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Comparison of Coleoptera emergent from various decay classes of downed coarse woody debris in Great Smoky Mountains National Park, USA

Michael L. Ferro
Louisiana State Arthropod Museum, spongymesophyll@gmail.com

Matthew L. Gimmel
Louisiana State University AgCenter, phalacrid@gmail.com

Kyle E. Harms
Louisiana State University, kharms@lsu.edu

Christopher E. Carlton
Louisiana State University Agricultural Center, ccarlton@agcenter.lsu.edu

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Michael L. Ferro
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University Agricultural Center
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
spongymesophyll@gmail.com

Matthew L. Gimmel
Division of Entomology
Department of Ecology & Evolutionary Biology
University of Kansas
1501 Crestline Drive, Suite 140
Lawrence, KS, 66045, U.S.A.
phalacrid@gmail.com

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

Christopher E. Carlton
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University Agricultural Center
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
ccarlton@agcenter.lsu.edu

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Michael L. Ferro
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University Agricultural Center
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
spongymesophyll@gmail.com

Matthew L. Gimmel
Division of Entomology
Department of Ecology & Evolutionary Biology
University of Kansas
1501 Crestline Drive, Suite 140
Lawrence, KS, 66045, U.S.A.
phalacrid@gmail.com

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

Christopher E. Carlton
Louisiana State Arthropod Museum, Department of Entomology
Louisiana State University Agricultural Center
402 Life Sciences Building
Baton Rouge, LA, 70803, U.S.A.
ccarlton@agcenter.lsu.edu

Abstract. Coleoptera species composition and succession in downed woody debris habitats are poorly known in eastern North America. A photoeclector emergence chamber was used to concentrate Coleoptera that emerged from various decay classes of fine and coarse woody debris (FWD and CWD, respectively) collected in primary and secondary forest sites in Great Smoky Mountains National Park, Tennessee, USA. A total of 5673 adult beetle specimens, representing 305 lowest identifiable taxa within 227 genera and 51 families, was collected. One hundred fifteen species (38%) were represented by single individuals. Many more specimens and species were collected from CWD (4129 and 247, respectively) than from FWD (1544 and 162, respectively), but species richness accumulation curves were not significantly different. 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). Species accumulation curves indicated higher richness in secondary forests. Based on a subset of 71 species represented by 10 or more specimens, 27 species were associated with fresh fine woody debris, 11 species with weathered fine woody debris, four with coarse woody debris decay class I, 14 with coarse woody debris decay class II, and eight with coarse woody debris decay class III–IV. Sixteen species were associated with secondary forests, whereas 28 species were associated with primary forests. Coarse woody debris decay class II taken in primary forests had highest absolute species richness with 156 species. In coarse woody debris species overlap decreased with increased difference in decay indicating faunal succession. Published works related to the study of the ecology of downed woody material are briefly summarized. Recommendations on developing a database of legacy trees for future researchers are given. Notes on the biology and photographs of the 71 species represented by 10 or more specimens are given to provide an atlas of eastern U.S. beetle species most commonly encountered in these habitats.

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

Introduction

Dead trees are unique habitats. No other habitat is 1) a contiguous patch of biological material that; 2) is 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 use 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 (1968) 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 program.

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 (Okland et al. 1996; Martikainen and Kaila 2004; Gibb et al. 2006a). 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 (Kruys and Jonsson 1999; Heilmann-Clausen and Christensen 2004; Norden et al. 2004) and that both FWD and CWD are important for maintaining beetle and fly species richness (Schiegg 2001; Lindhe et al. 2005; Jonsell et al. 2007; Brin et al. 2010). Studies of faunal succession within decaying wood and stumps show a general increase in species richness with an increase in wood age (Wallace 1953; Irmler et al. 1996; Hovemeyer and Schauermann 2003). Schlaghamersky (2000) surveyed and compared the saproxylic beetle and ant faunae in sites with different flood exposure in a forest in the Czech Republic and found higher species richness in the non-flooded forest. 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 (Jonsell et al. 2004; Lindhe and Lindelow 2004; Abrahamsson and Lindbladh 2006; Gibb et al. 2006b; Hedgren 2007), and snags (Kaila et al. 1997; Bouget et al. 2011b; 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 2012). 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 (Rotheray and MacGowan 2000; Siitonen and Saaristo 2000; Horak et al. 2011) and several conferences on conservation of European saproxylic beetles have been held (Bowen 2003; Barclay and Telnov 2005; 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 (Michaels and Bornemissza 1999; Grove 2002a,c; Baker 2006; 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-leaved 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 than 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 under way 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 and 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 softwood 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 et al. (2012a) 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 as from 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 (2009b) 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).

