or forest type. **References:** Downie and Arnett 1996; Dury 1888; Knull 1946 (as *Dirhagus imperfectus* (LeConte)); Majka 2007; Majka et al. 2011; Muona 2000.

HISTERIDAE

Many genera within this family are in need of revision. Keys do not exist for most species.

Bacanius tantillus LeConte (Fig. 7.46)
Range: probably throughout eastern United States, reported from Pennsylvania, New York, Indiana, Tennessee, and Louisiana. **Habitat:** reported from leaf litter and decaying wood. **Collection Method:** emergence, sifting/Berlese. **Biology:** reported from dry organic debris in tree cavities and sawdust piles, feeds mainly on fungal spores. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Casey 1893 (key to most species); Downie and Arnett 1996; Horn 1873; Kovarik and Caterino 2002; Peck and Thomas 1998; Wenzel 1960.

LEIODIDAE

Leiodinae

***Agathidium* spp.** (female) (Fig. 7.47)
This genus was represented in this research by males of four identifiable species; however none of the males were represented by more than 10 specimens. Information provided below is about the genus. **Range:** throughout eastern United States and worldwide. **Habitat:** high humidity locations, forests, leaf litter, dead wood. **Collection Method:** collection and dissection of slime molds (warming a slime mold in the laboratory will cause adults to move and become visible), sifting/Berlese leaf litter and dead wood, flight intercept traps, emergence chamber. **Biology:** winged and wingless species, strongly associated with slime molds (Myxomycetes), Wheeler and Miller (2005) provide a list of host associations for numerous species. **Ferro et al. (Chap. 6):** significantly higher abundance in leaf litter and primary forest, indifferent to season. **Present Study:** significantly higher abundance in primary forest. **References:** Blatchley 1910; Downie and Arnett 1996 (key out of date); Majka et al. 2011; Miller and Wheeler 2005; Peck and Thomas 1998; Wheeler and Miller 2005.

MELANDRYIDAE

Many genera within this family are in need of revision. Keys do not exist for most species.

Dircaea liturata (LeConte) (Fig. 7.48)
Range: north eastern North America, south to Tennessee, west to Missouri. **Habitat:** collected on moss of beech and maple trees, under dead maple bark. **Collection Method:** emergence. **Biology:** members of this tribe are considered xylophagous. **Present Study:** significantly higher abundance in primary forest. **References:** Blatchley 1910 (as *Phloeotrya quadrimaculata* Say); Downie and Arnett 1996; Felt 1906 (as *Phloeotrya liturata* LeConte); Majka et al. 2011; Peck and Thomas 1998; Pollock 2002a.

Hypulus simulator Newman (Fig. 7.49)
Range: northeastern North America south to Mississippi. **Habitat:** poorly known. **Collection Method:** emergence. **Biology:** poorly known. **Present Study:** not significantly associated with any substrate or forest type. **References:** Downie and Arnett 1996 (as *Mystaxus simulator* Newman); Majka et al. 2011; Packard 1890; Pollock 2002a.

PTILIIDAE

Ptiliidae is one of the least known families of Coleoptera. Most genera are in need of revision and many genera and species remain to be described. Until genera are revised identification to species will remain difficult or impossible.

Ptiliidae gen. spp. (Fig. 7.50)
Range: throughout North America. **Habitat:** moist areas with decaying plant and animal matter. **Collection Method:** sifting/Berlese organic material, flight intercept trap, emergence chamber. **Biology:** probably general detritivores. **Present Study:** significantly higher abundance in FWD2, CWD2, and primary forest. **References:** Blatchley 1910; Downie and Arnett 1996; Dybas 1990; Hall 2001.

Acrotrichinae

***Acrotrichis* spp.** (Fig. 7.51)
Range: throughout North America. **Habitat:** leaf litter, decaying logs, tree holes, fungi, animal dung, under bark, moist decaying organic matter. **Collection Method:** sifting/Berlese organic material, flight intercept trap, emergence chamber. **Biology:** De Coninck and Coessens (1981) studied *Acrotrichis intermedia* (Gillmeister): probably general detritivore, adults live about 150 days and produce ~10 eggs each, probably reproduction takes place throughout the year with overlap of generations. **Ferro et al. (Chap. 6):** significantly higher abundance in leaf litter, primary forest, and fall. **Present Study:** significantly higher abundance in CWD2 and primary forest. **References:** Blatchley 1910 (as *Trichopteryx* Kirby and Spence); De Coninck and Coessens 1981; Downie and Arnett 1996; Dybas 1990; Hall 2001; Peck and Thomas 1998.

Ptiliinae

***Pteryx* spp.** (Fig. 7.52)
Range: throughout North America. **Habitat:** forest floor debris, tree holes, logs, sphagnum bogs. **Collection Method:** sifting/Berlese organic material, emergence chamber. **Biology:** probably general detritivore. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, indifferent to forest type or season. **Present Study:** significantly higher abundance in FWD2, CWD2, and primary forest. **References:** Blatchley 1910; Downie and Arnett 1996; Dybas 1990; Hall 2001; Majka et al. 2011.

PYROCHROIDAE

Dendroides canadensis Latreille (Fig. 7.53)
Range: eastern North America, south to Florida, west to North Dakota. **Habitat:** larvae subcortical on the upper side of dead logs. **Collection Method:** at lights, beating foliage, emergence. **Biology:** reared larvae required wood inoculated by fungi to fully develop but could survive on sterilized wood, larval predators include millipedes, Elateridae larvae, and fly larvae, larvae are attached by the parasite *Zelia vertebrata* (Say) (Diptera: Tachinidae). **Present Study:** significantly higher abundance in FWD2, CWD2, and primary forest. **References:** Downie and Arnett 1996; Majka et al. 2011; Payne 1931; Peck and Thomas 1998; Young 1975, 1983, 2002.

Dendroides concolor (Newman) (Fig. 7.54)
Range: eastern North America, south to Tennessee, west to Minnesota. **Habitat:** larvae subcortical on the lower side of logs. **Collection Method:** at lights, beating foliage, emergence. **Biology:** swarming in males reported. **Present Study:** significantly higher abundance in primary forest. **References:** Blatchley 1910; Downie and Arnett 1996; MacGillivray and Houghton 1902; Majka et al. 2011; Packard 1890; Young 1975, 1983, 2002.

SALPINGIDAE

Rhinosimus viridiaeneus (Randall) (Fig. 7.55)
Range: northern North America from British Columbia to Maine, south to Indiana and Tennessee. **Habitat:** damp, shaded sites in association with dead wood, hanging dead leaves, moss, under lichens. **Collection Method:** beating dead branches, emergence. **Biology:** adults feed on bark of unthrifty alder and maple twigs, larvae feed on inner brown bark (see Howden and Howden (1981) notes on life history). **Present Study:** significantly higher abundance in FWD1 and primary forest. **References:** Blair 1932; Blatchley 1910; Downie and Arnett 1996; Howden and Howden 1981; Majka et al. 2011; Pollock 2002b.

STAPHYLINIDAE

Aleocharinae

Aleocharinae gen. sp. (Fig. 7.56)
These specimens could not be reliably identified to genus. Aleocharinae is the largest subfamily of Staphylinidae with 21 tribes, 183 genera, and 1385 described species known from North America and is badly in need of a comprehensive revision. See Newton et al. (2001) and references therein, for further information about this subfamily.
Range: throughout North America. **Habitat:** ubiquitous in terrestrial habitats. **Collection Method:** sifting/Berlese organic material, pitfall traps, bait traps, UV light, emergence chamber. **Biology:** virtually every mode of life (many very specialized) is known in this subfamily: free living, parasitic, herbivore, carnivore, fungivore, flier, walker, runner, swimmer, social, solitary, etc., but life history is almost unknown at the species level. **Ferro et al. (Chap. 6):** indifferent to substrate, forest type, and season. **Present Study:** significantly higher abundance FWD1, CWD2, and primary forest. **References:** Downie and Arnett 1996; Newton et al. 2001.

Athetini gen. spp. (Fig. 7.57)
These specimens could only be reliably identified to Athetini, which is a very large difficult tribe. Seevers (1978) characterization of the tribe and genera is inadequate. Currently 64 genera are recognized within the tribe in North America (Newton et al. 2001) but a complete revision is needed. Gusarov (2002a-e, 2003a-e, 2004a-b) has greatly contributed to our knowledge of many genera and Elven et al (2010) provided the first molecular phylogeny of the tribe, but more work needs to be done.

Range: throughout North America. **Habitat:** ubiquitous; decaying plants and animals, dung, bird and mammal nests, riparian areas, ant nests, under bark and logs. **Collection Method:** sifting/Berlese organic material, emergence. **Biology:** unknown; predators. **Ferro et al. (Chap. 6):** significantly higher abundance in leaf litter and spring, indifferent to forest type. **Present Study:** not significantly associated with any substrate or forest type. **References:** Downie and Arnett 1996; Elven et al. 2010; Gusarov 2002a-e, 2003a-e, 2004a-b; Newton et al. 2001; Seevers 1978.

Atheta spp. (Fig. 7.58)
These specimens could only be reliably identified to the genus Atheta *Thomson. Gusarov (2003) discussed the varying definitions of the genus and reviewed the types of the known species. Newton et al. (2001) report 176 species known in North America (as* Xenota *Mulsant and Rey).*
Range: throughout North America. **Habitat:** ubiquitous; decaying plants and animals, dung, bird and mammal nests, riparian areas, ant nests, under bark and logs. **Collection Method:** sifting/Berlese organic material, flight intercept trap, emergence. **Biology:** unknown, predators. **Present Study:** significantly higher abundance in CWD2 and primary forest. **References:** Blatchley 1910; Downie and Arnett 1996 (as *Xenota* sp.); Gusarov 2003e; Majka et al. 2011; Newton et al. (2001) (as *Xenota* sp.); Peck and Thomas 1998.

Leptusa carolinensis Pace (Fig. 7.59)
Range: northeastern North America south to North Carolina, west to Quebec. **Habitat:** occurs in sugar maple, red spruce, black spruce, and young, mature, and old growth red spruce/hemlock forests. **Collection Method:** pitfall traps, flight intercept traps, emergence. **Biology:** found under bark of beech, under maple log, in bracket fungi, associated with woody debris. **Present Study:** not significantly associated with any substrate or forest type. **References:** Gouix and Klimaszewski 2007; Klimaszewski et al. 2004; Pace 1989; Park et al. 2010; Webster et al. 2009.

Leptusa cribratula (Casey) (Fig. 7.60)
Range: northeastern North America south to Florida, west to Ohio. **Habitat:** poorly known. **Collection Method:** hand collecting, emergence. **Biology:** collected from under pine bark, associated with woody debris, adults have been collected year round. (Pace (1989) reported Casey (1906) taking this species under bark of old chestnuts, but no mention of this could be found.) **Present Study:** not significantly associated with any substrate or forest type. **References:** Casey 1906 (as *Ulitusa cribratula* Casey); Downie and Arnett 1996; Gouix and Klimaszewski 2007; Klimaszewski et al. 2004.

Leptusa pusio (Casey) (Fig. 7.61)
Range: Ohio, Tennessee. **Habitat:** forest leaf litter. **Collection Method:** sifting leaf litter (with Berlese funnel), and collected from dead wood with emergence chamber. **Biology:** unknown. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, primary forest, and spring. **Present Study:** significantly higher abundance in primary forest. **References:** Downie and Arnett 1996; Gusarov 2003e; Park et al. 2010.

***Leptusa* spp.** (Fig. 7.62)
Ten species of Leptusa *are known from GSMNP. Despite the revision by Park et al. (2010) some specimens could only be reliably identified to genus.*
Range: eastern United States. **Habitat:** forest leaf litter, rotten wood. **Collection Method:** sifting leaf litter (with Berlese funnel), and collected from dead wood with emergence chamber. **Biology:** unknown. **Ferro et al. (Chap. 6):** indifferent to substrate, forest type and season. **Present Study:** not significantly abundant in any subsamples. This is almost certainly a reflection of the habits of multiple species represented by these specimens. **References:** Blatchley 1910; Downie and Arnett 1996; Newton et al. 2001; Park et al. 2010.

Osoriinae

Thoracophorus costalis (Erichson) (Fig. 7.63)
Range: throughout eastern North America: New Jersey to Florida, west to Louisiana and Illinois. **Habitat:** under bark, in dead wood, forest litter. **Collection Method:** sifting litter, debris, and dead wood (with Berlese funnel), emergence chamber. **Biology:** unknown. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in FWD2, CWD3-4, and primary forest. **References:** Blatchley 1910; Downie and Arnett 1996 (figure is not *T. costalis*); Ferro and Gimmel (see Chapter 3); Horn 1871 (as *Glyptoma costale* Erichson, figure and key to common species in North America); Irmler 1985; Notman 1920; Majka et al. 2011; Peck and Thomas 1998.

Pselaphinae

Adranes lecontei Brendel (Fig. 7.64)
Range: Kentucky, Mississippi, New York, Pennsylvania, Tennessee. **Habitat:** lives in nests of *Lasius* spp. ants (Hymenoptera: Formicidae); nests have been found in beech logs in advance stages of decay. **Collection Method:** sifting *Lasius* spp. ant nests, rarely sifting/Berlese forest litter. **Biology:** obligate myrmecophile on *Lasius* spp. ants; adults feed on fluids obtained from their adult and immature hosts; possibly feed on dead immature ants; see Park (1932a) and Akre and Hill (1973) for interesting behavioral observations of the genus. **Ferro et al. (Chap. 6):** significantly higher abundance in secondary forest, indifferent to substrate or season, probably heavily influenced by their host. **Present Study:** significantly higher abundance in CWD3-4 and secondary forest. **References:** Akre and Hill 1973; Blatchley 1910; Downie and Arnett 1996; Hill et al. 1976; Newton et al. 2001; Park 1932a (with notes on life history), 1935, 1964; Wickham 1901.

***Batrisodes* spp.** (female) (Fig. 7.65)
Female Batrisodes *Reitter cannot be reliably identified. These female specimens are probably representative of the twelve described and five undescribed species that have been collected in GSMNP.*
Range: eastern North America. **Habitat:** within this genus some members are found in leaf litter, mosses, and rotten wood, others are associated with ants or troglobites. **Collection**

Method: sifting/Berlese litter, emergence. **Biology:** poorly known, but see Park (1932b) about feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte). **Ferro et al. (Chap. 6):** indifferent to substrate, forest type, and season. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Chandler 1990a; Downie and Arnett 1996; Park 1932b, 1947a, 1948; Majka et al. 2011; Newton et al. 2001; Peck and Thomas 1998.

Leptoplectus pertenuis (Casey) (Fig. 7.66)
Range: eastern United States, Pennsylvania south to Florida, west to Iowa. **Habitat:** reported from log mold, tree holes, and sawdust. **Collection Method:** sifting/Berlese, emergence. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in FWD2 and CWD3-4. **References:** Grigarick and Schuster 1980; Newton et al. 2001; Peck and Thomas 1998; Wagner 1975.

***Pycnoplectus* spp**. (female) (Fig. 7.67)
Female Pycnoplectus *Casey cannot be reliably identified. These female specimens are probably representative of the three species that have been collected in GSMNP.*
Range: northeastern North America, south to Florida, west to Oklahoma and Michigan. **Habitat:** log mold, stump mold, tree holes, and leaf litter. **Collection Method:** sifting/Berlese, at lights, emergence. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** not significantly associated with any substrate or forest type. **References:** Chandler 1990a; Grigarick and Schuster 1980; Newton et al. 2001; Peck and Thomas 1998; Wagner 1975.

***Sonoma* spp.** (female) (Fig. 7.68)
Female Sonoma *Casey cannot be reliably identified. These female specimens are probably representative of the eight described species that have been collected in GSMNP.*
Range: central eastern and western United States. **Habitat:** leaf litter, rhododendron litter, rotten wood. **Collection Method:** sifting litter and rotten wood (with Berlese funnel), Lindgren funnel, Malaise trap, flight intercept trap, rarely at UV light, emergence chamber. **Biology:** unknown, members of this subfamily are predacious. **Ferro et al. (Chap. 6):** significantly higher abundance in CWD5, indifferent to forest type and season. **Present Study:** significantly higher abundance in CWD3-4. **References:** Chandler 1990a; Downie and Arnett 1996; Ferro and Carlton 2010; Newton et al. 2001.

Trimioplectus obsoletus Brendel (Fig. 7.69)
Range: Pennsylvania south to North Carolina, west to Illinois. **Habitat:** rotting wood and tree holes. **Collection Method:** sifting/Berlese, emergence. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Brendel and Wickham 1890; Chandler 1990b; Grigarick and Schuster 1980; Park 1949.

Scydmaeninae

Nearly all the genera in the subfamily Scydmaeninae are in need of revision. Many have numerous undescribed species and/or have not been treated in the last 50-100 years. Until genera are revised identification to species will remain difficult or impossible. See O'Keefe (2001) (and references therein) and Grebennikov and Newton (2009) for up-to-date literature on the subfamily.

***Euconnus* (*Napochus*) spp.** Thomson (Fig. 7.70)
***Euconnus* (*Scopophus*) n. sp.** Casey (Fig. 7.71)
***Euconnus* (*Scopophus*) spp.** Casey (Fig. 7.72)
Range: mostly midwest, northeast, andsSoutheastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection Method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Ferro et al. (Chap. 6):** only *Euconnus* (*Napochus*) sp. was found in significantly higher abundance in leaf litter and secondary forest. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Downie and Arnett 1996 (usefulness of keys uncertain); Grebennikov and Newton 2009; O'Keefe 2001; Majka et al. 2011; Peck and Thomas 1998.

Staphylininae

Hesperus apicialis (Say) (Fig. 7.73)
Range: northeastern North America, southern Quebec south to Florida, west to Kansas and Nebraska. **Habitat:** found on old trees, fermenting sap under bark of oak, decaying wood of old fallen trees. **Collection Method:** at lights, malt trap, sifting/Berlese, emergence. **Biology:** poorly known. **Present Study:** significantly higher abundance in primary forest. **References:** Blatchley 1910 (as *Hesperus apicalis* (Say)); Downie and Arnett 1996 (as *H. apicalis*); Frank 1983; Horn 1884 (as *Philonthus apicalis* (Say)); Majka et al. 2011; Moore 1958; Peck and Thomas 1998; Smetana 1995.

Tachyporinae

Sepedophilus brachypterus Campbell (Fig. 7.74)
Range: eastern North America from Maine south to Mississippi, west to Texas and Iowa. **Habitat:** in leaf litter, wood trash, on fungus, underside of log. **Collection Method:** sifting/Berlese, emergence. **Biology:** recorded from undetermined Agaricales. **Present Study:** significantly higher abundance in CWD3-4 and primary forest. **References:** Campbell 1976; Downie and Arnett 1996; Majka et al. 2011; Newton 1984.

Sepedophilus cinctulus (Erichson) (Fig. 7.75)
Range: northeastern North America, south to Mississippi, west to Kansas. **Habitat:** specimens have been taken from under loose bark, mushrooms, dead logs, and trees holes. **Collection Method:** sifting/Berlese, emergence. **Biology:** this species is recorded from 8+ fungi and slime

mold species (see Newton 1984). **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Campbell 1976; Downie and Arnett 1996; Majka et al. 2011; Newton 1984.

Sepedophilus occultus (Casey) (Fig. 7.76)
Range: northeastern United States south to Mississippi, west to Iowa. **Habitat:** taken from under bark, brush pile, sifting humus. **Collection Method:** sifting/Berlese, emergence. **Biology:** members of this genus are considered mycetophagous. **Present Study:** not significantly associated with any substrate or forest type. **References:** Campbell 1976; Downie and Arnett 1996.

TENEBRIONIDAE

***Hymenorus* spp.** (female) (Fig. 7.77)
There are about 100 species of this genus known from North America. The last treatment was by Fall (1931). This genus is in need of revision. Natural history notes refer to the genus as a whole.
Range: widespread throughout North America. **Habitat:** generally associated with decaying hard and soft wood. **Collection Method:** flight intercept trap, emergence, at lights, Lindgren funnel. **Biology:** poorly known. **Present Study:** not significantly associated with any substrate or forest type. **References:** Fall 1931; Downie and Arnett 1996; Dunford and Young 2004; Majka et al. 2008, 2011; Packard 1890; Peck and Thomas 1998; Steiner 2008.

Strongylium crenatum Maklin (Fig. 7.78)
Range: Tennessee south to Florida, west to Texas and Ohio. **Habitat:** emergent from decayed ash log and moist decayed persimmon. **Collection Method:** tanglefoot screen, emergence. **Biology:** poorly known. **Present Study:** significantly higher abundance in secondary forest. **References:** Downie and Arnett 1996; Peck and Thomas 1998; Triplehorn and Spilman 1973.

THROSCIDAE

Aulonothroscus distans Blanchard (Fig. 7.79)
The entire family, including this genus, is in need of revision.
Range: reported from Massachusetts, New York, North Carolina, and Tennessee. **Habitat:** unknown. **Collection Method:** emergence. **Biology:** unknown, adults of the family are thought to be generalist pollen and mold feeders. **Present Study:** significantly higher abundance in FWD1, CWD1, and secondary forest. **References:** Blanchard 1917; Downie and Arnett 1996; Johnson 2002a.

Figure 7.9-7.14. Habitus images. 7.9) *Oligomerus obtusus* LeConte (Anobiidae: Anobiinae). 7.10) *Priobium sericeum* (Say) (Anobiidae: Anobiinae). 7.11) *Dicerca divaricata* (Say) (Buprestidae: Chrysochroinae). 7.12) *Gastrellarius honestus* (Say) (Carabidae: Harpalinae). 7.13) *Clinidium baldufi* Bell (Carabidae: Rhysodinae). 7.14) *Mioptachys flavicauda* (Say) (Carabidae: Trechinae).

Figure 7.15-7.20. Habitus images. 7.15) *Eupogonius pauper* LeConte (Cerambycidae: Lamiinae). 7.16) *Leptostylus transversus* (Gyllenhal) (Cerambycidae: Lamiinae). 7.17) *Microgoes oculatus* (LeConte) (Cerambycidae: Lamiinae). 7.18) *Urographis fasciatus* (Degeer) (Cerambycidae: Lamiinae). 7.19) *Analeptura lineola* Say (Cerambycidae: Lepturinae). 7.20) *Trachysida mutabilis* (Newman) (Cerambycidae: Lepturinae).

Figure 7.21-7.26. Habitus images. 7.21) *Cerylon castaneum* Say (Cerylonidae). 7.22) *Mychocerus striatus* (Sen Gupta and Crowson) (Cerylonidae). 7.23) *Philothermus glabriculus* (LeConte) (Cerylonidae). 7.24) *Ceracis singularis* (Dury) (Ciidae). 7.25) *Octotemnus laevis* Casey (Ciidae). 7.26) *Atomaria* sp. (Cryptophagidae).

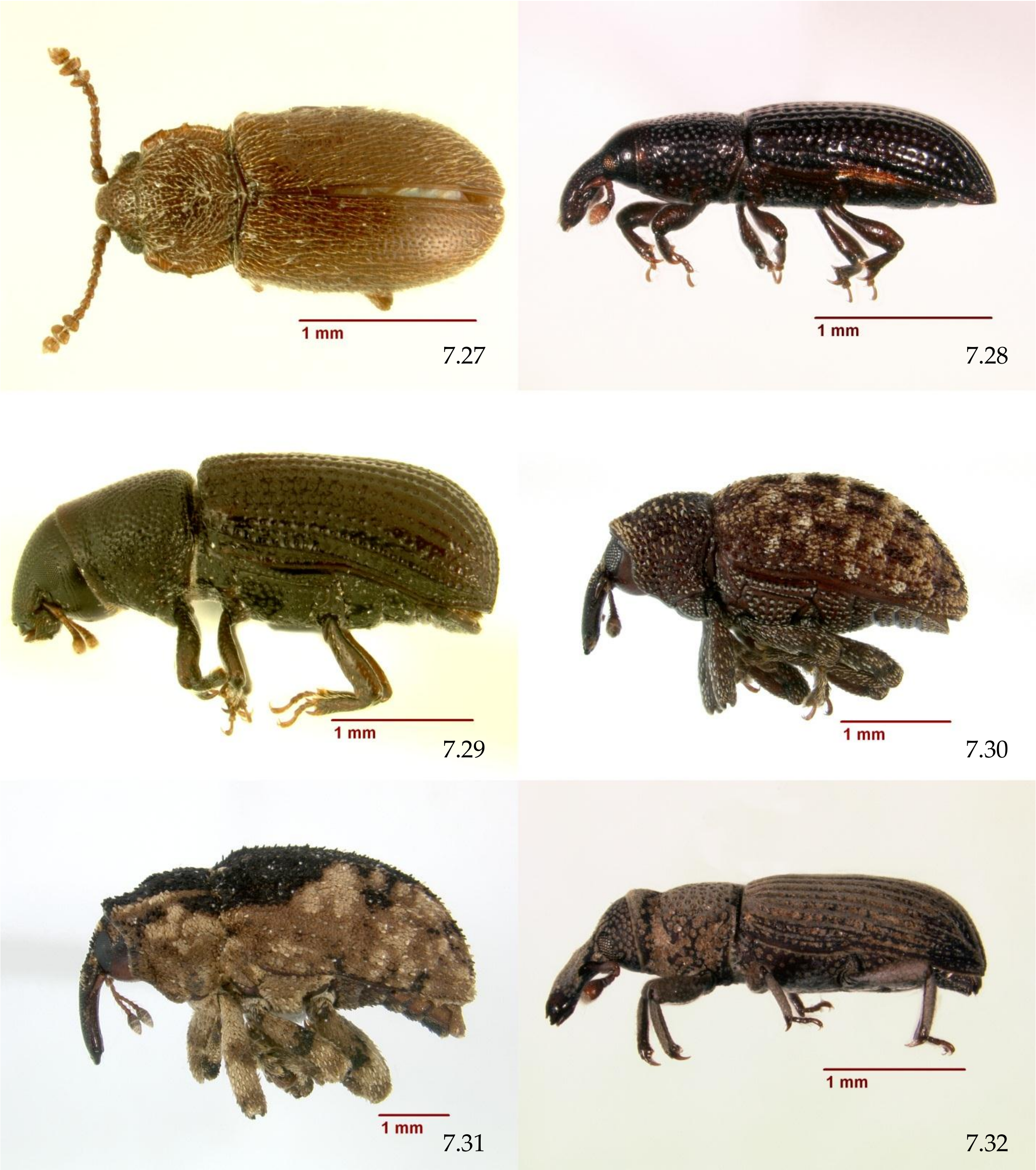

Figure 7.27-7.32. Habitus images. 7.27) *Cryptophagus* sp. (Cryptophagidae). 7.28) *Caulophilus dubius* (Horn) (Curculionidae: Cossoninae). 7.29) *Stenoscelis brevis* (Boheman) (Curculionidae: Cossoninae). 7.30) *Apteromechus ferratus* (Say) (Curculionidae: Cryptorhynchinae). 7.31) *Cophes fallax* (LeConte) (Curculionidae: Cryptorhynchinae). 7.32) *Dryophthorus americanus* (Bedel) (Curculionidae: Dryophthorinae).

Figure 7.33-7.38. Habitus images. 7.33) *Xyleborus atratus* Eichhoff (Curculionidae: Scolytinae). 7.34) *Xylosandrus crassiusculus* (Motschulsky) (Curculionidae: Scolytinae). 7.35) *Xylosandrus germanus* (Blandford) (Curculionidae: Scolytinae). 7.36) *Xyloterinus politus* (Say) (Curculionidae: Scolytinae). 7.37) *Ampedus areolatus* (Say) (Elateridae). 7.38) *Ampedus luteolus* (LeConte) (Elateridae).

Figure 7.39-7.44. Habitus images. 7.39) *Ampedus semicinctus* (Randall) (Elateridae). 7.40) *Bystus ulkei* (Crotch) (Endomychidae). 7.41) *Tohlezkus inexpectus* Vit (Eucinetidae). 7.42) *Isarthrus rufipes* (Melsheimer) (Eucnemidae). 7.43) *Isorhipis obliqua* (Say) (Eucnemidae). 7.44) *Melasis pectinicornis* Melsheimer (Eucnemidae).

Figure 7.45-7.50. Habitus images. 7.45) *Microrhagus subsinuatus* LeConte (Eucnemidae). 7.46) *Bacanius tantillus* LeConte (Histeridae). 7.47) *Agathidium* sp. (female) (Leiodidae: Leiodinae). 7.48) *Dircaea liturata* (LeConte) (Melandryidae). 7.49) *Hypulus simulator* Newman (Melandryidae). 7.50) Ptiliidae gen. sp. (Ptiliidae).

Figure 7.51-7.56. Habitus images. 7.51) *Acrotrichis* sp. (Ptiliidae: Acrotrichinae). 7.52) *Pteryx* sp. (Ptiliidae: Ptiliinae). 7.53) *Dendroides canadensis* Latreille (Pyrochroidae). 7.54) *Dendroides concolor* (Newman) (Pyrochroidae). 7.55) *Rhinosimus viridiaeneus* (Randall) (Salpingidae). 7.56) Aleocharinae gen. sp. (Staphylinidae: Aleocharinae).

Figure7. 57-7.62. Habitus images. 7.57) Athetini sp. (Staphylinidae: Aleocharinae). 7.58) *Atheta* sp. (Staphylinidae: Aleocharinae). 7.59) *Leptusa carolinensis* Pace (Staphylinidae: Aleocharinae). 7.60) *Leptusa cribratula* (Casey) (Staphylinidae: Aleocharinae). 7.61) *Leptusa pusio* (Casey) (Staphylinidae: Aleocharinae). 7.62) *Leptusa* spp. (Staphylinidae: Aleocharinae).

Figure 7.63-7.68. Habitus images. 7.63) *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae). 7.64) *Adranes lecontei* Brendel (Staphylinidae: Pselaphinae). 7.65) *Batrisodes* sp. (female) (Staphylinidae: Pselaphinae). 7.66) *Leptoplectus pertenuis* (Casey) (Staphylinidae: Pselaphinae). 7.67) *Pycnoplectus* sp. (female) (Staphylinidae: Pselaphinae). 7.68) *Sonoma* sp. (female) (Staphylinidae: Pselaphinae).

Figure 7.69-7.74. Habitus images. 7.69) *Trimioplectus obsoletus* Brendel (Staphylinidae: Pselaphinae). 7.70) *Euconnus* (*Napochus*) sp. (Staphylinidae: Scydmaeninae). 7.71) *Euconnus* (*Scopophus*) n. sp. (Staphylinidae: Scydmaeninae). 7.72) *Euconnus* (*Scopophus*) sp. (Staphylinidae: Scydmaeninae). 7.73) *Hesperus apicialis* (Say) (Staphylinidae: Tachyporinae). 7.74) *Sepedophilus brachypterus* Campbell (Staphylinidae: Tachyporinae).

Figure 7.75-7.79. Habitus images. 7.75) *Sepedophilus cinctulus* (Erichson) (Staphylinidae: Tachyporinae). 7.76) *Sepedophilus occultus* (Casey) (Staphylinidae: Tachyporinae). 7.77) *Hymenorus* spp. (female) (Tenebrionidae). 7.78) *Strongylium crenatum* Maklin (Tenebrionidae). 7.79) *Aulonothroscus distans* Blanchard (Throscidae).

CHAPTER 8: COMPARISON OF COLLECTION TECHNIQUES FOR CAPTURE OF COLEOPTERA, WITH AN EMPHASIS ON SAPROXYLIC SPECIES, IN GREAT SMOKY MOUNTAINS NATIONAL PARK, USA

8.1. INTRODUCTION

Concerning conservation of biodiversity, Aldo Leopold (1949) once admonished, "To keep every cog and wheel is the first precaution of intelligent tinkering." However, from a practical standpoint, an inventory of the "cogs" and "wheels" (species) at a location, in a community, or within a habitat can be quite daunting, especially for entomologists. The large number and similarity of many species, difficulty of identification of immature forms, relatively short adult life spans, wide variety of micro-niches, and apparent scarcity of some species all contrive to make full inventories difficult.

Habitat and collection method have a major influence over which species and how many specimens are collected. Hammond (1990), in his overview of early results from Project Wallace, where more than 1,000,000 tropical beetle specimens were collected using a wide variety of techniques, reported that 60% of species were collected from only one type of sample. Siitonen (1994) found that window traps collected more saproxylic beetle species associated with a wider variety of habitats than subcortical hand sampling in a northern Finland forest. Hammond (1997) found that window traps and emergence collections showed taxon bias when used to collect arthropods in a Canadian forest. Window traps collected 204 beetle species whereas emergence collected 161 and a 42% overlap of species between the two surveys was documented. Ranius and Jansson (2002) surveyed beetles in hollow oaks using pitfall traps, window traps, and hand searching through wood mold. They found significant differences in catch among the three collection methods despite limiting themselves to a very specific habitat that occupies a relatively small volume. Window traps collected a greater number and wider variety (based on microhabitat group) of species, but under-sampled eight species compared to the other methods. Touroult et al. (2010) compared seven methods used to collect longhorn beetles (Cerambycidae) in French Guiana. They found that time was an important factor in determining the efficiency of methods; emergence and flight intercept trapping (FIT) was most efficient during long studies, whereas direct collection (beating, hand collection) was most efficient during very short studies.

Species inventories and other comparative research are generally conducted by obtaining specimens (physical or observational) through "collecting" or "sampling" and here we differentiate the two activities. Collecting is a broad term for procuring specimens in any fashion or variety of fashions. It may be systematic, standardized, haphazard, eclectic, or serendipitous. Often specimens or groups of specimens obtained through collecting cannot be compared in any statistical sense to other groups, but this does not reduce the value of non-standardized collecting, which is vitally important for inventories, exploration of microhabitats, and obtaining specimens for taxonomic use.

However, often due to the nature of the question being asked, collecting *sensu lato* may not be appropriate and sampling, a type of collecting, must be employed. A sample is the subset representative of a larger set of entities (known as the "target statistical population") (Dauffy-Richard et al. 2009). A sample is more than the specimens obtained; it also contains information important for standardization (e.g., concerning scale, technique, effort, etc.) so that samples can be compared with one another, and meaningful statements, such as extrapolations, can be made about a total. Samples also help to overcome collector bias. Conducting appropriate ecological studies without "sampling" may be impossible, and for the remainder of this study the term "sample" is used in this strict sense.

These designations are meant to emphasize that general collecting and sampling are both important tools but are generally appropriate for answering different questions. Nageleisen and Bouget (2009, and chapters therein) provided an excellent overview of general considerations and techniques used for conducting inventories of insects in forests. They emphasized the need to develop *a priori* a sampling protocol designed to answer the specific question being asked. Additionally they stressed that observations should be, above all, biologically meaningful, and that any sampling design and statistics should be based on the question being asked, not vice versa.

Generally, no biotic inventory will yield a full census of species from an area and inventories are often constrained by limited resources. Attempts to maximize inventory returns by discovering the best habitat from which to collect, and/or most efficient collection method (based on some criteria, such as least use of resources or maximum number of species collected) are important. However, quantitative comparisons of catch among habitats and/or collection methods are challenging because standardization of methods is difficult. Commonly, surveys of different habitats or different collection methods can be compared only in relation to a single axis at a time, such as total cost, cost per species, time, materials, etc.

We standardized collections for this research by considering each to represent one "survey activity," a unit of sample that represents a reasonable collecting or sampling effort that uses a particular protocol to survey one or many habitats with one or many collection methods at a given location. In this research each survey activity is composed of a single collection method. Thus, while the collection method, habitat(s), type of samples, number of samples, and time of year differed among survey activities, each represents an independent, appropriate biotic survey and can be compared as such.

Concurrent research conducted at six sites in Great Smoky Mountains National Park (GSMNP), Tennessee, provided a unique opportunity to compare survey activities used to inventory Coleoptera. Ferro et al. (see Chapter 6) surveyed Coleoptera in two habitats, leaf litter and hardwood coarse woody debris decay class V, using a sifting/Berlese funneling (sifting/Berlese) collection method. Three samples of each substrate were taken at each location during Fall of 2006 and again Spring 2007 (total of 12 samples at each site). They collected a total of 2069 specimens and 128 species from both habitats combined at the two sites surveyed during this study.

Ferro et al. (see Chapter 7) used emergence chambers to survey saproxylic Coleoptera emergent from the general woody debris habitat. Three samples of each of the following were taken at each study site during April 2006: fine woody debris decay class I and decay class II; coarse woody debris decay class I; decay class II; and decay classes III and IV combined (total of 15 samples at each site). Each sample consisted of enough substrate to fill a 68-L emergence chamber three-fourths of its capacity. Chambers were sealed and specimens emergent from dead wood were collected over a two year period. They collected a total of 2630 specimens and 190 species at the two sites surveyed during this study.

The purpose of this research was to compare Coleoptera obtained from a survey activity using short-term FITs with those from sifting/Berlese and emergence survey activities. A secondary goal was to determine if short-term FITs could be substituted for emergence when attempting to collect saproxylic Coleoptera.

8.2. MATERIAL AND METHODS

Study Area. Great Smoky Mountains National Park was established in 1934, named as an International Biosphere Reserve in 1976, and a World Heritage Site in 1983. It encompasses 211,000 ha (521,490 acres) in Tennessee and North Carolina, USA. Five major forest communities are recognized in the park, though 80% may be broadly classified as eastern deciduous forest (Houk and Collier 1993). The eastern half of the park contains the largest remaining tract of old growth forest in the eastern U.S. (Davis 1996). See Chapter 7 for more details.

Study Sites. Overstory vegetation data were obtained from Madden (Geospatial Dataset-1047498), and understory vegetation data were obtained from Madden (Geospatial Dataset-1047499); see Welch et al. (2002) and Madden et al. (2004) for a description of how data were collected. Geology data were obtained from National Park Service (2006). Vegetation disturbance history data were obtained from National Park Service (2007). Data on forest type in 1938 were obtained from National Park Service (2009). Three locations within each study site were surveyed using a point relascope sampling technique (Brissette et al. 2003; Gove et al. 1999). Findings were averaged to obtain volume of CWD per hectare at each study site.

Collections took place at two locations in GSMNP:

1) Porters Creek (TN: Sevier Co.: N35˚40.790′ W83˚23.855′). The site was on Thunderhead Sandstone, has an acid cove forest overstory, and a medium rhododendron understory. Vegetation disturbance was light cut and during a 1938 survey this location was designated as cove hardwood. Coarse woody debris volume was 290 m^3/ha. Because of the history of minimal disturbance this site is referred to as "primary forest."

2) Greenbrier (TN: Sevier Co.: N35˚43.147′ W83˚23.349′). The site was on Roaring Fork Sandstone, has a successional hardwood overstory, and an herbaceous/deciduous understory. Vegetation disturbance was settlement class and during a 1938 survey this location was designated as grassland. Coarse woody debris volume was 143 m^3/ha. Because of the history of disturbance (heavily logged) this site is referred to as "secondary forest."

Sampling. Three ground-level FITs (see Schauff 2001 for basic design) were erected at each site on 1 July 2007 and removed on 8 July 2007. Each trap consisted of a vertical mesh pane 1 m high and 3 m long, a plastic horizontal rain fly 1 m wide and 3 m long, and eight collection containers with a combined collection surface of 1830 cm^2. Propylene glycol antifreeze (Prestone® Low Tox™ brand) was used as a killing and preserving agent. Position of traps was based on convenience, not based on proximity to snags or logs.

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 (primarily Arnett and Thomas (2001) and Arnett et al. (2002) and references therein, plus additional literature as needed), and/or comparison with authoritatively identified reference specimens. Specimens are deposited in the Louisiana State Arthropod Museum (LSAM), LSU AgCenter, Baton Rouge, Louisiana, and Great Smoky Mountains Natural History Museum (GSNP), Gatlinburg, Tennessee.

Data analysis. Individual-based rarefaction curves were used to compare species richness among survey activities (Gotelli and Colwell 2001). Curves were constructed using code developed by MLF and KEH and run in the R programming environment (R Development Core Team 2010). For each subset, 1000 rarefaction curves were created, an average curve and its 95% confidence limits were derived from the simulations, and a significant deviation from the simulated average occurred when an observed value fell outside the confidence interval. Each rarefaction curve is shown with a combination of these three lines and an average curve that lies outside the confidence interval of another curve can be considered different at least at the α=0.05 level.

Capture similarity was assessed using Sorensen's quotient of similarity (Southwood 1978).