Material and Methods

Study Area. Great Smoky Mountains National Park (GSMNP, Fig. 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 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) pro-

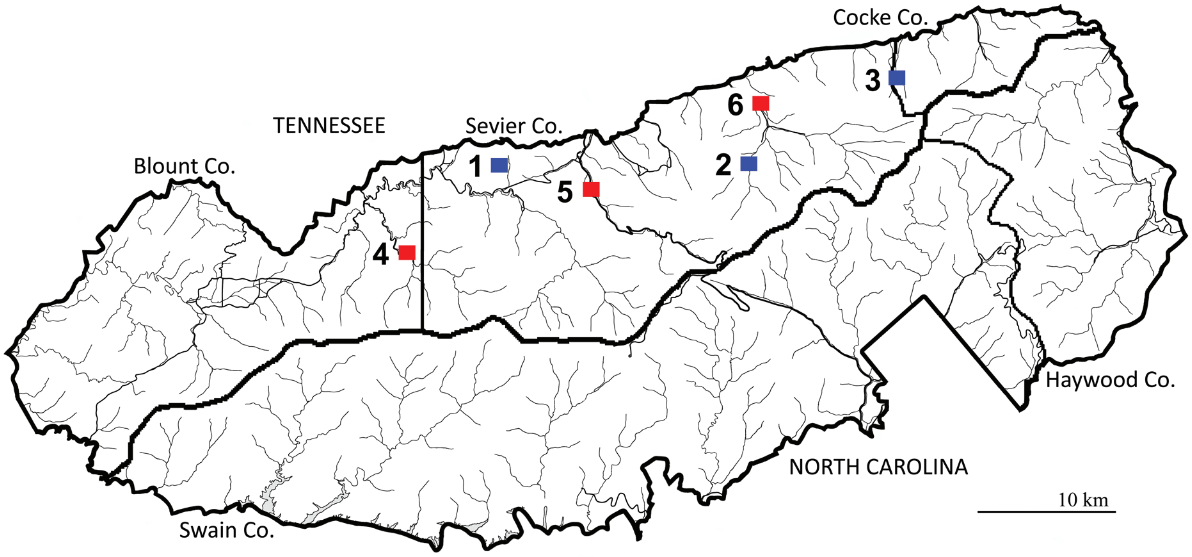


Figure 1. Map of collection locations in Great Smoky Mountains National Park. Primary forest sites: **1)** Laurel Falls; **2)** Porters Creek; **3)** Albright Grove. Secondary forest sites: **4)** Tremont; **5)** Sugarlands Quiet Walkway; **6)** Greenbrier.

vided 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 (Gove et al. 1999; Brissette et al. 2003). 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. 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 Ferro et al. 2012a) 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; Ferro and Gimmel 2011).

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 $\alpha = 0.05$ 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 $\alpha = 0.05$). 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 $\alpha = 0.05$). Chi square goodness of fit testing was performed for 71 species represented by 10 or more specimens total (degrees of freedom = 1 and $\alpha = 0.05$). 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 $\alpha = 0.05$ 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.

Results

Total. A total of 5673 adult beetle specimens, representing 305 lowest identifiable taxa within 227 genera and 51 families, was collected as part of this research (Appendix 1). 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.

Table 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 (α = 0.05), a = highest richness, b = second highest, etc.

		#Specimens	#Family	#Genus	#Species	SAC
1	Total	5673	51	227	305	/
2	FWD	1544	37	138	162	a
2	CWD	4129	46	192	247	a
3	Primary	3347	42	165	207	b
3	Secondary	2326	41	171	207	a
4	2006	1575	45	180	225	a
4	2007	4098	38	163	205	b
5	FWD1	803	24	78	91	b
5	FWD2	741	33	104	118	a
5	CWD1	1003	32	95	110	b
5	CWD2	1719	39	127	156	a
5	CWD3–4	1407	29	102	127	b
6	FWD1 – Primary	458	19	53	60	c
6	FWD2 – Primary	467	27	71	76	b
6	FWD1 – Secondary	345	17	47	51	c
6	FWD2 – Secondary	274	25	70	77	a
7	CWD1 – Primary	526	24	61	70	a
7	CWD2 – Primary	1091	32	88	107	a
7	CWD3–4 – Primary	477	26	65	84	a
7	CWD1 – Secondary	628	25	72	72	a
7	CWD2 – Secondary	805	24	67	86	a
7	CWD3–4 – Secondary	602	23	72	85	a

Staphylinidae were, 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 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. 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. 3) shows significantly higher species richness in secondary forest when normalized for number of specimens.