8.3. RESULTS

A total of 2472 adult beetle specimens, representing 217 lowest identifiable taxa within 164 genera and 42 families, were collected during the FIT survey activity. Of the 217 lowest identifiable taxa, 8 were identifiable only to family or tribe, 48 were identifiable only to genus, and 162 were identified to species (Appendix 4). Groups only identified to family, tribe, or genus may contain multiple species. For the remainder of the results and discussion all lowest identifiable taxa will be referred to as "species" in an attempt to reduce jargon and increase readability.

Staphylinidae was, by a wide margin, the most species rich family collected from the FIT survey activity with 66 species, followed by Leiodidae (25 spp.), Elateridae (11 spp.), and Curculionidae (10 spp.). Sixteen families were represented by a single species. Five species were represented by more than 100 specimens, and 87 species (40%) were singletons.

At the Porters Creek site 1393 adult beetle specimens, representing 131 species within 107 genera and 34 families, were collected. At the Greenbrier site 1079 adult beetle specimens, representing 160 species within 126 genera and 34 families, were collected.

Species richness based on species accumulation curve comparisons (Fig. 8.1.) was highest for all survey activity combined, followed by FIT, emergence, and lastly sifting/Berlese. All were significantly different from one another.

Sorensen's quotient of similarity for collection methods showed least similarity between sifting/Berlese and FIT (0.20), intermediate similarity between sifting/Berlese and emergence (0.22), and highest similarity between emergence and FIT (0.27).

8.4. DISCUSSION

All survey activities combined yielded 413 beetle species. The FIT survey collected 2472 specimens and 217 beetle species, compared to 2630 specimens and 190 species from the emergence survey, and 2069 specimens and 128 species from the sifting/Berlese survey (Appendix 4). Emergence and FIT surveys shared the most species (55, 16%) while sifting and

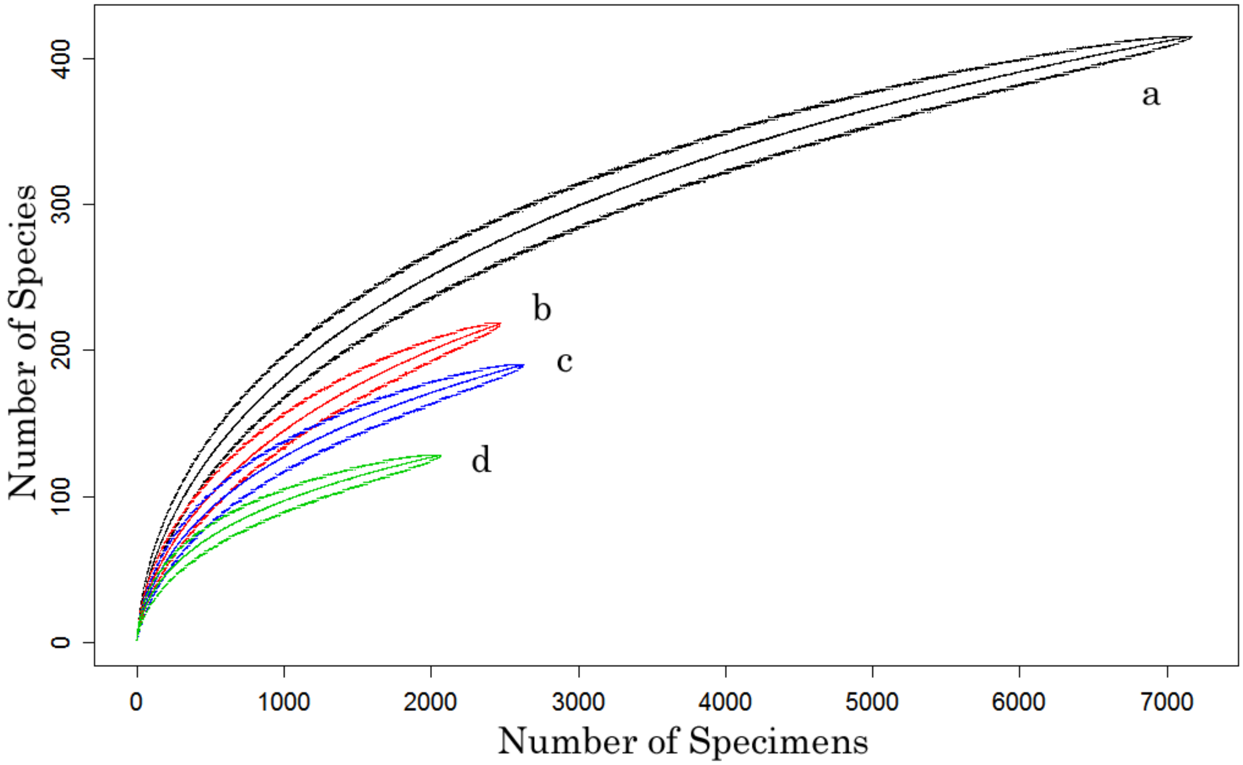

Figure 8.1. Species accumulation curves for a: all survey activities combined; b: FIT activity; c: emergence activity; d: sift/Berlese activity.

FIT surveys shared the fewest species (34, 11%) (Fig. 8.2.). Only 15 species (4%) were collected in all three surveys. In total 80% of species were collected in only a single survey activity. Hammond (1990) reported 60% of beetle species collected from a single collection type, but collected many more specimens (1,000,000+) and used a wider variety of survey activities.

The species accumulation curve for all surveys combined was significantly higher than any single survey activity. The individual influences of either habitat or collection method cannot be assessed based on this study, but it is clear that variation of those factors significantly increases species richness.

Of individual survey activities, the FIT survey collected significantly higher species richness than any other survey (Fig. 8.1.). However, surveys had low similarity, ranging from 0.20 to 0.27, which showed that each was about equally dissimilar from all others. Therefore, substitution of one survey activity for another would be ineffective at recovering similar species.

Saproxylic Coleoptera. Other researchers (Hammond 1997; Siitonen 1994) reported a wide overlap of saproxylic beetle species between flight intercept traps and other collection methods. However, their intercept traps were generally much smaller and placed immediately against target habitat such as snags. Additionally they trapped over a much longer period time, up to eight months over a two year period.

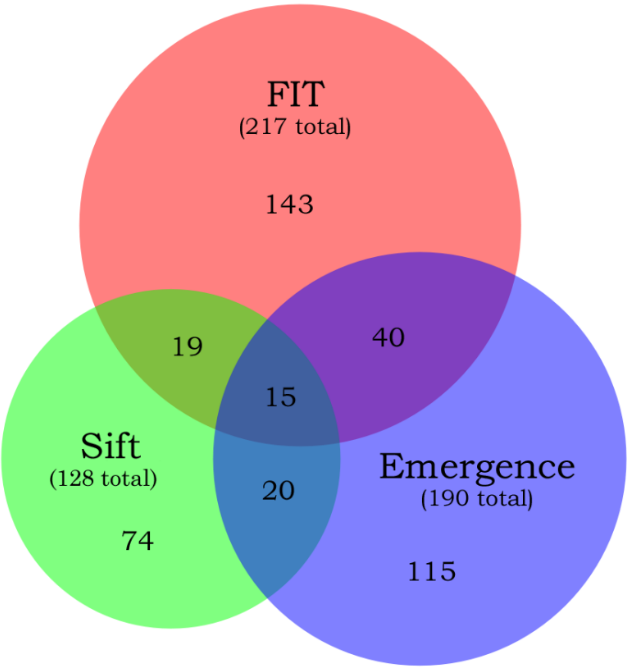

Figure 8.2. Species overlap among survey activities. Size of circle is proportional to species richness.

Within this research, most families with a high proportion of saproxylic species were poorly represented in the FIT survey compared to the emergence survey. However, Leiodidae, Mordellidae, and Nitidulidae, families with some saproxylic species, were better represented in the FIT survey than either emergence or sifting/Berlese surveys (Appendix 4). Overlap of catch between the FIT and emergence surveys was too low to justify substitution. Therefore, an appropriate survey activity composed of the FIT collection protocol used in this research is not an effective alternative to emergence surveys when attempting to collect saproxylic Coleoptera.

Related Research. This publication represents a portion of a larger body of research, specifically the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007). See Chapter 7 for a list of publications resultant from this research.

Conclusion. An accurate survey of the Coleoptera in a given area is difficult owing to the wide variety of species and their habits. The three separate survey activities utilizing different collection methods and targeting different habitats resulted in the total collection of 7171 specimens and 413 beetle species at two sites in GSMNP. However, there was very little overlap in catch among survey activities, indicating that a variety of survey activities would increase catch richness, and that substitution of one survey activity for another will not yield similar species.

CHAPTER 9: SUMMARY

In eastern North America dead wood is still largely an unexplored habitat. Elucidation of the species that require dead wood is at an early stage. Taxonomy precedes ecology and taxonomic work of any scale makes a lasting contribution. Descriptions of unknown species, clarification of identities of known species, identification keys, and natural history observations are needed for many taxa. The taxonomic portions of this study described 15 new species associated with dead wood, and clarified the identity of another dead wood associate. Even these small steps will make a lasting impression on future biotic surveys and ecological studies.

Collection of additional specimens of undescribed species with accompanying locality and habitat information will aid future workers in taxonomic endeavors. The current research advertised areas where taxonomic knowledge was lacking, something generally only known to specialists. As our taxonomic ignorance becomes better known more researchers and land managers will seek funds for taxonomic research, and more granting agencies should be willing to provide funds for taxonomic research.

The studies conducted during this research are a far cry from the early comprehensive works of Packard (1890), Felt (1906), Blatchley (1910), and Blackman and Stage (1918, 1924). However, where those studies excelled in the comprehensive treatment of their respective subjects, the studies conducted during this research offer better quantification of samples and habitats, and a wider treatment of beetle taxa associated with dead wood. Additionally, these current studies highlighted otherwise overlooked habitats such as fine woody debris and extremely decayed downed coarse woody debris. Now that researchers, land managers, and conservationists are aware that these habitats contain unique communities, they can be studied and managed more appropriately.

Study of the succession of organisms in dead wood is difficult because of the time required. This research documented succession of beetles in dead wood by sampling substrate in different stages of decay, showing that otherwise lengthy studies can be conducted in shorter periods of time. Many species collected during this research were documented from a specific habitat for the first time. Use of emergence chambers to survey beetles is cheap, fast, and provides natural history information for the species collected. Emergence chambers are important tools for future forest surveys and can be used to compare saproxylic species among habitats ranging from intact forests ("reference" forests) to highly managed areas such as tree plantations. Using the sifting and emergence protocols outlined in this work a comprehensive survey of the common beetles found in various decay stages of dead wood in eastern North America could be performed by a few dedicated, appropriately funded researchers in less than a decade.

When represented by a sufficient number of specimens, species collected during this research were photographed and notes on their biology were summarized. In some ways this level of treatment moved beyond the early works that imaged few species and tended to emphasize species of economic importance. Advances in technology, particularly digital photography and electronic disseminate of information, make the possibility of photographs and species accounts, complete with links to original works, for every species of saproxylic beetle a real possibility.

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APPENDIX 1. 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	*Discotenes nigrotuberculata* (Schaeffer, 1904)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Anthribidae	*Ischnocerus infuscatus* Fahraeus, 1839	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Anthribidae	*Ormiscus eusphyroides* (Schaeffer, 1906)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Bostrichidae	*Amphicerus* sp.	*Prosopis glandulosa* Torr. var. *glandulosa*	Average 9.1 mm	Associated with twigs girdled by *Oncideres rhodosticta* Bates (Cerambycidae)	TX	Polk and Ueckert 1973
Bostrichidae	*Xylobiops basilaris* (Say)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Bostrichidae	*Xylobiops* sp.	*Prosopis glandulosa* Torr. var. *glandulosa*	Average 9.1 mm	Live twig girdled by parent	TX	Polk and Ueckert 1973
Bostrichidae	2 spp.	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	*Acmaeodera neoneglecta* Fisher, 1949	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Buprestidae	*Agrilus neoprosopidis* Knull, 1938	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	*Agrilus otiosus* Say, 1833	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Anthaxia quercata* (Fabricius, 1801)	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	*Anthaxia viridicornis* (Say, 1823)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Anthaxia viridifrons* Gory, 1841	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Chrysobothris analis* LeConte, 1860	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Buprestidae	*Chrysobothris dentipes* (Germar, 1824)	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	*Chrysobothris femorata* (Olivier, 1790)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Chrysobothris rotundicollis* Gory & Laporte, 1837 [as *Chrysobothris blanchardi*	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	Horn]					
Buprestidae	*Chrysobothris sexsignata* Say, 1839	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Chrysobothris sexsignata* Say, 1839	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Buprestidae	*Dicerca lurida* (Fabricius, 1775)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Buprestidae	*Phaenops fulvoguttata* (Harris, 1829) [as *Melanophila fulvoguttata* (Harris)]	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	*Achryson surinamum* (Linnaeus, 1767)			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Achryson surinamum* (Linnaeus, 1767)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Aegomorphus modestus* (Gyllenhal, 1817) [as *A. dicipiens* Haldeman]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Anelaphus debilis* (LeConte, 1854)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Anelaphus inermis*			Associated with twigs		Linsley

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	(Newman, 1840) [as *Anoplium truncatum* LeConte]			girdled by *Oncideres pustulata* LeConte (Cerambycidae)		1940
Cerambycidae	*Astylopsis sexguttata* (Say, 1826) [as *Leptostylus sex-guttatus* (Say)]	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	*Ataxia crypta* (Say, 1831)			Associated with twigs girdled by *Oncideres cingulata texana* Horn (Cerambycidae)		Linsley 1940
Cerambycidae	*Cyrtophorus verrucosus* (Olivier, 1795)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Dorcaschema cinereum* (Olivier, 1795) [as *Hetoemis cinerea* (Olivier)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Dorcaschema nigrum* (Say, 1826)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Eburia mutica* LeConte, 1853	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Ecyrus arcuatus* Gahan, 1892 [as *Ecyrus texanus* Schaeffer]			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Euderces reichei* LeConte,			Associated with twigs		Linsley

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	1873 [as *Euderces exilis* Casey]			girdled by *Oncideres pustulata* LeConte (Cerambycidae)		1940
Cerambycidae	*Euderces picipes* (Fabricius, 1787)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Geropa concolor* (LeConte, 1873) [as *Achryson concolor* LeConte]			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Geropa concolor* (LeConte, 1873)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Gnaphalodes trachyderoides* Thomson, 1860	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Heterachthes quadrimaculatus* Haldeman, 1847	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Anelaphus villosus* (Fabricius, 1792) [as *Hypermallus villosus* (Fabricius)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Knulliana cincta* (Drury, 1773) [as *Chion cinctus* Drury]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Lepturges angulatus* (LeConte, 1852) [as	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres*	TX	Hovore and

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	Lepturges angulatus canus Casey]			*pustulata* LeConte (Cerambycidae)		Penrose 1982
Cerambycidae	*Lepturges infilatus* Bates, 1872	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Liopinus* nr. *alpha* (Say, 1827) [as *Leiopus* nr. *alpha* (Say)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Liopinus mimeticus* (Casey, 1891) [as *Leiopus houstoni* Casey and *Leiopus texana* Casey]			Associated with twigs girdled by *Oncideres pustulata* LeConte and *O. cingulata texana* Horn (Cerambycidae)		Linsley 1940
Cerambycidae	*Liopinus mimeticus* (Casey, 1891) [as *Sternidius mimeticus* (Casey) and *Sternidius texanus* (Casey)]	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Liopinus wiltii* (Horn, 1880) [as *Leiopus wiltii* Horn]			Associated with twigs girdled by *Oncideres pustulata* LeConte and *O. cingulata texana* Horn (Cerambycidae)		Linsley 1940
Cerambycidae	*Lochmaeocles cornuticeps cornuticeps* Schaeffer, 1906	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Molorchus bimaculatus* Say, 1824	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say	NY	Blackman and Stage

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
				(Scolytinae)		1924
Cerambycidae	*Neoclytus acuminatus* (Fabricius, 1775)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Neoclytus leucozonus* Laporte & Gory, 1835 [as *Neoclytus longipes* (Kirby)]	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Cerambycidae	*Neocompsa exclamationis* (Thomson, 1860) [as *Ibidion exclamationis* Thomson]			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Neocompsa exclamationis* (Thomson, 1860)	*Leucaena pulverulenta* (Schltdl.) Benth.	56 mm	Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Neocompsa mexicana* (Thomson, 1865) [as *Ibidion townsendi* Linell]			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Neocompsa mexicana* (Thomson, 1865)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Obrium maculatum* (Olivier, 1795)			Associated with twigs girdled by *Oncideres pustulata* LeConte and *O. cingulata texana* Horn (Cerambycidae)		Linsley 1940
Cerambycidae	*Obrium maculatum*	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs	TX	Hovore

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	(Olivier, 1795)			girdled by *Oncideres pustulata* LeConte (Cerambycidae)		and Penrose 1982
Cerambycidae	*Obrium mozinnae* Linell, 1897	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Oncideres cingulata texana* Horn, 1885 [as *Oncideres texana* Horn]	*Acacia*, probably also *Prosopis* and *Ebenopsis* [as *Pithecolobium*]		Live twig girdled by parent		Linsley 1940
Cerambycidae	*Oncideres pustulata* LeConte, 1854	*Acacia farnesiana* (L.) Willd., *Ebenopsis ebano* (Berl.) Barneby & Grimes [as *Pithecolobium flexicaulis* (Benth.) J.M. Coult.], *Prosopis glandulosa* Torr., *Acacia berlandieri* Benth., *Parkinsonia aculeata* L., *Mimosa aculeaticarpa* Ortega [as *Mimosa lindheimeri* A. Gray]	20 - 40 mm	Live twig girdled by parent		Linsley 1940
Cerambycidae	*Oncideres pustulata* LeConte, 1854	*Leucaena pulverulenta* (Schltdl.) Benth.		Live twig girdled by parent	TX	Hovore and Penrose 1982
Cerambycidae	*Oncideres rhodosticta* Bates, 1885	*Prosopis glandulosa* Torr. var. *glandulosa*	Average 9.1 mm	Live twig girdled by parent	TX	Polk and Ueckert 1973
Cerambycidae	*Placosternus difficilis* (Chevrolat, 1862)			Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)		Linsley 1940
Cerambycidae	*Pogonocherus mixtus* Haldeman, 1847	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
						1918
Cerambycidae	*Psyrassa unicolor* (Randall, 1838) [as *Pseudibidion unicolor* (Randall)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Purpuricenus axillaris* Haldeman, 1847	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Saperda discoidea* Fabricius, 1798	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Sphaenothecus bivittata* Dupont, 1838			Associated with twigs girdled by *Oncideres cingulata texana* Horn (Cerambycidae)		Linsley 1940
Cerambycidae	*Sphaenothecus bivittata* Dupont, 1838 [as *Taranomis bivittata bivittata* (Dupont)]	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Stenosphenus lugens* LeConte, 1862	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Stenosphenus notatus* (Olivier, 1795)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Thryallis undatus* (Chevrolat, 1834)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Cerambycidae	*Trachyderes mandibularis* (Dupont in Audinet-Serville, 1834) [as *Dendrobias mandibularis* (Audinet-Serville)]	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Urgleptes celtis* (Schaeffer, 1905)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cerambycidae	*Urgleptes querci* (Fitch, 1858) [as *Lepturges querci* (Fitch)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cerambycidae	*Xylotrechus colonus* (Fabricius, 1775)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	*Chariessa pilosa* (Forster, 1771)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	*Cymatodera inornata* (Say, 1835)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	*Enoclerus quadrisignatus* (Say, 1835)	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cleridae	*Enoclerus* sp.	*Prosopis glandulosa* Torr. var. *glandulosa*	Average 9.1 mm	Associated with twigs girdled by *Oncideres rhodosticta* Bates (Cerambycidae)	TX	Polk and Ueckert 1973
Cleridae	*Madoniella dislocatus*	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown	NY	Blackman

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
	(Say, 1825) [as *Phyllobaenus dislocatus* (Say)]			cause		and Stage 1918
Cleridae	*Madoniella dislocatus* (Say, 1825) [as *Phyllobaenus dislocatus* (Say)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	*Monophylla pallipes* Schaeffer, 1908	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Cleridae	*Monophylla terminata* (Say, 1835)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Cleridae	*Pyticeroides laticornis* (Say, 1835) [as *Neichnea laticornis* (Say)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Chramesus hicoriae* LeConte, 1868	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Cophes fallax* (LeConte, 1876) [as *Cryptorhynchus fallax* LeConte]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Hylocurus rudis* (LeConte, 1876) [as *Hylocurus biorbis* Blackman]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Magdalis olyra* (Herbst, 1797)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Curculionidae	*Magdalis pandura* (Say, 1831)	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Polygraphus rufipennis* (Kirby, 1837)	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Curculionidae	*Sciaphilus asperatus* (Bonsdorff, 1785) [as *Sciaphilus muricatus* (Fabricius)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Curculionidae	*Scolytus piceae* (Swaine, 1910) [as *Eccoptogaster piceae* Swaine]	*Larix laricina* (Du Roi) K. Koch.	2.5 – 5 cm	Dead tree, unknown cause	NY	Blackman and Stage 1918
Curculionidae	*Scolytus quadrispinosus* Say, 1824 [as *Eccoptogaster quadrispinosus* (Say)]	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm		NY	Blackman and Stage 1924
Melandryidae	*Orchesia castanea* Melsheimer, 1846	*Carya glabra* (Mill.) Sweet [as *Hicoria glabra* Mill.]	< 6.4 cm	Tree killed by *Scolytus quadrispinosus* Say (Scolytinae)	NY	Blackman and Stage 1924
Mordellidae	1 sp.	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982
Tenebrionidae	1 sp.	*Leucaena pulverulenta* (Schltdl.) Benth.		Associated with twigs girdled by *Oncideres pustulata* LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

Appendix 1 cont.

Coleoptera family	Coleoptera species	Plant species	Substrate diameter	Substrate origin	State	Reference
Trogossitidae	Temnoscheila sp.	*Leucaena pulverulenta (Schltdl.) Benth.*		Associated with twigs girdled by Oncideres pustulata LeConte (Cerambycidae)	TX	Hovore and Penrose 1982

APPENDIX 2. LIST OF TAXA AND NUMBER OF SPECIMENS COLLECTED FROM LEAF LITTER AND CWD5

Chi-square goodness of fit testing was performed for all taxa represented by 10 or more specimens. (F) = unidentified female specimens. For all tests degrees of freedom = 1 and α=0.05. X = chi-square value. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$

SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
AGYRTIDAE							
1 *Necrophilus pettitii* Horn	1	0	1	0	0	1	1
BRENTIDAE							
2 *Apion* spp.	0	3	1	2	0	3	3
CANTHARIDAE							
3 *Rhagonycha* sp.	0	1	0	1	1	0	1
CARABIDAE							
4 *Acupalpus testaceus* Dejean	0	1	1	0	1	0	1
5 *Amphasia interstitialis* (Say)	0	6	0	6	4	2	6
6 *Anillinus cherokee* Sokolov and Carlton	2	14**	16****	0	13*	3	16
	X = 9	*P = 0.0027*	X = 16	*P < 0.0001*	X = 6.25	*P = 0.0124*	
7 *Anillinus langdoni* Sokolov and Carlton	13	543****	467****	89	252	304*	556
	X = 505.2158	*P < 0.0001*	X = 256.9856	*P < 0.0001*	X = 4.8633	*P = 0.0274*	
8 *Anillinus loweae* Sokolov and Carlton	0	2	2	0	0	2	2
9 *Apenes lucidulus* (Dejean)	0	2	0	2	2	0	2
10 *Carabus* (*s.str.*) *goryi* Dejean	0	1	1	0	1	0	1
11 *Clinidium valentinei* Bell	7	3	2	8	5	5	10
	X = 1.6	*P = 0.2059*	X = 3.6	*P = 0.0577*	X = 0	*P = 1*	
12 *Cyclotrachelus freitagi* Bousquet	0	2	0	2	2	0	2
13 *Dicaelus* (*Paradicaelus*) *dilatatus* Say	0	1	0	1	0	1	1
14 *Gastrellarius blanchardi* (Horn)	0	8	7	1	5	3	8
15 *Gastrellarius honestus* (Say)	4	0	1	3	3	1	4

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
16	*Harpalus spadiceus* Dejean	1	6	7	0	7	0	7
17	*Lebia viridis* Say	0	2	1	1	0	2	2
18	*Olisthopus parmatus* (Say)	1	2	0	3	2	1	3
19	*Polyderis laevis* (Say)	3	34****	2	35****	27**	10	37
		X = 25.973	*P < 0.0001*	X = 29.4324	*P < 0.0001*	X = 7.8108	*P = 0.0051*	
20	*Pterostichus* (*Steropus*) *moestus* (Say)	1	0	1	0	1	0	1
21	*Scaphinotus* (*Maronetus*) spp.	0	3	3	0	3	0	3
22	*Serranillus dunavani* (Jeannel)	2	0	1	1	2	0	2
23	*Serranillus* sp.	1	0	0	1	1	0	1
24	*Sphaeroderus bicarinatus* (LeConte)	0	1	1	0	0	1	1
25	*Sphaeroderus canadensis lengi* Darlington	0	1	1	0	1	0	1
26	*Sphaeroderus stenostomus lecontei* Dejean	0	2	0	2	2	0	2
27	*Trechus* (*Microtrechus*) *pisgahensis* Barr	23	33	56****	0	28	28	56
		X = 1.7857	*P = 0.1814*	X = 56	*P < 0.0001*	X = 0	*P = 1*	
28	*Trichotichnus autumnalis* (Say)	0	1	0	1	1	0	1
CERYLONIDAE								
29	*Mychocerus striatus* (Sen Gupta and Crowson)	246****	4	68	182****	153***	97	250
		X = 234.256	*P < 0.0001*	X = 51.984	*P < 0.0001*	X = 12.544	*P = 0.0004*	
30	*Philothermus glabriculus* LeConte	4	2	4	2	6	0	6
31	*Philothermus stephani* Gimmel and Slipinski	4	0	4	0	0	4	4
CHRYSOMELIDAE								
32	*Altica* spp.	1	3	4	0	2	2	4
33	*Capraita subvittata* (Horn)	0	3	3	0	1	2	3
34	*Disonycha leptolineata* Blatchley	0	1	1	0	0	1	1
35	*Disonycha xanthomelas* (Dalman)	0	1	1	0	0	1	1
36	*Odontota dorsalis* (Thunberg)	1	8	3	6	4	5	9

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
37	*Psylliodes appalachianus* Konstantinov and Tishechkin	0	6	6	0	3	3	6
	CIIDAE							
38	*Ceracis* sp.	1	0	0	1	0	1	1
39	*Strigocis opalescens* (Casey)	1	0	1	0	1	0	1
	CLAMBIDAE							
40	*Clambus* sp.	0	1	1	0	0	1	1
	CORYLOPHIDAE							
41	*Holopsis* spp.	2	21****	2	21****	13	10	23
		X = 15.6957	*P < 0.0001*	X = 15.6957	*P < 0.0001*	X = 0.3913	*P = 0.5316*	
	CRYPTOPHAGIDAE							
42	*Cryptophagus* sp.	0	1	1	0	1	0	1
43	*Henoticus serratus* (Gyllenhal)	0	1	1	0	0	1	1
	CURCULIONIDAE							
44	*Acalles* spp.	0	9	5	4	9	0	9
45	*Anthonomus* sp.	0	1	1	0	1	0	1
46	*Caulophilus dubius* (Horn)	4	45****	30	19	38***	11	49
		X = 34.3061	*P < 0.0001*	X = 2.4694	*P = 0.1161*	X = 14.8776	*P = 0.0001*	
47	*Conotrachelus* spp.	0	7	7	0	6	1	7
48	*Craponius inaequalis* (Say)	0	1	0	1	1	0	1
49	Curculionidae gen. spp.	1	3	3	1	2	2	4
50	*Cyrtepistomus castaneus* (Roelofs)	0	1	0	1	1	0	1

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
51	*Dryophthorus americanus* (Bedel)	20****	0	0	20****	17**	3	20
		$X = 20$	$P < 0.0001$	$X = 20$	$P < 0.0001$	$X = 9.8$	$P = 0.0017$	
52	*Epacalles* spp.	0	4	1	3	0	4	4
53	*Eurhoptus* n. sp.	1	38****	4	35****	24	15	39
		$X = 35.1026$	$P < 0.0001$	$X = 24.641$	$P < 0.0001$	$X = 2.0769$	$P = 0.1495$	
54	*Eurhoptus pyriformis* LeConte	0	55****	44****	11	34	21	55
		$X = 55$	$P < 0.0001$	$X = 19.8$	$P < 0.0001$	$X = 3.0727$	$P = 0.0796$	
55	*Lechriops oculatus* (Say)	1	0	1	0	1	0	1
56	*Microhyus* n.sp.	0	2	2	0	1	1	2
57	*Microhyus setiger* LeConte	2	0	2	0	2	0	2
58	*Myosides seriehispidus* Roelofs	2	7	0	9	8	1	9
59	*Odontopus calceatus* (Say)	0	1	1	0	0	1	1
60	*Panscopus impressus* Pierce	0	12***	10*	2	2	10*	12
		$X = 12$	$P = 0.0005$	$X = 5.3333$	$P = 0.0209$	$X = 5.3333$	$P = 0.0209$	
61	*Pseudanthonomus* spp.	0	3	2	1	2	1	3
62	*Xylosandrus crassiusculus* (Motschulsky)	1	0	0	1	0	1	1
63	*Xyloterinus politus* (Say)	0	1	1	0	1	0	1
ELATERIDAE								
64	*Ampedus rubicus* (Say)	1	0	1	0	0	1	1
65	*Ampedus* sp.	1	0	1	0	0	1	1
66	*Dalopius* sp.	0	1	1	0	0	1	1
67	*Limonius nimbatus* (Say)	0	1	0	1	1	0	1
EROTYLIDAE								
68	*Tritoma unicolor* Say	0	1	0	1	1	0	1

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
EUCINETIDAE								
69	*Tohlezkus inexpectus* Vit	34****	1	31****	4	30****	5	35
		X = 31.1143	$P < 0.0001$	X = 20.8286	$P < 0.0001$	X = 17.8571	$P < 0.0001$	
HISTERIDAE								
70	*Bacanius tantillus* LeConte	2	1	2	1	2	1	3
HYDROPHILIDAE								
71	*Cercyon occallatus* (Say)	0	4	4	0	2	2	4
LATRIDIIDAE								
72	*Dienerella costulata* (Reitter)	2	2	3	1	0	4	4
LEIODIDAE								
73	*Agathidium compressidens* Fall	1	0	1	0	0	1	1
74	*Agathidium divaricatum* Miller and Wheeler	0	2	2	0	1	1	2
75	*Agathidium gallititillo* Miller and Wheeler	0	2	2	0	0	2	2
76	*Agathidium kimberlae* Miller and Wheeler	0	3	2	1	2	1	3
77	*Agathidium* n.sp.	0	5	4	1	3	2	5
78	*Agathidium oniscoides* Beauvois	4	0	4	0	4	0	4
79	*Agathidium rubellum* Fall	2	0	1	1	1	1	2
80	*Agathidium* spp. (F)	7	18*	18*	7	13	12	25
		X = 4.84	$P = 0.0278$	X = 4.84	$P = 0.0278$	X = 0.04	$P = 0.8415$	
81	*Aglyptinus laevis* (LeConte)	3	0	0	3	1	2	3
82	*Cainosternum imbricatum* Notman	0	1	1	0	0	1	1
83	*Catopocerus appalachianus* Peck	0	5	3	2	3	2	5
84	*Catopocerus* n.sp.	0	4	3	1	2	2	4

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
85	*Catopocerus* spp. (F)	0	16****	11	5	11	5	16
		X = 16	*P < 0.0001*	X = 2.25	*P = 0.1336*	X = 2.25	*P = 0.1336*	
86	*Catops paramericanus* Peck and Cook	0	1	1	0	1	0	1
87	*Colenis impunctata* LeConte	0	7	0	7	7	0	7
88	*Colon megasetosum* Peck and Stephan	0	4	0	4	0	4	4
89	*Gelae* spp. (F)	1	0	1	0	1	0	1
90	*Hydnobius substriatus* LeConte	0	2	0	2	0	2	2
91	*Ptomaphagus appalachianus* (Peck)	9	25**	31****	3	6	28***	34
		X = 7.5294	*P = 0.0061*	X = 23.0588	*P < 0.0001*	X = 14.2353	*P = 0.0002*	
92	*Ptomaphagus* spp. (F)	9	32***	36****	5	16	25	41
		X = 12.9024	*P = 0.0003*	X = 23.439	*P < 0.0001*	X = 1.9756	*P = 0.1599*	
93	*Sciodrepoides watsoni* (Spence)	1	0	1	0	1	0	1
LUCANIDAE								
94	*Platycerus virescens* (Fabricius)	0	1	1	0	1	0	1
MONOTOMIDAE								
95	*Bactridium* sp.	0	1	0	1	0	1	1
NITIDULIDAE								
96	*Epuraea* sp.	0	1	0	1	1	0	1
97	*Pallodes pallidus* (Beauvois)	0	2	2	0	1	1	2
98	*Stelidota geminata* (Say)	0	2	0	2	2	0	2
99	*Stelidota octomaculata* (Say)	0	41****	13	28*	26	15	41
		X = 41	*P < 0.0001*	X = 5.4878	*P = 0.0191*	X = 2.9512	*P = 0.0858*	
PHALACRIDAE								
100	*Acylomus* n.sp.	0	1	0	1	0	1	1

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
PTILIIDAE								
101	*Acrotrichis* spp.	17	460****	470****	7	207	270**	477
		X = 411.4235	*P < 0.0001*	X = 449.4109	*P < 0.0001*	X = 8.3208	*P = 0.0039*	
102	*Micridium* sp.	0	1	0	1	0	1	1
103	*Nossidium* spp.	4	1	5	0	5	0	5
104	*Pteryx* spp.	15**	2	8	9	9	8	17
		X = 9.9412	*P = 0.0016*	X = 0.0588	*P = 0.8084*	X = 0.0588	*P = 0.8084*	
105	Ptiliidae gen. spp.	2	0	1	1	2	0	2
SCARABAEIDAE								
106	*Dialytellus tragicus* (Schmidt)	2	37****	38****	1	30***	9	39
		X = 31.4103	*P < 0.0001*	X = 35.1026	*P < 0.0001*	X = 11.3077	*P = 0.0007*	
107	*Serica* spp.	0	6	3	3	6	0	6
STAPHYLINIDAE								
Aleocharinae								
108	*Aleodorus bilobatus* (Say)	0	28****	28****	0	3	25****	28
		X = 28	*P < 0.0001*	X = 28	*P < 0.0001*	X = 17.2857	*P < 0.0001*	
109	Athetini gen. spp.	0	13***	9	4	11*	2	13
		X = 13	*P = 0.0003*	X = 1.9231	*P = 0.1655*	X = 6.2308	*P = 0.0125*	
110	*Euvira* spp.	0	5	2	3	3	2	5
111	*Gyrophaena* sp.	0	1	0	1	0	1	1
112	*Hoplandria laeviventris* Casey	0	2	0	2	0	2	2
113	*Leptusa carolinensis* Pace	1	0	1	0	0	1	1
114	*Leptusa cribratula* (Casey)	7	0	0	7	5	2	7
115	*Leptusa gimmeli* Park and Carlton	0	101****	101****	0	37	64**	101
		X = 101	*P < 0.0001*	X = 101	*P < 0.0001*	X = 7.2178	*P = 0.0072*	
116	*Leptusa pseudosmokyiensis* Park and Carlton	0	2	2	0	2	0	2

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
117	*Leptusa pusio* (Casey)	11*	2	13***	0	11*	2	13
		X = 6.2308	$P = 0.0125$	X = 13	$P = 0.0003$	X = 6.2308	$P = 0.0125$	
118	*Leptusa* spp.	24	16	18	22	21	19	40
		X = 1.6	$P = 0.2059$	X = 0.4	$P = 0.5271$	X = 0.1	$P = 0.7518$	
119	*Myllaena* spp.	13	11	4	20**	14	10	24
		X = 0.1667	$P = 0.6831$	X = 10.6667	$P = 0.0011$	X = 0.6667	$P = 0.4142$	
120	*Oxypoda* spp.	0	4	1	3	0	4	4
121	*Phanerota* sp.	0	1	0	1	1	0	1
122	Aleocharinae gen. spp.	4	8	7	5	8	4	12
		X = 1.3333	$P = 0.2482$	X = 0.3333	$P = 0.5637$	X = 1.3333	$P = 0.2482$	
Dasycerinae								
123	*Dasycerus* spp.	0	20****	0	20****	17**	3	20
		X = 20	$P < 0.0001$	X = 20	$P < 0.0001$	X = 9.8	$P = 0.0017$	
Euaesthetinae								
124	*Edaphus americanus* Puthz	5	1	2	4	2	4	6
125	*Stictocranius puncticeps* LeConte	1	3	0	4	1	3	4
Osoriinae								
126	*Thoracophorus costalis* (Erichson)	17*	5	2	20***	21****	1	22
		X = 6.5455	$P = 0.0105$	X = 14.7273	$P = 0.0001$	X = 18.1818	$P < 0.0001$	
Oxytelinae								
127	*Anotylus* spp.	0	86****	83****	3	80****	6	86
		X = 86	$P < 0.0001$	X = 74.4186	$P < 0.0001$	X = 63.6744	$P < 0.0001$	
128	*Carpelimus* sp. 1	0	12***	11**	1	1	11**	12
		X = 12	$P = 0.0005$	X = 8.3333	$P = 0.0038$	X = 8.3333	$P = 0.0038$	
129	*Carpelimus* sp. 2	1	0	1	0	1	0	1
130	*Oxytelus convergens* LeConte	0	1	1	0	1	0	1
131	*Oxytelus* spp. (F)	0	2	2	0	2	0	2

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
Paederinae								
132	*Achenomorphus corticinus* (Gravenhorst)	0	3	0	3	1	2	3
133	*Homaeotarsus* sp.	0	1	0	1	0	1	1
134	*Lathrobium* spp.	0	3	0	3	1	2	3
135	*Ochthephilum* sp.	0	1	0	1	0	1	1
136	*Palaminus fraternus* Casey	0	3	0	3	0	3	3
137	*Palaminus* spp. (F)	0	6	0	6	4	2	6
138	*Palaminus testaceus* Erichson	0	1	0	1	0	1	1
139	*Stilicopsis paradoxa* Sachse	0	2	0	2	2	0	2
140	*Sunius confluentus* (Say)	2	0	0	2	2	0	2
141	*Sunius rufipes* (Casey)	9	602****	375****	236	282	329	611
		X = 575.5303	*P < 0.0001*	X = 31.6219	*P < 0.0001*	X = 3.6154	*P = 0.0572*	
Pselaphinae								
142	*Actiastes fundatum* Grigarick and Schuster	1	41****	42****	0	16	26	42
		X = 38.0952	*P < 0.0001*	X = 42	*P < 0.0001*	X = 2.381	*P = 0.1228*	
143	*Actiastes* spp. (F)	1	98****	97****	2	59	40	99
		X = 95.0404	*P < 0.0001*	X = 91.1616	*P < 0.0001*	X = 3.6465	*P = 0.0561*	
144	*Actiastes suteri* (Park)	0	7	6	1	5	2	7
145	*Adranes lecontei* Brendel	8	7	0	15***	10	5	15
		X = 0.0667	*P = 0.7963*	X = 15	*P = 0.0001*	X = 1.6667	*P = 0.1967*	
146	*Arianops digitata* Barr	1	0	1	0	0	1	1
147	*Batrisodes auerbachi* Park	3	1	2	2	2	2	4
148	*Batrisodes beyeri* Schaeffer	1	11**	11**	1	4	8	12
		X = 8.3333	*P = 0.0038*	X = 8.3333	*P = 0.0038*	X = 1.3333	*P = 0.2482*	
149	*Batrisodes denticollis* (Casey)	0	3	0	3	3	0	3
150	*Batrisodes lineaticollis* (Aubé)	3	1	3	1	2	2	4
151	*Batrisodes* spp. (F)	11	12	13	10	15	8	23
		X = 0.0435	*P = 0.8348*	X = 0.3913	*P = 0.5316*	X = 2.1304	*P = 0.1444*	