Table 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. 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. 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.

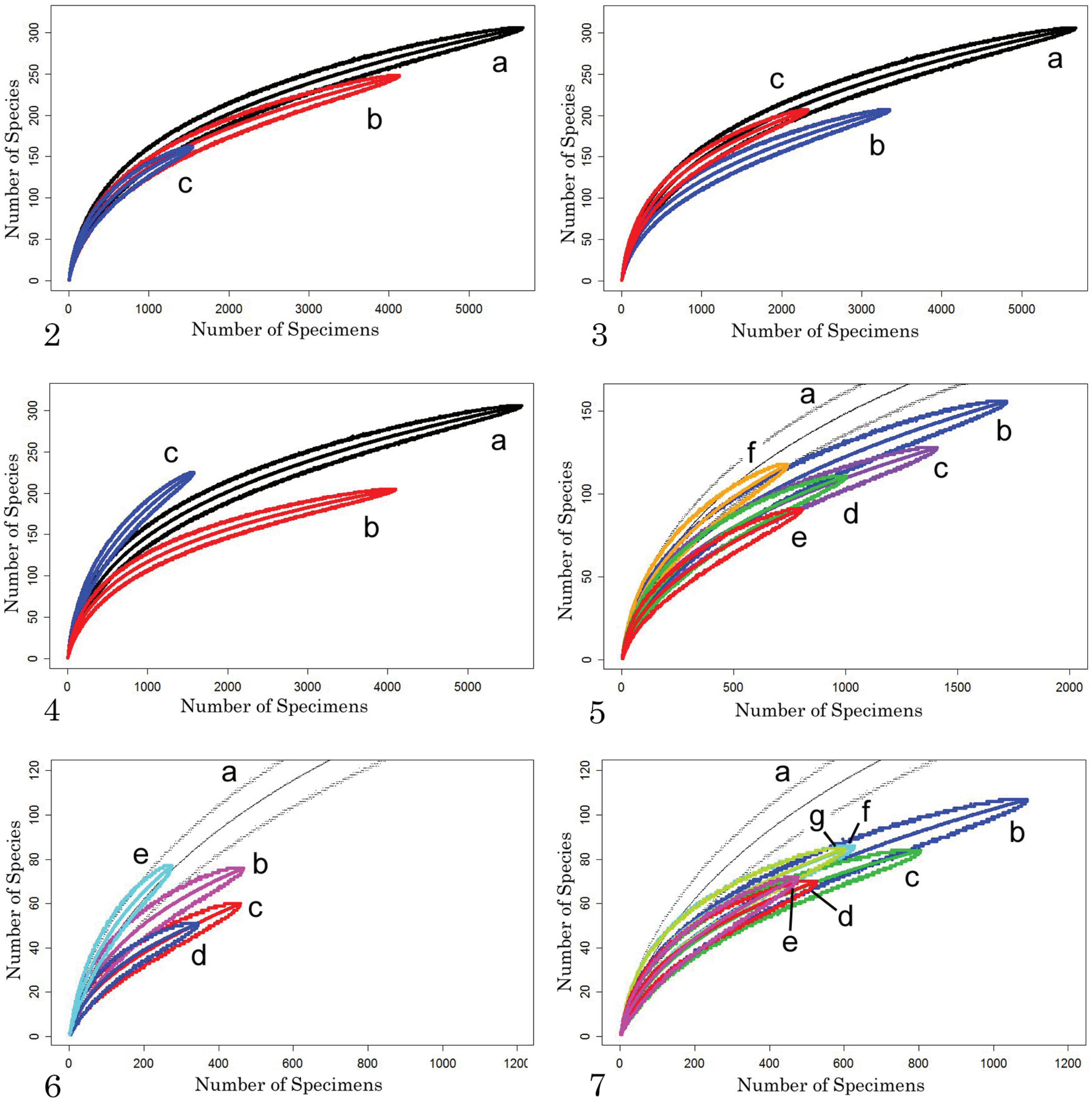
Sorensen's quotient of similarity for these substrates (Table 2) showed the least similarity between FWD1 and CWD3–4 (0.38) and the greatest similarity (0.50) between the following combinations: FWD1 and CWD1; CWD1 and CWD2; and CWD2 and CWD3–4. The null Sorensen's quotient of similarity was 0.37 (range 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. 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) 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 1) 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.