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
152	*Bibloplectus ruficeps* (Motschulsky)	3	0	0	3	3	0	3
153	*Bibloplectus* spp. (F)	2	0	0	2	2	0	2
154	*Conoplectus canaliculatus* (LeConte)	20***	3	1	22****	9	14	23
		X = 12.5652	*P = 0.0003*	X = 19.1739	*P < 0.0001*	X = 1.087	*P = 0.2971*	
155	*Ctenisodes* spp.	1	29****	1	29****	8	22*	30
		X = 26.1333	*P < 0.0001*	X = 26.1333	*P < 0.0001*	X = 6.5333	*P = 0.0105*	
156	*Custotychus daggyi* (Park)	0	1	0	1	0	1	1
157	*Custotychus spiculifer* (Casey)	0	2	0	2	1	1	2
158	*Custotychus* spp. (F)	1	3	0	4	3	1	4
159	*Decarthron nigrocavum* Park	0	2	0	2	2	0	2
160	*Euboarhexius perscitus* (Fletcher)	0	56****	55****	1	24	32	56
		X = 56	*P < 0.0001*	X = 52.0714	*P < 0.0001*	X = 1.1429	*P = 0.2850*	
161	*Euboarhexius trogasteroides* (Brendel)	0	4	3	1	4	0	4
162	*Euplectus* sp. (F)	1	0	0	1	1	0	1
163	*Eutyphlus dybasi* Park	1	14***	15***	0	4	11	15
		X = 11.2667	*P = 0.0007*	X = 15	*P = 0.0001*	X = 3.2667	*P = 0.0707*	
164	*Eutyphlus* spp. (F)	3	176****	162****	17	94	85	179
		X = 167.2011	*P < 0.0001*	X = 117.4581	*P < 0.0001*	X = 0.4525	*P = 0.5011*	
165	*Eutyphlus thoracicus* Park	0	1	1	0	1	0	1
166	*Leptoplectus pertenuis* (Casey)	6	2	0	8	6	2	8
167	*Machaerodes carinatus* (Brendel)	3	50****	53****	0	27	26	53
		X = 41.6792	*P < 0.0001*	X = 53	*P < 0.0001*	X = 0.0189	*P = 0.8907*	
168	*Mipseltyrus nicolayi* Park	1	33****	34****	0	27***	7	34
		X = 30.1176	*P < 0.0001*	X = 34	*P < 0.0001*	X = 11.7647	*P = 0.0006*	
169	*Prespelea copelandi* Park	0	1	1	0	1	0	1
170	*Prespelea quirsfeldi* Park	0	4	4	0	2	2	4
171	*Pseudactium arcuatum* (LeConte)	2	16***	3	15**	1	17***	18
		X = 10.8889	*P = 0.0009*	X = 8	*P = 0.0046*	X = 14.2222	*P = 0.0002*	

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
172	*Pycnoplectus infossus* (Raffray)	1	0	0	1	0	1	1
173	*Pycnoplectus interruptus* (LeConte)	1	0	1	0	1	0	1
174	*Pycnoplectus* spp. (F)	2	0	1	1	2	0	2
175	*Rhexius schmitti* Brendel	0	10**	0	10**	9*	1	10
		X = 10	*P = 0.0015*	X = 10	*P = 0.0015*	X = 6.4	*P = 0.0114*	
176	*Rhexius* spp. (F)	2	11*	0	13***	9	4	13
		X = 6.2308	*P = 0.0125*	X = 13	*P = 0.0003*	X = 1.9231	*P = 0.1655*	
177	*Sonoma chouljenkoi* Ferro and Carlton	2	1	1	2	2	1	3
178	*Sonoma gilae* Ferro and Carlton	5	0	5	0	4	1	5
179	*Sonoma gimmeli* Ferro and Carlton	1	2	0	3	2	1	3
180	*Sonoma* spp. (F)	22**	6	10	18	13	15	28
		X = 9.1429	*P = 0.0024*	X = 2.2857	*P = 0.1306*	X = 0.1429	*P = 0.7055*	
181	*Tmesiphorus* sp.	1	0	0	1	1	0	1
182	*Trimiomelba dubia* (LeConte)	1	11**	0	12***	12***	0	12
		X = 8.3333	*P = 0.0038*	X = 12	*P = 0.0005*	X = 12	*P = 0.0005*	
Scaphidiinae								
183	*Baeocera pallida* Casey	2	8	0	10**	6	4	10
		X = 3.6	*P = 0.0577*	X = 10	*P = 0.0015*	X = 0.4	*P = 0.5271*	
184	*Baeocera* spp.	2	0	0	2	2	0	2
185	*Scaphisoma suturale* LeConte	0	3	1	2	3	0	3
186	*Toxidium gammaroides* LeConte	1	2	0	3	2	1	3
Scydmaeninae								
187	*Brachycepsis* sp.	0	1	0	1	1	0	1
188	*Euconnus* (*Napochus*) spp.	22	116****	27	111****	68	70	138
		X = 64.029	*P < 0.0001*	X = 51.1304	*P < 0.0001*	X = 0.029	*P = 0.8648*	
189	*Euconnus* (*Napoconnus*) sp.	1	0	0	1	0	1	1
190	*Euconnus* (*Scopophus*) spp.	38	25	34	29	35	28	63
		X = 2.6825	*P = 0.1015*	X = 0.3968	*P = 0.5287*	X = 0.7778	*P = 0.3778*	

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
191	*Euconnus* spp.	15	12	11	16	13	14	27
		X = 0.3333	*P = 0.5637*	X = 0.9259	*P = 0.3359*	X = 0.037	*P = 0.8474*	
192	*Leptoscydmus* spp.	6	1	1	6	4	3	7
193	*Microscydmus* (*Delius*) sp.	1	0	0	1	0	1	1
194	*Microscydmus* (*Neladius*) sp.	1	0	1	0	0	1	1
195	*Microscydmus (s. str.)* spp.	3	0	0	3	2	1	3
196	*Parascydmus* spp.	3	10	12**	1	13***	0	13
		X = 3.7692	*P = 0.0522*	X = 9.3077	*P = 0.0022*	X = 13	*P = 0.0003*	
197	*Scydmaenus* spp.	0	15***	6	9	5	10	15
		X = 15	*P = 0.0001*	X = 0.6	*P = 0.4386*	X = 1.6667	*P = 0.1967*	
198	*Stenichnus* sp.	0	1	1	0	1	0	1
Staphylininae								
199	*Atrecus americanus* (Casey)	1	0	1	0	0	1	1
200	*Erichsonius patella* (Horn)	0	3	0	3	2	1	3
201	*Gabrius fallaciosus* (Horn)	1	0	1	0	1	0	1
202	*Philonthus* spp.	0	2	2	0	0	2	2
203	*Platydracus cinnamopterus* (Gravenhorst)	0	3	0	3	3	0	3
Steninae								
204	*Stenus* spp.	2	38****	40****	0	30**	10	40
		X = 32.4	*P < 0.0001*	X = 40	*P < 0.0001*	X = 10	*P = 0.0015*	
Tachyporinae								
205	*Bryoporus rufescens* LeConte	0	8	0	8	6	2	8
206	*Ischnosoma lecontei* Campbell	1	29****	25***	5	27****	3	30
		X = 26.1333	*P < 0.0001*	X = 13.3333	*P = 0.0002*	X = 19.2	*P < 0.0001*	
207	*Mycetoporus americanus* Erichson	0	1	1	0	1	0	1
208	*Sepedophilus basalis* (Erichson)	1	2	0	3	3	0	3
209	*Sepedophilus brachypterus* Campbell	7	0	4	3	5	2	7
210	*Sepedophilus cinctulus* (Erichson)	1	0	0	1	1	0	1

Appendix 2 cont.

	SPECIES	CWD5	Leaf Litter	Primary	Secondary	Spring	Fall	Total
211	*Sepedophilus crassus* (Gravenhorst)	1	0	1	0	1	0	1
212	*Sepedophilus occultus* (Casey)	2	0	2	0	0	2	2
213	*Sepedophilus versicolor* (Casey)	4	0	0	4	3	1	4
TENEBRIONIDAE								
214	*Anaedus brunneus* (Ziegler)	0	10**	0	10**	9*	1	10
		X = 10	*P = 0.0015*	X = 10	*P = 0.0015*	X = 6.4	*P = 0.0114*	
215	*Paratenetus* spp.	0	7	1	6	1	6	7
THROSCIDAE								
216	*Aulonothroscus punctatus* (Bonvouloir)	0	1	0	1	1	0	1
	Significant Associations	8	40	28	19	19	9	

APPENDIX 3. LIST OF TAXA AND NUMBER OF SPECIMENS EMERGENT FROM WOODY DERBIS

Chi-square goodness of fit testing was performed for all taxa represented by 10 or more specimens from FWD (degrees of freedom = 1), all taxa represented by 15 or more specimens from CWD (degrees of freedom = 2), and all taxa represented by 10 or more total specimens (degrees of freedom = 1). For all tests α=0.05. †From Ferro et al. (Chap. 6), a= significantly associated with CWD5. X = chi-square value. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Aderidae										
1	*Vanonus huronicus* Casey	0	0	1	1	0	1	1	2	-
Anobiidae										
2	*Hadrobregmus notatus* (Say)	0	0	3	0	1	4	0	4	-
3	*Lasioderma semirufum* Fall	1	0	0	0	0	1	0	1	-
4	*Oligomerus obtusus* LeConte	2	12**	0	0	0	13**	1	14	-
		X=7.14	P=0.0075				X=10.29	P=0.0013		
5	*Petalium incisum* Ford	0	2	0	0	0	2	0	2	-
6	*Priobium sericeum* (Say)	17*	5	17**	5	0	15	29*	44	-
		X=6.55	P=0.0105	P=0.0017	P=0.6907	P=0.0256	X=4.45	P=0.0348		
7	*Sculptotheca puberula* (LeConte)	1	4	1	1	1	8	0	8	-
8	*Trichodesma klagesi* Fall	5	2	0	1	1	6	3	9	-
9	*Vrilletta laurentina* Fall	0	1	0	0	0	1	0	1	-
10	*Xyletinus* spp.	0	1	0	1	0	0	2	2	-
Anthribidae										
11	*Eurymycter tricarinatus* Pierce	0	1	0	0	1	1	1	2	-
12	*Ormiscus* spp.	1	0	0	1	0	2	0	2	-
Buprestidae										
13	*Agrilus masculinus* Horn	2	0	0	0	0	2	0	2	-
14	*Agrilus* spp.	3	0	0	0	0	3	0	3	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
15	*Dicerca divaricata* (Say)	0	3	5	2	0	6	4	10	-
							X=0.40	*P*=0.5271		
Carabidae										
16	*Agonum ferreum* Haldeman	1	0	0	0	0	0	1	1	-
17	*Anillinus loweae* Sokolov and Carlton	0	0	0	0	1	0	1	1	-
18	Carabidae gen. sp. (teneral specimen)	0	0	0	1	0	1	0	1	-
19	*Clinidium baldufi* Bell	0	4	0	2	7	4	9	13	-
							X=1.92	*P*=0.1655		
20	*Clinidium rosenbergi* Bell	0	1	0	0	0	0	1	1	-
21	*Clinidium sculptile* (Newman)	0	0	0	0	1	1	0	1	-
22	*Gastrellarius honestus* (Say)	1	3	1	7	14*	11	15	26	4
				P=0.0648	*P*=0.9901	*P*=0.0483	X=0.61	*P*=0.4328		
23	*Harpalus spadiceus* Dejean	0	0	0	0	1	0	1	1	1
24	*Mioptachys flavicauda* (Say)	0	1	2	8	0	8	3	11	-
							X=2.27	*P*=0.1317		
25	*Polyderis laevis* (Say)	0	0	0	0	1	1	0	1	3
26	*Pterostichus tristis* (Dejean)	0	0	0	1	0	0	1	1	-
27	*Trechus (Microtrechus) pisgahensis* Barr	0	0	0	0	2	0	2	2	23
Cerambycidae										
28	*Aegomorphus modestus* (Gyllenhal)	0	1	0	4	0	5	0	5	-
29	*Aegomorphus quadrigibbus* (Say)	0	2	0	0	0	0	2	2	-
30	*Analeptura lineola* Say	0	25****	0	0	1	4	22***	26	-
		X=25.00	*P*<0.0001				X=12.46	*P*=0.0004		
31	*Anoplodera pubera* (Say)	0	0	0	1	0	0	1	1	-
32	*Astylopsis maculata* (Say)	3	1	0	1	0	4	1	5	-
33	*Bellamira scalaris* (Say)	0	0	0	3	0	3	0	3	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
34	*Clytus ruricola* (Olivier)	1	1	0	0	1	0	3	3	-
35	*Cyrtophorus verrucosus* (Olivier)	0	1	0	1	0	1	1	2	-
36	*Elaphidion mucronatum* (Say)	0	0	4	0	0	4	0	4	-
37	*Eupogonius pauper* LeConte	27****	0	0	0	0	27****	0	27	-
		X=27.00	*P*<0.0001				X=27.00	*P*<0.0001		
38	*Grammoptera exigua* (Newman)	0	1	0	0	0	1	0	1	-
39	*Hyperplatys aspersa* (Say)	0	2	0	0	0	2	0	2	-
40	*Leptorhabdium pictum* (Haldeman)	0	0	2	0	0	0	2	2	-
41	*Leptostylus transversus* (Gyllenhal)	2	0	7	4	1	14***	0	14	-
							X=14.00	*P*=0.0002		
42	*Lepturges confluens* (Haldeman)	0	1	0	0	0	1	0	1	-
43	*Microgoes oculatus* (LeConte)	13	8	8	2	0	9	22*	31	-
		X=1.19	*P*=0.2752				X=5.45	*P*=0.0196		
44	*Molorchus b. bimaculatus* Say	4	0	0	0	0	4	0	4	-
45	*Neandra brunnea* (Fabricius)	1	0	1	3	0	1	4	5	-
46	*Oplosia nubila* (LeConte)	2	0	0	5	0	5	2	7	-
47	*Pidonia ruficollis* (Say)	0	1	1	1	0	0	3	3	-
48	*Saperda vestita* Say	0	0	0	1	0	1	0	1	-
49	*Strangalepta abbreviata* (Germar)	0	1	0	0	0	1	0	1	-
50	*Strangalia luteicornis* (Fabricius)	0	2	0	0	0	2	0	2	-
51	*Trachysida mutabilis* (Newman)	2	16***	22*	13	4	14	43***	57	-
		X=10.89	*P*=0.0009	*P*=0.0443	*P*=1.0000	*P*=0.0443	X=14.75	*P*=0.0001		
52	*Typocerus velutinus* (Olivier)	0	2	0	0	3	4	1	5	-
53	*Urgleptes foveatocollis* (Hamilton)	0	1	0	0	0	1	0	1	-
54	*Urgleptes querci* (Fitch)	2	1	0	0	0	2	1	3	-
55	*Urographis fasciatus* (DeGeer)	0	0	13	0	0	0	13***	13	-
							X=13.00	*P*=0.0003		
56	*Xylotrechus nitidus* (Horn)	1	0	0	0	0	1	0	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Cerylonidae										
57	*Cerylon castaneum* Say	0	0	4	8	0	0	12***	12	-
							X=12	*P*=0.0005		
58	*Cerylon unicolor* Ziegler	0	0	1	0	0	1	0	1	-
59	*Hypodacne punctata* LeConte	0	1	0	0	0	1	0	1	-
60	*Mychocerus striatus*	0	0	0	0	15****	14***	1	15	246 (a)
	(Sen Gupta and Crowson)			*P*=0.0820	*P*=0.0820	*P*<0.0001	X=11.27	*P*=0.0008		
61	*Philothermus glabriculus* (LeConte)	0	7	4	16	12	17	22	39	4
				P=0.1243	*P*=0.2631	*P*=0.9185	X=0.64	*P*=0.4233		
Chrysomelidae										
62	*Cryptocephalus quadruplex* Newman	0	1	0	0	0	0	1	1	-
63	*Tymnes* sp.	0	0	0	1	0	0	1	1	-
Ciidae										
64	*Ceracis sallei* Mellie	0	0	0	4	0	4	0	4	-
65	*Ceracis singularis* (Dury)	0	0	0	16****	1	16***	1	17	-
				P=0.0587	*P*<0.0001	*P*=0.1466	X=13.24	*P*=0.0002		
66	*Ceracis* spp.	0	0	0	7	0	7	0	7	1
67	*Ceracis thoracicornis* Ziegler	0	0	0	3	0	3	0	3	-
68	Ciidae gen. spp.	1	1	0	1	1	1	3	4	-
69	*Cis fuscipes* Mellie	0	0	4	0	2	0	6	6	-
70	*Cis miles* (Casey)	0	0	0	0	1	1	0	1	-
71	*Octotemnus laevis* Casey	42****	0	0	1	3	2	44****	46	-
		X=42.00	*P*<0.0001				X=38.35	*P*<0.0001		
72	*Rhopalodontus* sp.	1	0	0	0	0	0	1	1	-

Appendix 3 cont.

Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Cleridae									
73 *Cymatodera bicolor* (Say)	0	0	0	0	1	1	0	1	-
Colydiidae									
74 *Paha laticollis* (LeConte)	0	1	0	0	0	1	0	1	-
75 *Synchita fuliginosa* Melsheimer	0	0	0	2	0	0	2	2	-
Corylophidae									
76 Corylophidae gen. sp.	0	0	0	1	0	0	1	1	-
77 *Sericoderus* spp.	0	0	1	1	0	1	1	2	-
Cryptophagidae									
78 *Atomaria* spp.	2	11*	6	4	3	13	13	26	-
	X=6.23	*P*=0.0125				X=0.00	P=1		
79 *Caenoscelis* spp.	0	0	0	2	0	0	2	2	-
80 *Cryptophagus* spp.	23*	10	23	46*	23	60	65	125	-
	X=5.12	*P*=0.0236	*P*=0.3828	*P*=0.0216	*P*=0.3828	X=0.20	*P*=0.6547		
Cucujidae									
81 *Cucujus clavipes* Fabricius	0	0	0	1	0	1	0	1	-
Cupedidae									
82 *Cupes capitatus* Fabricius	0	1	1	1	0	1	2	3	-
Curculionidae									
83 *Acalles carinatus* LeConte	2	1	0	0	0	1	2	3	-
84 *Acoptus suturalis* LeConte	1	0	0	1	0	1	1	2	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
85	*Apteromechus ferratus* (Say)	2	1	10	0	0	13***	0	13	-
							X=13.00	*P*=0.0003		
86	*Caulophilus dubius* Horn	2	22****	13	20	24	30	51*	81	4
		X=16.67	*P*<0.0001	*P*=0.3886	*P*=0.9753	*P*=0.5168	X=5.44	*P*=0.0196		
87	*Cercopeus* sp.	0	0	1	0	0	0	1	1	-
88	*Cophes fallax* (LeConte)	19****	0	0	0	0	19****	0	19	-
		X=19.00	*P*<0.0001				X=19.00	*P*<0.0001		
89	*Cophes obtentus* (Herbst)	1	0	0	0	0	0	1	1	-
90	*Cossonus impressifrons* Boheman	0	0	0	3	0	3	0	3	-
91	Curculionidae gen. spp.	0	0	2	0	2	3	1	4	-
92	*Cyrtepistomus castaneus* (Roelofs)	0	0	0	1	0	0	1	1	-
93	*Dryophthorus americanus* Bedel	39**	19	69	125****	54	112	194****	306	20 (a)
		X=6.90	*P*=0.0086	*P*=0.3230	*P*<0.0001	*P*=0.0069	X=21.97	*P*<0.0001		
94	*Eurhoptus* n. sp.	0	2	0	0	0	0	2	2	1
95	*Hylesinus pruniosus* Eichhoff	0	0	3	0	0	0	3	3	-
96	*Hylesinus* sp.	1	0	0	0	0	0	1	1	-
97	*Hypothenemus* spp.	5	1	0	3	0	9	0	9	-
98	*Micromimus corticalis* Boheman	1	0	0	1	0	2	0	2	-
99	*Myosides seriehispidus* Roelofs	0	1	0	1	0	2	0	2	2
100	*Pityophthorus annectens* LeConte	9	0	0	0	0	9	0	9	-
101	*Pseudopentarthrum* sp.	1	1	0	0	0	2	0	2	-
102	*Pseudopityophthorus asperulus* (LeConte)	0	0	0	0	1	0	1	1	-
103	*Stenoscelis brevis* (Boheman)	14	23	26	49*	28	88**	52	140	-
		X=2.19	*P*=0.1390	*P*=0.3328	*P*=0.0435	*P*=0.5571	X=9.26	*P*=0.0023		
104	*Xyleborus affinis* Eichhoff	0	0	1	0	0	0	1	1	-
105	*Xyleborus atratus* Eichhoff	1	1	9	0	0	4	7	11	-
							X=0.82	*P*=0.3657		
106	*Xyleborus californicus* Wood	0	0	1	0	0	0	1	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
107	*Xyleborus ferrugineus* (Fabricius)	0	0	1	0	0	0	1	1	-
108	*Xyleborus pulliculosus* Eichhoff	1	0	0	0	0	1	0	1	-
109	*Xylosandrus crassiusculus* (Motschulsky)	1	0	1	12	0	14***	0	14	1
							$X=14.00$	$P=0.0002$		
110	*Xylosandrus germanus* (Blandford)	14***	0	2	6	0	5	17*	22	-
		$X=14.00$	$P=0.0002$				$X=6.55$	$P=0.0105$		
111	*Xylosandrus* spp.	0	0	0	2	0	2	0	2	-
112	*Xyloterinus politus* (Say)	2	0	24****	0	0	5	21**	26	-
				$P<0.0001$	$P=0.0183$	$P=0.0183$	$X=9.85$	$P=0.0017$		
Elateridae										
113	*Ampedus areolatus* (Say)	1	1	3	24**	8	10	27**	37	-
				$P=0.0399$	$P=0.0014$	$P=0.5627$	$X=7.81$	$P=0.0051$		
114	*Ampedus luteolus* (LeConte)	0	0	0	0	13	9	4	13	-
							$X=1.92$	$P=0.1655$		
115	*Ampedus rubricus* (Say)	0	0	0	0	1	1	0	1	1
116	*Ampedus semicinctus* (Randall)	1	2	3	1	3	8	2	10	-
							$X=3.60$	$P=0.0577$		
117	*Ampedus* sp.	0	0	0	0	1	0	1	1	1
118	*Athous cucullatus* (Say)	0	1	0	0	5	6	0	6	-
119	*Athous rufifrons* (Randall)	0	0	0	1	0	0	1	1	-
120	*Athous scapularis* (Say)	0	1	2	3	0	2	4	6	-
121	*Denticollis denticornis* (Kirby)	0	0	0	0	1	0	1	1	-
122	*Lacon discoideus* (Weber)	0	0	1	1	1	2	1	3	-
123	*Melanotus decumanus* (Erichson)	1	0	0	0	0	0	1	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Endomychidae										
124	*Bystus ulkei* (Crotch)	3	4	7	0	1	4	11	15	-
							X=3.27	*P*=0.0707		
125	*Endomychus biguttatus* Say	0	0	2	0	0	0	2	2	-
126	*Micropsephodes lundgreni* Leschen and Carlton	0	0	1	0	0	1	0	1	-
127	*Mycetina perpulchra* (Newman)	0	0	1	0	0	1	0	1	-
128	*Phymaphora pulchella* Newman	0	0	0	0	1	0	1	1	-
Erotylidae										
129	*Microsternus ulkei* (Crotch)	0	0	0	0	3	3	0	3	-
Eucinetidae										
130	*Tohlezkus inexpectus* Vit	0	13***	14	9	127****	13	150****	163	34 (a)
		X=13.00	*P*=0.0003	*P*<0.0001	*P*<0.0001	*P*<0.0001	X=115.15	*P*<0.0001		
Eucnemidae										
131	*Dirrhagofarsus lewisi* (Fleutiaux)	0	0	0	1	0	0	1	1	-
132	*Dromaeolus cylindricollis* (Say)	2	0	1	0	0	1	2	3	-
133	*Entomophthalmus rufiolus* (LeConte)	0	0	0	3	3	6	0	6	-
134	*Isarthrus rufipes* (Melsheimer)	0	3	0	1	10	0	14***	14	-
							X=14.00	*P*=0.0002		
135	*Isorhipis obliqua* (Say)	3	0	7	24***	0	34****	0	34	-
				P=0.5827	*P*=0.0001	*P*=0.0057	X=34.00	*P*<0.0001		
136	*Melasis pectinicornis* Melsheimer	0	0	1	24****	0	24****	1	25	-
				P=0.0397	*P*<0.0001	*P*=0.0155	X=21.16	*P*<0.0001		
137	*Microrhagus subsinuatus* LeConte	0	0	0	2	14	10	6	16	-
							X=1	*P*=0.3173		

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Histeridae										
138	*Aeletes floridae* (Marseul)	0	0	0	1	0	0	1	1	-
139	*Bacanius tantillus* LeConte	2	3	1	6	4	5	11	16	2
							X=2.25	*P*=0.1336		
140	*Caerosternus americanus* (LeConte)	0	0	0	0	1	0	1	1	-
141	*Paromalus bistriatus* Erichson	0	0	1	4	1	4	2	6	-
Hydrophilidae										
142	*Cercyon assecla* Smetana	0	1	1	1	1	4	0	4	-
143	*Cercyon occallatus* (Say)	1	0	0	0	0	0	1	1	-
144	*Cercyon versicolor* Smetana	0	0	0	1	0	0	1	1	-
Laemophloeidae										
145	*Charaphloeus adustus* (LeConte)	0	0	0	2	0	2	0	2	-
146	*Laemophloeus biguttatus* (Say)	0	0	0	1	0	1	0	1	-
147	*Laemophloeus megacephalus* Grouvelle	0	0	0	9	0	9	0	9	-
148	*Placonotus zimmermanni* (LeConte)	2	0	0	0	0	2	0	2	-
Lampyridae										
149	*Lucidota* spp.	0	0	1	5	0	0	6	6	-
Leiodidae										
150	*Agathidium atronitens* Fall	0	0	0	0	4	0	4	4	-
151	*Agathidium exiguum* Melsheimer	0	0	0	0	1	0	1	1	-
152	*Agathidium oniscoides* Beauvois	1	2	1	4	0	1	7	8	4
153	*Agathidium rubellum* Fall	0	0	0	0	1	1	0	1	2
154	*Agathidium* spp. (female)	4	7	1	13	7	9	23*	32	7
		X=0.82	*P*=0.3657	*P*=0.0765	*P*=0.0765	*P*=1.0000	X=6.13	*P*=0.0133		

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
155	*Anisotoma* n. sp.	0	0	0	1	0	0	1	1	-
156	*Catopocerus appalachianus* Peck	0	0	0	1	0	0	1	1	-
157	*Catopocerus* spp. (female)	0	0	0	0	2	1	1	2	-
158	*Catops davidsoni* Salgado	0	0	1	0	0	0	1	1	-
159	*Nemadus triangulum* Jeannel	0	2	0	1	1	2	2	4	-
160	*Sciodrepoides latinotum* Peck and Cook	1	0	3	2	0	1	5	6	-
Lucanidae										
161	*Platycerus virescens* (Fabricius)	0	3	0	0	0	0	3	3	-
Lycidae										
162	*Plateros* sp.	0	1	0	0	0	1	0	1	-
Lymexylidae										
163	*Elateroides lugubris* (Say)	0	0	0	1	0	0	1	1	-
Melandryidae										
164	*Dircaea liturata* (LeConte)	0	0	0	13	0	12**	1	13	-
							X=9.31	*P*=0.0022		
165	*Emmesa connectens* (Newman)	0	3	0	1	2	1	5	6	-
166	*Hypulus simulator* Newman	0	0	0	8	2	8	2	10	-
							X=3.60	*P*=0.0577		
167	*Microtonus sericans* LeConte	0	1	2	0	2	1	4	5	-
168	*Orchesia castanea* (Melsheimer)	0	0	2	0	0	0	2	2	-
169	*Phloeotrya vaudoueri* Mulsant	0	2	0	0	0	0	2	2	-
170	*Prothalpia undata* (LeConte)	0	2	0	0	0	0	2	2	-
171	*Symphora rugosa* (Haldeman)	0	1	0	1	0	0	2	2	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Melyridae										
172	*Hypebaeus apicalis* Say	0	0	2	0	0	2	0	2	-
173	*Melyrodes cribratus* (LeConte)	0	0	0	1	0	1	0	1	-
Monotomidae										
174	*Rhizophagus dimidiatus* Mannerheim	0	0	0	1	0	0	1	1	-
Mordellidae										
175	*Falsomordellistena bihamata* (Melsheimer)	0	3	0	0	0	3	0	3	-
176	*Glipostenoda ambusta* (LeConte)	0	0	0	1	2	1	2	3	-
177	*Mordella* sp.	0	0	0	0	1	1	0	1	-
178	*Mordellaria serval* (Say)	0	0	0	2	0	0	2	2	-
179	*Mordellistena* spp.	0	0	0	0	8	0	8	8	-
180	*Mordellochroa scapularis* (Say)	0	0	1	0	0	0	1	1	-
181	*Paramordellaria triloba* (Say)	0	1	0	0	0	0	1	1	-
Mycetophagidae										
182	*Mycetophagus flexuosus* Say	0	0	0	0	1	0	1	1	-
Nitidulidae										
183	*Carpophilus* spp.	1	0	3	0	1	5	0	5	-
184	*Epuraea* spp.	1	1	1	2	0	4	1	5	-
185	*Glischrochilus confluentus* (Say)	0	1	0	0	0	1	0	1	-
Oedemeridae										
186	*Asclera ruficollis* (Say)	0	0	2	0	0	0	2	2	-

Appendix 3 cont.

Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Ptiliidae									
187 *Acrotrichis* spp.	0	0	1	21****	1	1	22*	23	17
			P=0.0550	*P*<0.0001	*P*=0.0550	X=19.18	*P*<0.0001		
188 *Micridium* sp.	1	0	0	0	0	0	1	1	-
189 *Pteryx* spp.	2	44****	2	251****	105	108	296****	404	15 (a)
	X=38.35	*P*<0.0001	*P*<0.0001	*P*<0.0001	*P*=0.4231	X=87.49	*P*<0.0001		
190 Ptiliidae gen. spp.	10	25*	4	70****	26	55	80*	135	2
	X=6.43	*P*=0.0112	*P*<0.0001	*P*<0.0001	*P*=0.4470	X=4.63	*P*=0.0314		
Ptilodactylidae									
191 *Ptilodactyla carinata* Johnson and Freytag	0	0	0	0	4	3	1	4	-
192 *Ptilodactyla* spp. (female)	1	0	0	1	0	0	2	2	-
Pyrochroidae									
193 *Dendroides canadensis* Latreille	1	15***	1	16****	0	7	26***	33	-
	X=12.25	*P*=0.0004	*P*=0.1466	*P*<0.0001	*P*=0.0587	X=10.94	*P*=0.0009		
194 *Dendroides concolor* (Newman)	0	8	0	2	0	0	10**	10	-
						X=10.00	*P*=0.0015		
195 *Neopyrochroa flabellata* (Fabricius)	0	0	0	2	4	0	6	6	-
Salpingidae									
196 *Rhinosimus viridiaeneus* (Randall)	10**	0	4	1	0	3	12*	15	-
	X=10.00	*P*=0.0015				X=5.40	*P*=0.0201		
Scarabaeidae									
197 *Gnorimella maculosa* (Knoch)	0	0	0	1	0	1	0	1	-
Scraptiidae									
198 *Canifa* sp.	1	0	0	0	0	1	0	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Silvanidae										
199	*Cathartosilvanus imbellis* (LeConte)	0	1	0	0	0	1	0	1	-
200	*Silvanus muticus* Sharp	0	6	0	0	0	0	6	6	-
201	*Uleiota dubia* (Fabricius)	0	0	1	0	0	1	0	1	-
Staphylinidae										
Aleocharinae										
202	Aleocharinae gen. spp.	14*	5	13	34*	18	27	57**	84	4
		X=4.26	*P*=0.0389	*P*=0.1764	*P*=0.0298	*P*=0.7334	X=10.71	*P*=0.0011		
203	*Aleodorus bilobatus* (Say)	0	0	0	0	2	0	2	2	-
204	*Atheta* spp.	16	15	35	65***	23	36	118****	154	-
		X=0.03	*P*=0.8575	*P*=0.6440	*P*=0.0009	*P*=0.0192	X=43.66	*P*<0.0001		
205	Athetini gen. spp.	1	2	3	5	2	5	8	13	-
							X=0.69	*P*=0.4054		
206	*Earota* spp.	1	0	0	0	0	0	1	1	-
207	*Leptusa carolinensis* Pace	2	1	3	8	2	8	8	16	1
							X=0.00	*P*=1.0000		
208	*Leptusa cribratula* (Casey)	4	0	3	3	4	6	8	14	7
							X=0.29	*P*=0.5930		
209	*Leptusa ferroi* Park and Carlton	0	1	0	0	0	1	0	1	-
210	*Leptusa gimmeli* Park and Carlton	0	0	0	1	0	0	1	1	-
211	*Leptusa pusio* (Casey)	1	1	3	4	4	2	11*	13	11 (a)
							X=6.23	*P*=0.0125		
212	*Leptusa* spp.	1	4	2	6	3	5	11	16	24
							X=2.25	*P*=0.1336		
213	*Myrmecocephalus cingulatus* (LeConte)	4	0	0	1	0	0	5	5	-
214	*Placusa* sp.	0	0	0	1	0	0	1	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
Euaesthetinae										
215	*Edaphus americanus* Puthz	0	0	0	1	3	3	1	4	5
Omaliinae										
216	*Hapalaraea hamata* (Fauvel)	0	0	1	0	0	1	0	1	-
217	*Omalium fractum* Fauvel	1	0	1	1	1	3	1	4	-
Osoriinae										
218	*Thoracophorus costalis* (Erichson)	18	127****	24	224	463****	193	663****	856	17 (a)
		X=81.94	*P*<0.0001	*P*<0.0001	*P*=0.7011	*P*<0.0001	X=258.06	*P*<0.0001		
Oxytelinae										
219	*Anotylus* sp.	0	1	0	0	0	0	1	1	-
Paederinae										
220	*Sunius* spp.	0	1	0	2	0	1	2	3	-
Phloeocharinae										
221	*Charhyphus picipennis* (LeConte)	0	0	1	0	0	0	1	1	-
Piestinae										
222	*Siagonium americanum* (Melsheimer)	0	0	1	0	0	1	0	1	-
223	*Siagonium punctatum* LeConte	0	0	0	2	0	0	2	2	-
Proteininae										
224	*Proteinus* spp.	0	0	3	0	0	0	3	3	-
Pselaphinae										
225	*Actiastes* sp. (female)	0	0	1	0	0	0	1	1	1
226	*Actiastes suteri* Park	0	1	0	0	0	0	1	1	-
227	*Adranes lecontei* Brendel	0	0	1	0	39****	39****	1	40	8
				P=0.0033	*P*=0.0012	*P*<0.0001	X=36.10	*P*<0.0001		
228	*Batrisodes beyeri* Schaeffer	0	0	0	2	1	1	2	3	1
229	*Batrisodes ionae* LeConte	0	0	0	0	1	1	0	1	-
230	*Batrisodes lineaticollis* Aube	0	0	2	1	5	1	7	8	3
231	*Batrisodes schaumi* Aube	0	0	0	0	1	0	1	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
232	*Batrisodes* spp. (female)	1	2	3	5	6	5	12	17	11
							X=2.88	*P*=0.0895		
233	*Bibloplectus* sp. (female)	1	0	0	0	0	1	0	1	2
234	*Cedius cruralis* Park	0	0	1	0	0	1	0	1	-
235	*Cedius spinosus* LeConte	1	1	0	3	2	1	6	7	-
236	*Ctenisodes* sp.	0	0	0	1	0	1	0	1	1
237	*Custotychus* sp.	0	0	0	0	1	1	0	1	1
238	*Dalmosella tenuis* Casey	0	0	1	0	1	2	0	2	-
239	*Euboarhexius perscitus* Fletcher	0	1	0	0	0	0	1	1	-
240	*Euplectus confluens* LeConte	0	0	1	0	0	0	1	1	-
241	*Euplectus longicollis* Casey	0	0	0	1	1	1	1	2	-
242	*Euplectus* sp. (female)	0	1	0	0	0	0	1	1	1
243	*Eutyphlus similis* LeConte	0	0	0	1	0	0	1	1	-
244	*Eutyphlus* sp. (female)	0	0	0	1	0	0	1	1	3
245	*Leptoplectus pertenuis* (Casey)	0	16****	0	12	20*	25	23	48	6
		X=16.00	*P*<0.0001	*P*=0.0048	*P*=0.9185	*P*=0.0168	X=0.08	*P*=0.7728		
246	*Pycnoplectus cediosus* Wagner	0	0	0	1	0	0	1	1	-
247	*Pycnoplectus infossus* Raffray	0	2	0	1	1	3	1	4	1
248	*Pycnoplectus linearis* LeConte	0	1	0	0	0	0	1	1	-
249	*Pycnoplectus* spp. (female)	0	5	2	14	10	14	17	31	2
				P=0.0769	*P*=0.1939	*P*=0.9003	X=0.29	*P*=0.5900		
250	*Rhexius schmitti* Brendel	0	0	0	0	1	1	0	1	-
251	*Rhexius* sp. (female)	0	0	1	0	0	1	0	1	2
252	*Sonoma chouljenkoi* Ferro and Carlton	0	1	0	1	3	1	4	5	2
253	*Sonoma gilae* Ferro and Carlton	0	0	0	0	4	1	3	4	5
254	*Sonoma gimmeli* Ferro and Carlton	0	1	0	0	6	6	1	7	1
255	*Sonoma* spp. (female)	0	4	2	3	23****	19	13	32	22 (a)
				P=0.0561	*P*=0.1164	*P*<0.0001	X=1.12	*P*=0.2888		

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
256	*Thesium cavifrons* LeConte	1	0	0	1	1	1	2	3	-
257	*Thesium* spp. (female)	0	0	0	2	0	0	2	2	-
258	*Trimiomelba dubia* LeConte	0	2	1	2	2	5	2	7	1
259	*Trimioplectus obsoletus* Brendel	1	6	4	4	2	6	11	17	-
							X=1.47	*P*=0.2253		
260	*Tyrus* spp.	0	0	0	2	0	2	0	2	-
Scaphidiinae										
261	*Scaphisoma convexum* Say	1	1	0	1	0	2	1	3	-
Scydmaeninae										
262	*Euconnus (Napochus)* spp.	0	3	1	7	11	12	10	22	22
				P=0.1059	*P*=0.9656	*P*=0.1790	X=0.18	*P*=0.6698		
263	*Euconnus (Napoconnus)* spp.	0	2	0	1	1	1	3	4	1
264	*Euconnus (Scopophus)* n. spp.	0	3	1	2	7	6	7	13	-
							X=0.08	*P*=0.7815		
265	*Euconnus (Scopophus)* spp.	0	4	0	4	10	6	12	18	38
							X=2.00	*P*=0.1573		
266	*Microscydmus (Delius)* sp.	0	0	0	1	0	1	0	1	1
267	*Parascydmus* spp.	0	0	1	2	3	2	4	6	3
268	*Scydmaenus* sp.	0	0	0	1	0	0	1	1	-
Staphylininae										
269	*Belonuchus rufipennis* (Fabricius)	2	3	0	2	1	4	4	8	-
270	*Bisnius blandus* (Gravenhorst)	0	0	1	0	0	1	0	1	-
271	*Erichsonius* n. sp.	0	0	0	2	0	0	2	2	-
272	*Gabrius fallaciosus* (Horn)	0	5	1	0	0	0	6	6	1
273	*Hesperus apicialis* (Say)	22	15	59	62	36	68	126****	194	-
		X=1.32	*P*=0.2498	*P*=0.6537	*P*=0.4086	*P*=0.0780	X=17.34	*P*<0.0001		
274	*Hesperus baltimorensis* (Gravenhorst)	1	0	2	0	0	2	1	3	-
275	*Hypnogyra gularis* (LeConte)	0	0	0	0	1	0	1	1	-

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
276	*Platydracus violaceus* (Gravenhorst)	0	0	0	0	1	1	0	1	-
277	*Platydracus viridanus* (Horn)	0	1	0	0	0	1	0	1	-
Tachyporinae										
278	*Sepedophilus brachypterus* Campbell	1	0	0	3	17***	1	20****	21	7
				P=0.0356	*P*=0.3642	*P*=0.0003	X=17.19	*P*<0.0001		
279	*Sepedophilus cinctulus* (Erichson)	4	6	15	31**	8	41*	23	64	-
		X=0.40	*P*=0.5271	*P*=0.7788	*P*=0.0091	*P*=0.0620	X=5.06	*P*=0.0244		
280	*Sepedophilus crassus* (Gravenhorst)	0	0	0	1	0	0	1	1	1
281	*Sepedophilus occultus* (Casey)	1	0	8	11	1	14	7	21	2
				P=0.8737	*P*=0.2441	*P*=0.0898	X=2.33	*P*=0.1266		
282	*Sepedophilus* sp.	0	0	0	0	1	0	1	1	-
283	*Sepedophilus testaceus* (Fabricius)	0	0	0	1	1	0	2	2	-
Stenotrachelidae										
284	*Cephaloon lepturides* Newman	0	3	0	0	0	0	3	3	-
Synchroidae										
285	*Synchroa punctata* Newman	0	0	0	0	1	0	1	1	-
Tenebrionidae										
286	*Alobates pennsylvanicus* (DeGeer)	0	0	0	0	1	1	0	1	-
287	*Anaedus brunneus* (Ziegler)	0	0	0	0	1	1	0	1	-
288	*Arthromacra aenea lengi* Parsons	0	1	0	0	0	1	0	1	-
289	*Centronopus calcaratus* (Fabricius)	0	0	0	0	9	1	8	9	-
290	*Haplandrus fulvipes* (Herbst)	0	0	0	0	1	1	0	1	-
291	*Hymenorus* spp. (female)	4	5	5	9	6	16	13	29	-
				P=0.8105	*P*=0.6636	*P*=0.9656	X=0.31	*P*=0.5775		

Appendix 3 cont.