Figures 2–7. 2) Species accumulation curves for a: total; b: CWD; c: FWD.**3)** Species accumulation curves for a: total; b: primary forest; c: secondary forest. **4)** Species accumulation curves for a: total; b: 2007; c: 2006. **5)** Species accumulation curves for a: total; b: CWD2; c: CWD3-4; d: CWD1; e: FWD1; f: FWD2. **6)** Species accumulation curves for a: total; b: primary FWD2; c: primary FWD1; d: secondary FWD1; e: secondary FWD2. **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.

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 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.

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 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 1) 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. 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 2012), 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 1) 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. 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 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

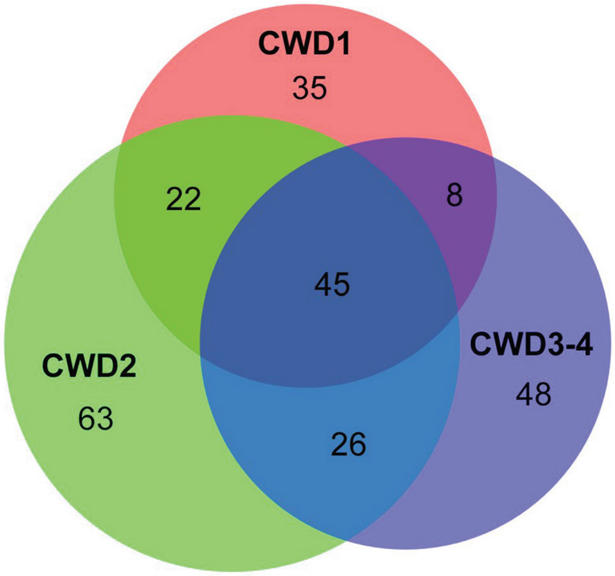


Figure 8. Species overlap among CWD decay stages. Size of circle is proportional to species richness.

for statistical evaluation (Appendix 1), 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 et al. (2012a). 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 et al. (2012a) 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 1). 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 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.

Table 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

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. 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 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 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. 3). However, primary forest had more statistically associated species than secondary forest (Appendix 1). 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 et al. (2012a) 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 1). 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 et al. (2012a) 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 was 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* Motschulsky, Ferro and Gimmel (2011) 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 (Ferro et al. 2012a) and flight intercept traps were used to compare their effectiveness at sampling saproxylic Coleoptera with sifting and emergence (Ferro et al. 2012b).

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); Osoriinae: *Thoracophorus* (Ferro and Gimmel 2011); 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.

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.

BUPRESTIDAE
Chrysochroinae

Dicerca divaricata (Say) (Fig. 9)
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:** Packard 1890; Blatchley 1910; Nelson 1975; Downie and Arnett 1996; MacRae 2006; Nelson et al. 2008; Majka et al. 2011.

CARABIDAE
Harpalinae

Gastrellarius honestus (Say) (Fig. 10)
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:** Blatchley 1910 (as *Pterostichus honestus* Say); Lindroth 1961–1969 (as *P. honestus*); Bousquet and Larochelle 1993; Downie and Arnett 1996; Ciegler 2000; Ball and Bousquet 2001; Majka et al. 2011.

Trechinae

Mioptachys flavicauda (Say) (Fig. 11)
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:** Ulke 1903 (as *Tachys flavicauda* Say); Blatchley 1910 (as *T. flavicauda*); Lindroth 1961–1969 (as *T. flavicauda*); Nelson 1991; Bousquet and Larochelle 1993; Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2000; Majka et al. 2011.

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 (Linsley 1961, 1962a,b, 1963, 1964; Chemsak 1963; 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). Cerambycidae of northeastern North America are treated in a field guide by Yanega (1996).

Lamiinae

Eupogonius pauper LeConte (Fig. 12)
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:** Linsley and Chemsak 1984, 1997; Downie and Arnett 1996; Peck and Thomas 1998; Lingafelter 2007; Majka et al. 2011.

Leptostylus transversus (Gyllenhal) (Fig. 13)
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:** Linsley and Chemsak 1995, 1997; Downie and Arnett 1996; Peck and Thomas 1998; Lingafelter 2007.

Microgoes oculatus (LeConte) (Fig. 14)
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:** Linsley and Chemsak 1984, 1997; Downie and Arnett 1996; Turnbow and Thomas 2002; Lingafelter 2007; Majka et al. 2011.

Urographis fasciatus (DeGeer) (Fig. 15)
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:** Packard 1890; Linsley and Chemsak 1995, 1997; Downie and Arnett 1996; Peck and Thomas 1998; Lingafelter 2007.