	Species	FWD1	FWD2	CWD1	CWD2	CWD3-4	Secondary	Primary	Total	CWD5†
292	*Hymenorus* sp. a	0	0	0	1	0	1	0	1	-
293	*Hymenorus* sp. b	0	0	0	1	0	1	0	1	-
294	*Hymenorus* sp. c	0	0	1	0	0	0	1	1	-
295	*Meracantha contracta* (Beauvois)	0	4	0	0	1	5	0	5	-
296	*Prateus fusculus* LeConte	0	0	0	0	1	1	0	1	-
297	*Strongylium crenatum* Maklin	0	0	0	0	12	12***	0	12	-
							X=12.00	*P*=0.0005		
298	*Strongylium terminatum* (Say)	0	1	0	0	0	1	0	1	-
299	Tenebrionidae gen. spp.	0	0	2	5	1	5	3	8	-
300	*Uloma impressa* Melsheimer	0	0	0	0	1	1	0	1	-
Tetratomidae										
301	*Holostrophus bifasciatus* (Say)	0	1	0	0	0	0	1	1	-
Throscidae										
302	*Aulonothroscus distans* Blanchard	371****	111	416****	201	31	608*	522	1130	-
		X=140.25	*P*<0.0001	*P*<0.0001	*P*=0.5945	*P*<0.0001	X=6.55	*P*=0.0105		
303	*Aulonothroscus* spp.	1	0	2	2	0	2	3	5	-
Trogossitidae										
304	*Airora cylindrica* (Serville)	0	0	1	0	0	1	0	1	-
305	*Thymalus marginicollis* Chevrolat	0	0	0	1	0	1	0	1	-
	Associates	10	11	4	14	8	16	27	5673	8

APPENDIX 4. LIST OF TAXA AND NUMBER OF SPECIMENS COLLECTED AT GREENBRIER AND PORTERS CREEK SITES

Sifting/Berlese data are from Ferro et al. (see Chapter 6), and emergence data are from Ferro et al. (see Chapter 7).

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
Aderidae							
1	*Vanonus huronicus* Casey	—	1	1	—	—	—
Agyrtidae							
2	*Necrophilus pettitii* Horn	—	—	—	1	—	—
Anobiidae							
3	*Caenocara* spp.	—	—	1	—	—	4
4	*Priobium sericeum* (Say)	—	5	1	—	6	1
5	*Protheca hispida* LeConte	—	—	4	—	—	—
6	*Sculptotheca puberula* (LeConte)	—	1	3	—	—	—
7	*Trichodesma klagesi* Fall	—	—	—	—	3	—
8	*Vrilletta laurentina* Fall	—	1	—	—	—	—
Anthicidae							
9	*Ischalia costata* (LeConte)	—	—	1	—	—	1
Anthribidae							
10	*Eurymycter tricarinatus* Pierce	—	—	1	—	—	—
Artematopodidae							
11	*Eurypogon niger* (Melsheimer)	—	—	—	—	—	1

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
Buprestidae							
12	*Dicerca divaricata* (Say)	—	1	1	—	3	—
Cantharidae							
13	Cantharidae gen. sp.	—	—	—	—	—	1
Carabidae							
14	*Agonum ferreum* Haldeman	—	—	—	—	1	—
15	*Anillinus langdoni* Sokolov and Carlton	88	—	—	107	—	—
16	*Apenes lucidulus* (Dejean)	1	—	—	—	—	—
17	Carabidae gen. sp. (teneral specimen)	—	1	—	—	—	—
18	*Carabus goryi* Dejean	—	—	—	—	—	1
19	*Clinidium baldufi* Bell	—	2	—	—	2	—
20	*Clinidium rosenbergi* Bell	—	—	—	—	1	—
21	*Clinidium valentinei* Bell	3	—	—	—	—	—
22	*Cyclotrachelus freitagi* Bousquet	2	—	—	—	—	—
23	*Dicaelus (Paradicaelus) dilatatus* Say	1	—	—	—	—	—
24	*Gastrellarius blanchardi* (Horn)	—	—	—	1	—	—
25	*Gastrellarius honestus* (Say)	1	3	—	—	6	—
26	*Mioptachys flavicauda* (Say)	—	7	—	—	1	—
27	*Platynus parmarginatus* Hamilton	—	—	—	—	—	3
28	*Polyderis laevis* (Say)	—	1	—	—	—	—
29	*Pterostichus (Steropus) moestus* (Say)	—	—	—	1	—	—
30	*Scaphinotus (Maronetus)* spp.	—	—	—	3	—	—
31	*Serranillus* sp.	1	—	—	—	—	—
32	*Sphaeroderus stenostomus lecontei* Dejean	1	—	—	—	—	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
33	*Trechus (Microtrechus) pisgahensis* Barr	—	—	—	2	—	—
34	*Trichotichnus autumnalis* (Say)	1	—	—	—	—	—
	Cerambycidae						
35	*Aegomorphus modestus* (Gyllenhal)	—	1	—	—	—	—
36	*Aegomorphus quadrigibbus* (Say)	—	—	—	—	2	—
37	*Analeptura lineola* Say	—	4	—	—	—	—
38	*Astylopsis maculata* (Say)	—	3	—	—	—	—
39	*Clytus ruricola* (Olivier)	—	—	—	—	1	—
40	*Cyrtophorus verrucosus* (Olivier)	—	—	—	—	1	—
41	*Grammoptera exigua* (Newman)	—	1	—	—	—	—
42	*Graphisurus fasciatus* (DeGeer)	—	—	—	—	13	—
43	*Leptorhabdium pictum* (Haldeman)	—	—	—	—	2	—
44	*Leptostylus transversus* (Gyllenhal)	—	1	—	—	—	—
45	*Metacmaeops vittata* (Swederus)	—	—	—	—	—	2
46	*Microgoes oculatus* (LeConte)	—	4	1	—	10	—
47	*Molorchus b. bimaculatus* Say	—	3	—	—	—	—
48	*Neandra brunnea* (Fabricius)	—	1	—	—	1	—
49	*Oplosia nubila* (LeConte)	—	5	—	—	—	—
50	*Saperda vestita* Say	—	1	—	—	—	—
51	*Strangalepta abbreviata* (Germar)	—	1	1	—	—	—
52	*Trachysida mutabilis* (Newman)	—	1	—	—	12	—
53	*Tragosoma depsarium* (Linnaeus)	—	—	—	—	—	1
54	*Urgleptes querci* (Fitch)	—	1	—	—	—	—
	Cerylonidae						
55	*Cerylon castaneum* Say	—	—	—	—	3	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
56	*Cerylon unicolor* Ziegler	—	1	—	—	—	—
57	*Hypodacne punctata* LeConte	—	1	—	—	—	—
58	*Mychocerus striatus* (Sen Gupta and Crowson)	100	9	—	31	—	—
59	*Philothermus glabriculus* (LeConte)	—	8	—	—	16	—
60	*Philothermus stephani* Gimmel and Slipinski	—	—	—	2	—	—
Chrysomelidae							
61	*Altica* sp.	—	—	—	—	—	1
62	*Disonycha leptolineata* Blatchley	—	—	—	1	—	—
63	*Disonycha xanthomelas* (Dalman)	—	—	—	1	—	1
64	*Odontota dorsalis* (Thunberg)	—	—	—	2	—	—
65	*Psylliodes appalachianus* Konstantinov and Tishechkin	—	—	—	6	—	21
66	*Rhabdopterus* spp. (female)	—	—	—	—	—	4
67	*Sumitrosis inaequalis* (Weber)	—	—	—	—	—	19
68	*Sumitrosis rosea* (Weber)	—	—	—	—	—	3
69	*Tymnes* sp.	—	—	1	—	—	—
Ciidae							
70	*Ceracis sallei* (Mellie)	—	3	—	—	—	—
71	*Ceracis singularis* (Dury)	—	—	1	—	1	—
72	*Ceracis* spp.	—	4	1	—	—	—
73	*Ceracis thoracicornis* (Ziegler)	—	3	—	—	—	—
74	Ciidae gen. spp.	—	—	1	—	2	—
75	*Cis fuscipes* Mellie	—	—	—	—	2	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
76	*Octotemnus laevis* Casey	—	—	—	—	42	—
77	*Rhopalodontus* sp.	—	—	—	—	1	—
Clambidae							
78	*Clambus* sp.	—	—	—	1	—	—
Colydiidae							
79	*Paha laticollis* (LeConte)	—	1	—	—	—	—
80	*Synchita fuliginosa* Melsheimer	—	—	—	—	2	—
Corylophidae							
81	*Holopsis* spp.	2	—	—	—	—	—
Corylophidae							
82	*Sericoderus* sp.	—	—	—	—	1	—
Cryptophagidae							
83	*Atomaria* spp.	—	13	—	—	7	—
84	*Cryptophagus* spp.	—	14	—	1	28	—
Cucujidae							
85	*Cucujus clavipes* Fabricius	—	1	—	—	—	—
Cupedidae							
86	*Cupes capitatus* Fabricius	—	1	—	—	1	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
Curculionidae							
87	*Acalles carinatus* LeConte	—	1	—	—	2	—
88	*Acalles* spp.	—	—	—	3	—	—
89	*Caulophilus dubius* (Horn)	6	17	—	21	3	—
90	*Cophes obtentus* (Herbst)	—	—	—	—	1	—
91	*Cossonus impressifrons* Boheman	—	3	—	—	—	—
92	Curculionidae gen. spp.	1	1	3	3	—	—
93	*Cyrtepistomus castaneus* (Roelofs)	1	—	—	—	1	—
94	*Dryophthorus americanus* Bedel	7	57	52	—	134	23
95	*Eurhoptus* n. sp.	25	—	—	—	—	—
96	*Eurhoptus pyriformis* LeConte	1	—	—	5	—	—
97	*Hylesinus pruniosus* Eichhoff	—	—	—	—	3	—
98	*Hylesinus* sp.	—	—	—	—	1	—
99	*Hypothenemus* spp.	—	3	—	—	—	1
100	*Lechriops oculatus* (Say)	—	—	2	—	—	—
101	*Microhyus setiger* LeConte	—	—	—	2	—	1
102	*Micromimus corticalis* Boheman	—	2	—	—	—	—
103	*Myosides seriehispidus* Roelofs	9	2	—	—	—	—
104	*Panscopus impressus* Pierce	—	—	—	1	—	—
105	*Stenoscelis brevis* (Boheman)	—	9	—	—	18	—
106	*Xyleborinus saxeseni* (Ratzeburg)	—	—	1	—	—	—
107	*Xyleborus affinis* Eichhoff	—	—	—	—	1	—
108	*Xyleborus atratus* Eichhoff	—	—	3	—	6	—
109	*Xyleborus californicus* Wood	—	—	—	—	1	—
110	*Xyleborus ferrugineus* (Fabricius)	—	—	2	—	1	—
111	*Xylosandrus germanus* (Blandford)	—	—	1	—	14	6
112	*Xyloterinus politus* (Say)	—	1	17	—	2	—

Appendix 4 cont.

			Greenbrier			Porters Creek	
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
Dermestidae							
113	*Anthrenus* spp.	—	—	1	—	—	3
Elateridae							
114	*Ampedus areolatus* (Say)	—	10	—	—	13	—
115	*Ampedus luteolus* (LeConte)	—	5	—	—	1	—
116	*Ampedus rubricus* (Say)	—	—	—	1	—	—
117	*Ampedus semicinctus* (Randall)	—	1	—	—	1	—
118	*Athous acanthus* (Say)	—	—	—	—	—	1
119	*Athous brightwelli* (Kirby)	—	—	2	—	—	1
120	*Athous cucullatus* (Say)	—	2	—	—	—	—
121	*Athous rufifrons* (Randall)	—	—	—	—	1	—
122	*Athous scapularis* (Say)	—	1	—	—	3	—
123	*Cardiophorus* sp.	—	—	1	—	—	—
124	*Ctenicera mimica* Becker	—	—	1	—	—	3
125	*Dalopius* sp.	—	—	—	1	—	—
126	Elateridae gen. spp.	—	—	1	—	—	1
127	*Hemicrepidius memnonius* (Herbst)	—	—	—	—	—	2
128	*Limonius aurifer* LeConte	—	—	1	—	—	—
129	*Limonius griseus* (Beauvois)	—	—	1	—	—	—
130	*Limonius nimbatus* (Say)	1	—	—	—	—	—
131	*Melanotus decumanus* (Erichson)	—	—	—	—	1	—
132	*Melanotus parallelus* Blatchley	—	—	1	—	—	—
133	*Melanotus sagittarius* (LeConte)	—	—	1	—	—	—
134	*Pityobius anguinus* LeConte	—	—	1	—	—	—

Appendix 4 cont.

		Greenbrier			Porters Creek	
Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
Endomychidae						
135 *Bystus ulkei* (Crotch)	—	3	—	—	8	—
136 *Endomychus biguttatus* Say	—	—	1	—	2	1
137 *Micropsephodes lundgreni* Leschen and Carlton	—	1	—	—	—	—
138 *Mycetina perpulchra* (Newman)	—	—	3	—	—	—
Erotylidae						
139 *Tritoma humeralis* Fabricius	—	—	—	—	—	1
140 *Tritoma mimetica* (Crotch)	—	—	2	—	—	—
141 *Tritoma unicolor* Say	1	—	1	—	—	—
Eucinetidae						
142 *Tohlezkus inexpectus* Vit	4	8	—	6	127	—
Eucnemidae						
143 *Dirrhagofarsus lewisi* (Fleutiaux)	—	—	1	—	—	—
144 *Dromaeolus cylindricollis* (Say)	—	—	1	—	1	—
145 *Entomophthalmus rufiolus* (LeConte)	—	3	—	—	—	—
146 *Isarthrus rufipes* (Melsheimer)	—	—	—	—	5	—
147 *Isorhipis obliqua* (Say)	—	—	1	—	—	—
148 *Melasis pectinicornis* Melsheimer	—	24	—	—	—	—
149 *Microrhagus subsinuatus* LeConte	—	6	1	—	4	7
Geotrupidae						
150 *Geotrupes balyi* Jekel	—	—	2	—	—	—
151 *Geotrupes splendidus* (Fabricius)	—	—	1	—	—	—

Appendix 4 cont.

	Species	Greenbrier sift (77)	emergence (123)	FIT (159)	Porters Creek sift (81)	emergence (130)	FIT (131)
152	*Odonteus liebecki* (Wallis)	—	—	1	—	—	—
Histeridae							
153	*Aeletes floridae* (Marseul)	—	—	3	—	—	—
154	*Bacanius tantillus* LeConte	—	3	—	—	6	—
155	*Geomysaprinus* sp.	—	—	—	—	—	4
156	*Hololepta lucida* LeConte	—	—	2	—	—	—
157	*Margarinotus lecontei* Wenzel	—	—	29	—	—	84
158	*Onthophilus pluricostatus* LeConte	—	—	21	—	—	—
159	*Xestipyge geminatum* (LeConte)	—	—	2	—	—	—
Hydrophilidae							
160	*Cercyon assecla* Smetana	—	1	1	—	—	8
161	*Cercyon occallatus* (Say)	—	—	88	4	1	297
162	*Cercyon pygmaeus* (Illiger)	—	—	2	—	—	1
163	*Cymbiodyta blanchardi* Horn	—	—	1	—	—	—
164	*Pemelus costatus* (LeConte)	—	—	5	—	—	—
165	*Tectosternum naviculare* (Zimmermann)	—	—	1	—	—	—
Lampyridae							
166	Lampyridae gen. spp.	—	—	1	—	—	1
167	*Lucidota* spp.	—	—	—	—	4	—
168	*Photinus* spp.	—	—	—	—	—	11
Latridiidae							
169	*Corticarina fuscula* (Gyllenhal)	—	—	—	—	—	1

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
170	*Melanophthalma americana* (Mannerheim)	—	—	1	—	—	1
	Leiodidae						
171	*Agathidium compressidens* Fall	—	—	—	1	—	—
172	*Agathidium kimberlae* Miller and Wheeler	1	—	—	—	—	—
173	*Agathidium* n. sp.	1	—	—	—	—	—
174	*Agathidium oniscoides* Beauvois	—	1	1	2	3	—
175	*Agathidium* spp. (female)	6	6	—	4	11	1
176	*Aglyptinus laevis* (LeConte)	1	—	—	—	—	—
177	*Anisotoma bifoveata* Wheeler	—	—	2	—	—	2
178	*Anisotoma blanchardi* (Horn)	—	—	2	—	—	—
179	*Anisotoma discolor* (Melsheimer)	—	—	1	—	—	—
180	*Anisotoma geminata* (Horn)	—	—	—	—	—	1
181	*Anisotoma* spp. (female)	—	—	3	—	—	2
182	*Anogdus puritanus* (Fall)	—	—	1	—	—	—
183	*Catopocerus appalachianus* Peck	2	—	—	2	—	—
184	*Catopocerus* n. sp.	1	—	—	2	—	—
185	*Catopocerus* spp. (female)	5	1	—	8	1	—
186	*Catops basilaris* Say	—	—	—	—	—	1
187	*Colenis impunctata* LeConte	7	—	6	—	—	4
188	*Colon dentatum* LeConte	—	—	1	—	—	—
189	*Colon megasetosum* Stephan and Peck	—	—	1	—	—	1
190	*Colon oblongum* Blatchley	—	—	2	—	—	—
191	*Colon* spp. (female)	—	—	7	—	—	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
192	*Dissochaetus oblitus* Peck	—	—	1	—	—	—
193	*Gelae* spp. (female)	—	—	2	—	—	1
194	*Hydnobius substriatus* (LeConte)	1	—	—	—	—	—
195	*Leiodes appalachiana* Baranowski	—	—	1	—	—	—
196	*Leiodes impressa* Baranowski	—	—	1	—	—	1
197	*Liocyrtusa luggeri* (Hatch)	—	—	2	—	—	—
198	*Nemadus* spp. (female)	—	—	2	—	—	—
199	*Nemadus triangulum* Jeannel	—	2	—	—	—	—
200	*Ptomaphagus (Adelops) brevior* Jeannel	—	—	2	—	—	16
201	*Ptomaphagus (Adelops) ulkei* Horn	—	—	—	—	—	1
202	*Ptomaphagus (Appadelopsis) appalachianus* (Peck)	—	—	—	25	—	—
203	*Ptomaphagus (Appadelopsis) richlandensis* (Peck)	—	—	—	—	—	1
204	*Ptomaphagus* spp.	1	—	1	20	—	—
205	*Sciodrepoides latinotum* Peck and Cook	—	1	—	—	1	—
206	*Sciodrepoides* sp. (female)	—	—	—	—	—	1
207	*Sciodrepoides watsoni* (Spence)	—	—	—	1	—	—
Lucanidae							
208	*Ceruchus piceus* (Weber)	—	—	—	—	—	3
209	*Platycerus virescens* (Fabricius)	—	—	—	1	—	—
Lycidae							
210	Lycidae gen. spp.	—	—	1	—	—	1

Appendix 4 cont.

	Species	Greenbrier sift (77)	 emergence (123)	 FIT (159)	Porters Creek sift (81)	 emergence (130)	 FIT (131)
211	*Plateros* spp.	—	1	1	—	—	2
Melandryidae							
212	*Dircaea liturata* (LeConte)	—	—	1	—	—	—
213	*Emmesa connectens* (Newman)	—	—	—	—	2	—
214	*Hypulus simulator* Newman	—	8	—	—	2	—
215	*Microtonus sericans* LeConte	—	—	—	—	1	—
216	*Phloeotrya vaudoueri* Mulsant	—	—	—	—	2	—
Monotomidae							
217	*Europs pallipennis* (LeConte)	—	—	1	—	—	—
Mordellidae							
218	*Falsomordellistena bihamata* (Melsheimer)	—	3	6	—	—	4
219	*Falsomordellistena pubescens* (Fabricius)	—	—	1	—	—	—
220	*Glipostenoda ambusta* (LeConte)	—	—	1	—	2	6
221	*Mordellistena frosti* Liljeblad	—	—	1	—	—	1
222	*Mordellistena trifasciata* Ray	—	—	1	—	—	—
223	*Paramordellaria triloba* (Say)	—	—	7	—	—	—
Nitidulidae							
224	*Brassicogethes simplipes* (Easton)	—	—	—	—	—	2
225	*Carpophilus* spp.	—	1	1	—	—	—
226	*Epuraea* spp.	1	1	—	—	—	2
227	*Glischrochilus confluentus* (Say)	—	1	—	—	—	—
228	*Glischrochilus sanguinolentus* (Olivier)	—	—	1	—	—	2

Appendix 4 cont.

		Greenbrier			Porters Creek	
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
229	*Pallodes pallidus* (Beauvois)	—	—	22	2	—	25
230	*Phenolia grossa* (Fabricius)	—	—	—	—	—	1
231	*Stelidota geminata* (Say)	1	—	45	—	—	9
232	*Stelidota octomaculata* (Say)	19	—	—	4	—	—
Oedemeridae							
233	*Asclera ruficollis* (Say)	—	—	—	—	2	—
Phalacridae							
234	*Acylomus* n. sp.	1	—	—	—	—	—
Ptiliidae							
235	*Acrotrichis* spp.	—	1	27	461	—	73
236	*Micridium* sp.	—	—	—	—	1	—
237	*Nossidium* spp.	—	—	10	5	—	2
238	*Ptenidium* sp.	—	—	1	—	—	1
239	*Pteryx* spp.	2	84	—	2	56	—
240	Ptiliidae gen. spp.	—	22	42	1	9	39
Ptilodactylidae							
241	*Ptilodactyla angustata* Horn	—	—	5	—	—	1
242	*Ptilodactyla carinata* Johnson and Freytag	—	3	—	—	1	1
243	*Ptilodactyla* spp. (female)	—	—	2	—	2	2
Pyrochroidae							
244	*Dendroides canadensis* Latreille	—	7	—	—	22	—

Appendix 4 cont.

		Greenbrier			Porters Creek		
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
245	*Dendroides concolor* (Newman)	—	—	—	—	5	—
246	*Neopyrochroa flabellata* (Fabricius)	—	—	2	—	5	1
Salpingidae							
247	*Rhinosimus viridiaeneus* (Randall)	—	—	—	—	11	—
Scarabaeidae							
248	*Canthon chalcites* (Haldeman)	—	—	1	—	—	1
249	*Canthon viridis* (Beauvois)	—	—	2	—	—	—
250	*Dialytellus tragicus* (Schmidt)	—	—	—	38	—	—
251	*Dialytes ulkei* Horn	—	—	1	—	—	—
252	*Gnorimella maculosa* (Knoch)	—	1	—	—	—	—
253	*Onthophagus hecate* (Panzer)	—	—	1	—	—	—
254	*Onthophagus orpheus* (Fabricius)	—	—	12	—	—	2
255	*Onthophagus striatulus* (Beauvois)	—	—	5	—	—	—
256	*Onthophagus taurus* (Schreber)	—	—	1	—	—	2
257	*Serica* spp. (female)	2	—	4	2	—	2
Scraptiidae							
258	*Anaspis rufa* Say	—	—	—	—	—	19
Silphidae							
259	*Nicrophorus defodiens* Mannerheim	—	—	—	—	—	3
260	*Nicrophorus orbicollis* Say	—	—	18	—	—	3
Silvanidae							
261	*Uleiota dubia* (Fabricius)	—	1	—	—	—	—

Appendix 4 cont.

	Species	Greenbrier sift (77)	 emergence (123)	 FIT (159)	Porters Creek sift (81)	 emergence (130)	 FIT (131)
Sphindidae							
262	*Eurysphindus comatulus* McHugh	—	—	—	—	—	2
Staphylinidae							
Aleocharinae							
263	Aleocharinae gen. spp.	—	13	41	3	24	45
264	*Aleodorus bilobatus* (Say)	—	—	—	28	2	3
265	*Atheta* spp.	—	21	57	—	26	27
266	Athetini gen. spp.	4	1	15	5	1	29
267	*Borboropora quadriceps* (LeConte)	—	—	3	—	—	1
268	*Earota* spp.	—	—	—	—	1	—
269	*Euvira* sp.	3	—	—	2	—	—
270	*Gyrophaena* sp.	1	—	—	—	—	—
271	*Hoplandria klimaszewskii* Genier	—	—	7	—	—	16
272	*Leptusa cribratula* (Casey)	—	3	—	—	8	—
273	*Leptusa pseudosmokyiensis* Park and Carlton	—	—	—	1	—	—
274	*Leptusa pusio* (Casey)	—	1	—	13	11	—
275	*Leptusa* spp.	1	4	—	5	5	1
276	*Meronera venustula* (Erichson)	—	—	—	—	—	2
277	*Myllaena* spp.	—	—	—	4	—	—
278	*Myrmecocephalus cingulatus* (LeConte)	—	—	2	—	5	—
279	*Myrmedonota* n. sp.	—	—	5	—	—	277
280	*Oxypoda* sp.	—	—	—	1	—	—
281	*Placusa* spp.	—	—	—	—	—	2
Dasycerinae							
282	*Dasycerus* spp.	20	—	—	—	—	—

Appendix 4 cont.

Species		Greenbrier			Porters Creek	
	sift (77)	emergence (123)	FIT (159)	sift (81)	emergence (130)	FIT (131)
Euaesthetinae						
283 *Edaphus americanus* Puthz	4	3	—	1	1	—
Megalopsidiinae						
284 *Megalopinus caelatus* (Gravenhorst)	—	—	1	—	—	—
Omaliinae						
285 *Omalium fractum* Fauvel	—	1	—	—	1	—
Osoriinae						
286 *Thoracophorus costalis* (Erichson)	—	41	1	—	610	3
Oxyporinae						
287 *Oxyporus vittatus* Gravenhorst	—	—	1	—	—	—
Oxytelinae						
288 *Anotylus* spp.	—	—	16	83	1	27
289 *Carpelimus* sp. 1	—	—	—	11	—	—
290 *Oxytelus convergens* LeConte	—	—	—	1	—	2
291 *Oxytelus* spp. (female)	—	—	2	2	—	5
Paederinae						
292 *Achenomorphus corticinus* (Gravenhorst)	1	—	3	—	—	1
293 *Palaminus fraternus* Casey	1	—	—	—	—	—
294 *Palaminus* sp. (female)	1	—	—	—	—	—
295 *Rugilus* spp.	—	—	2	—	—	3
296 *Stilicopsis paradoxa* Sachse	2	—	—	—	—	—
297 *Sunius rufipes* (Casey)	154	—	—	93	—	—
298 *Sunius* spp.	—	—	1	—	1	—
Phloeocharinae						
299 *Charhyphus picipennis* (LeConte)	—	—	—	—	1	—
Piestinae						

Appendix 4 cont.

			Greenbrier			Porters Creek	
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
300	*Siagonium americanum* (Melsheimer)	—	—	—	—	—	1
Proteininae							
301	*Proteinus* spp.	—	—	5	—	—	1
Pselaphinae							
302	*Actiastes fundatum* Grigarick and Schuster	—	—	—	38	—	3
303	*Actiastes* spp. (female)	—	—	—	76	1	1
304	*Actiastes suteri* (Park)	—	—	—	—	1	—
305	*Adranes lecontei* Brendel	7	11	—	—	—	—
306	*Batrisodes auerbachi* Park	—	—	1	—	—	2
307	*Batrisodes beyeri* Schaeffer	—	—	—	9	1	—
308	*Batrisodes ionae* (LeConte)	—	—	1	—	—	—
309	*Batrisodes lineaticollis* Aube	1	—	1	3	5	—
310	*Batrisodes schaumi* (Aube)	—	—	—	—	1	2
311	*Batrisodes* sp. 2	2	—	—	8	—	1
312	*Batrisodes* spp. (female)	—	1	1	—	6	—
313	*Bibloplectus* sp. (female)	—	1	—	—	—	—
314	*Cedius cruralis* Park	—	1	—	—	—	—
315	*Cedius spinosus* LeConte	—	—	—	—	3	—
316	*Conoplectus canaliculatus* (Brendel)	1	—	3	—	—	—
317	*Ctenisodes* spp.	19	—	—	—	—	—
318	*Custotychus spiculifer* (Casey)	2	—	—	—	—	—
319	*Custotychus* spp.	4	1	—	—	—	—
320	*Dalmosella tenuis* Casey	—	1	—	—	—	—
321	*Decarthron nigrocavum* Park	2	—	—	—	—	—
322	*Euboarhexius perscitus* (Fletcher)	—	—	—	55	—	—
323	*Euboarhexius trogasteroides* Brendel	1	—	—	3	—	—

Appendix 4 cont.

			Greenbrier			Porters Creek	
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
324	*Euplectus confluens* LeConte	—	—	—	—	1	—
325	*Euplectus longicollis* Casey	—	1	—	—	—	—
326	*Euplectus* spp. (female)	—	—	3	—	—	2
327	*Eutyphlus dybasi* Park	—	—	—	3	—	—
328	*Eutyphlus similis* LeConte	—	—	—	—	1	—
329	*Eutyphlus* sp. (female)	17	—	—	56	—	—
330	*Leptoplectus pertenuis* (Casey)	3	17	2	—	22	—
331	*Prespelea quirsfeldi* Park	—	—	—	3	—	—
332	*Pseudactium arcuatum* (LeConte)	15	—	—	—	—	—
333	*Pycnoplectus difficilis* (LeConte)	—	—	—	—	—	1
334	*Pycnoplectus infossus* (Raffray)	1	3	—	—	—	—
335	*Pycnoplectus interruptus* (LeConte)	—	—	—	1	—	—
336	*Pycnoplectus* spp. (female)	1	9	—	1	3	—
337	*Rhexius schmitti* Brendel	1	1	—	—	—	—
338	*Rhexius* spp. (female)	1	1	—	—	—	—
339	*Sonoma chouljenkoi* Ferro and Carlton	—	1	—	1	4	—
340	*Sonoma gilae* Ferro and Carlton	—	1	—	—	—	—
341	*Sonoma gimmeli* Ferro and Carlton	3	6	—	—	—	—
342	*Sonoma* spp. (female)	7	14	—	7	6	—
343	*Thesium cavifrons* (LeConte)	—	—	—	—	2	—
344	*Thesium* spp. (female)	—	—	—	—	2	—
345	*Trimiomelba dubia* (LeConte)	—	2	3	—	1	—
346	*Trimioplectus obsoletus* Brendel	—	5	—	—	3	—
Scaphidiinae							
347	*Baeocera pallida* Casey	—	—	—	—	—	1
348	*Baeocera* spp.	—	—	2	—	—	—
349	*Cyparium concolor* (Fabricius)	—	—	5	—	—	2

Appendix 4 cont.

	Species	sift (77)	Greenbrier emergence (123)	FIT (159)	sift (81)	Porters Creek emergence (130)	FIT (131)
350	*Scaphisoma carolinae* Casey	—	—	1	—	—	—
351	*Scaphisoma convexum* Say	—	1	2	—	1	—
352	*Scaphisoma suturale* LeConte	2	—	—	—	—	1
353	*Toxidium gammaroides* LeConte	2	—	1	—	—	—
Scydmaeninae							
354	*Brachycepsis* sp.	1	—	—	—	—	—
355	*Euconnus (Napochus)* spp.	81	5	11	20	3	3
356	*Euconnus (Napoconnus)* spp.	—	—	—	—	2	—
357	*Euconnus (Scopophus)* n. sp.	—	3	—	—	4	1
358	*Euconnus (Scopophus)* spp.	12	5	3	18	7	8
359	*Euconnus* spp.	6	—	—	1	—	—
360	*Euthiconus* sp.	1	—	1	—	—	—
361	*Microscydmus (Delius)* sp.	—	1	—	—	—	—
362	*Microscydmus (Neladius)* sp.	—	—	1	—	—	—
363	*Parascydmus* spp.	—	2	7	—	1	2
364	*Scydmaenus* spp.	—	—	1	6	1	—
365	*Stenichnus* spp.	—	—	2	—	—	—
Staphylininae							
366	*Atrecus americanus* (Casey)	—	—	—	—	—	1
367	*Belonuchus rufipennis* (Fabricius)	—	1	—	—	2	—
368	*Bisnius blandus* (Gravenhorst)	—	1	50	—	—	39
369	*Gabrius fallaciosus* (Horn)	—	—	—	—	5	3
370	*Hesperus apicialis* (Say)	—	51	—	—	36	—
371	*Hesperus baltimorensis* (Gravenhorst)	—	1	—	—	1	—
372	*Ontholestes cingulatus* (Gravenhorst)	—	—	30	—	—	25
373	*Philonthus asper* Horn	—	—	—	—	—	5
374	*Philonthus caeruleipennis* Mannerheim	—	—	163	—	—	29

Appendix 4 cont.

			Greenbrier			**Porters Creek**	
	Species	**sift (77)**	**emergence (123)**	**FIT (159)**	**sift (81)**	**emergence (130)**	**FIT (131)**
375	*Philonthus* spp.	—	—	4	1	—	2
376	*Platydracus violaceus* (Gravenhorst)	—	—	7	—	—	3
377	*Platydracus viridanus* (Horn)	—	1	—	—	—	—
378	*Tympanophorus puncticollis* Erichson	—	—	1	—	—	—
Steninae							
379	*Stenus* spp.	—	—	—	2	—	—
Tachyporinae							
380	*Bryoporus rufescens* LeConte	5	—	21	—	—	2
381	*Bryoporus testaceus* LeConte	—	—	1	—	—	1
382	*Ischnosoma lecontei* Campbell	5	—	—	3	—	—
383	*Lordithon cinctus* (Gravenhorst)	—	—	1	—	—	—
384	*Lordithon facilis* (Casey)	—	—	—	—	—	1
385	*Lordithon notabilis* Campbell	—	—	2	—	—	5
386	*Mycetoporus americanus* Erichson	—	—	—	1	—	—
387	*Mycetoporus consors* LeConte	—	—	—	—	—	1
388	*Sepedophilus brachypterus* Campbell	—	—	—	2	4	—
389	*Sepedophilus cinctulus* (Erichson)	—	13	7	—	6	—
390	*Sepedophilus crassus* (Gravenhorst)	—	—	2	—	—	3
391	*Sepedophilus occultus* (Casey)	—	10	2	—	1	—
392	*Sepedophilus opicus* (Say)	—	—	1	—	—	—
393	*Sepedophilus* sp.	—	—	—	—	1	—
394	*Tachinus canadensis* Horn	—	—	—	—	—	1
395	*Tachinus fimbriatus* Gravenhorst	—	—	24	—	—	10
396	*Tachinus fumipennis* (Say)	—	—	—	—	—	3
397	*Tachinus luridus* Erichson	—	—	1	—	—	11

Appendix 4 cont.

Species	Greenbrier sift (77)	emergence (123)	FIT (159)	Porters Creek sift (81)	emergence (130)	FIT (131)
Stenotrachelidae						
398 *Cephaloon lepturides* Newman	—	—	—	—	1	—
Tenebrionidae						
399 *Anaedus brunneus* (Ziegler)	1	1	—	—	—	—
400 *Arthromacra aenea lengi* Parsons	—	1	—	—	—	—
401 *Centronopus calcaratus* (Fabricius)	—	—	—	—	8	—
402 *Dioedus punctatus* LeConte	—	—	—	—	—	1
403 *Hymenorus* spp. (female)	—	5	—	—	7	—
404 *Meracantha contracta* (Beauvois)	—	3	—	—	—	—
405 *Paratenetus* sp. 1	4	—	—	1	—	—
406 Tenebrionidae gen. spp.	—	4	—	—	1	—
Tetratomidae						
407 *Eustrophopsis bicolor* (Fabricius)	—	—	1	—	—	—
408 *Holostrophus bifasciatus* (Say)	—	—	—	—	1	—
409 *Synstrophus repandus* (Horn)	—	—	—	—	—	1
Throscidae						
410 *Aulonothroscus distans* Blanchard	—	248	1	—	158	—
411 *Aulonothroscus* spp.	—	—	—	—	1	—
Trogidae						
412 *Trox variolatus* Melsheimer	—	—	—	—	—	2

Appendix 4 cont.

	Species	Greenbrier sift (77)	 emergence (123)	 FIT (159)	Porters Creek sift (81)	 emergence (130)	 FIT (131)
Trogossitidae							
413	*Thymalus marginicollis* Chevrolat	—	1	—	—	—	—
	Total (specimens/species)	709/77	941/123	1079/159	1360/81	1689/130	1393/131

APPENDIX 5. LETTER OF PERMISSION FOR CHAPTER 2

from	Paul Skelley insectamundi@gmail.com
to	Mike Ferro <spongymesophyll@gmail.com>
date	Wed, Sep 28, 2011 at 8:20 PM
subject	Re: Permission Request

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APPENDIX 6. LETTER OF PERMISSION FOR CHAPTERS 4 AND 5

from Ronald D Cave beetleeditor@gmail.com
to Mike Ferro <spongymesophyll@gmail.com>
date Thu, Sep 29, 2011 at 12:05 PM
subject Re: Permission Request

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Congratulations for completing your dissertation.

Best regards,
Ron

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VITA

Michael Leslie Ferro was born in Clinton, Missouri, and spent much of his youth covered in mud while roaming the creeks, fields, and forests of the family farm. Michael saw his first insect collection at the age of 7 or 8 at the Missouri State Fair and a few years later, with the help of his mother, built his first insect collection as a 4-H project. During high school Michael took a 4-H sponsored trip to Washington, D.C., and a personal trip to Thailand, both of which provided invaluable knowledge about the wider world. After high school Michael attended Central Missouri State University where he received a full-ride scholarship allowing him to explore a wide variety of classes including marine ecology (twice!) with laboratory sessions in Jamaica and Belize. While there he was invited to participate in the McNair Scholars Program, which sponsored his first entomological research. Michael also taught Supplemental Instruction for various biology courses for seven semesters. After graduation Michael attended the University of Missouri – Columbia and obtained a master's degree in entomology. During that time Michael also received a Brown Graduate Research Fellowship, which allowed him to return to Thailand and conduct research on dragonflies, an invaluable professional and personal experience. Additionally he received the Thomas R. Yonke Award in Insect Biodiversity, which allowed him to participate in the VIIIth International Symposium on Neuropterology in College Station, Texas with a two-week collecting excursion throughout Texas, New Mexico, and Arizona, his first trip to that part of the world. After leaving Missouri, Michael became a graduate student at Louisiana State University where he attended an Organization of Tropical Studies coarse on tropical ecology in Costa Rica and participated in Louisiana State Arthropod Museum collection excursions to Taiwan, Ecuador, Great Smoky Mountains National Park, and the Chiricahua Mountains. Michael was a teaching assistant for a general studies course called Science and Society for 10 semesters and the teaching assistant for a special topics course in aquatic entomology. An avid reader, Michael has been heavily influenced by the works of Ayaan Hirsi Ali, Douglas Adams, Jared Diamond, Stephen Fry, Peter F. Hamilton, Marvin Harris, George McDonald Fraser, Herman Melville, Redmond O'Hanlon, George Orwell, Carl Sagan, Mark Twain, and Kurt Vonnegut Jr. If all goes well Michael will graduate with a doctorate from Louisiana State University, Baton Rouge, in December 2011.