Lepturinae

Analeptura lineola Say (Fig. 16)
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:** Linsley and Chemsak 1976, 1997; Downie and Arnett 1996; Peck and Thomas 1998; Turnbow and Thomas 2002; Lingafelter 2007; Majka et al. 2011.

Trachysida mutabilis (Newman) (Fig. 17)
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:** Linsley and Chemsak 1976, 1997; Downie and Arnett 1996; Lingafelter 2007; Majka et al. 2011.

CERYLONIDAE

Cerylon castaneum Say (Fig. 18)
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; Lawrence and Stephan 1975; Lawrence 1982a; Downie and Arnett 1996; Majka et al. 2011.

Mychocerus striatus (Sen Gupta and Crowson) (Fig. 19)
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. (2012a):** significantly more abundant in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in CWD3–4 and secondary forest. **References:** Sen Gupta and Crowson 1973 (as *Lapecautomus striatus* Sen Gupta and Crowson); Lawrence and Stephan 1975 (as *Lapethus striatus* (Sen Gupta and Crowson)); Lawrence 1982a.

Philothermus glabriculus (LeConte) (Fig. 20)
Range: eastern North America, Ontario and Maine 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; Lawrence and Stephan 1975; Lawrence 1982a; Downie and Arnett 1996; Peck and Thomas 1998; Gimmel and Slipinski 2007; Majka et al. 2011.

CIIDAE

Ceracis singularis (Dury) (Fig. 21)
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. and D. Sacc. **Collection Method:** emergence. **Biology:** breeds in polypore fungi. **Present Study:** significantly higher abundance in CWD2 and secondary forest. **References:** Lawrence 1967, 1971, 1982b; Downie and Arnett 1996; Peck and Thomas 1998.

Octotemnus laevis Casey (Fig. 22)
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; Lawrence 1971, 1973, 1982b; Downie and Arnett 1996; Thayer and Lawrence 2002; Majka et al. 2011.

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. 23)
Comments. 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. 24)
Comments. 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; Woodroffe and Coombs 1961; Bousquet 1989, 1990; Downie and Arnett 1996 (usefulness of keys unknown); Leschen 1996; Peck and Thomas 1998; Leschen and Skelley 2002; Majka and Langor 2010; Majka et al. 2011.

CURCULIONIDAE

Cossoninae

Caulophilus dubius (Horn) (Fig. 25)
Range: throughout eastern United States: New York to Florida, west to Michigan and Texas. **Habitat:** under bark of dead trees and *Vitis* (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. (2012a):** 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); Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2010.

Stenoscelis brevis (Boheman) (Fig. 26)
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:** Packard 1890; Blatchley and Leng 1916; Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2010; Majka et al. 2011.

Cryptorhynchinae

Apteromechus ferratus (Say) (Fig. 27)
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:** Blatchley and Leng 1916; Whitehead 1979; Downie and Arnett 1996; Peck and Thomas 1998; Anderson 2002; Ciegler 2010.

Cophes fallax (LeConte) (Fig. 28)
Comments. *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:** Blatchley and Leng 1916 (as *Cryptorhynchus fallax* LeConte); Downie and Arnett 1996; Peck and Thomas 1998; Anderson 2002; Ciegler 2010.

Dryophthorinae

Dryophthorus americanus (Bedel) (Fig. 29)
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. (2012a):** significantly higher abundance in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in FWD1, CWD2, and primary forest. **References:** Blatchley and Leng 1916; Anderson 2002; Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2010; Majka et al. 2011.

Scolytinae

Xyleborus atratus Eichhoff (Fig. 30)
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; Peck and Thomas 1998; Vandenberg et al. 2000; Majka et al. 2011.

Xylosandrus crassiusculus (Motschulsky) (Fig. 31)
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:** Wood 1982 (and references therein); Peck and Thomas 1998; Rabaglia 2003.

Xylosandrus germanus (Blandford) (Fig. 32)
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:** Hoffmann 1941; Wood 1982; Downie and Arnett 1996; Peck and Thomas 1998; Rabaglia 2003; Majka et al. 2011.

Xyloterinus politus (Say) (Fig. 33)
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:** Wood 1982; Downie and Arnett 1996; Anderson 2002; Majka et al. 2011.

ELATERIDAE

Elateridae are the ninth most diverse family of beetles in the world but are 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. 34)
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:** LeConte 1853 (as *Elater areolatus* Say); Blatchley 1910 (as *E. areolatus*); Dietrich 1945; Downie and Arnett 1996; Peck and Thomas 1998; Majka and Johnson 2008; Majka et al. 2011.

Ampedus luteolus (LeConte) (Fig. 35)
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:** LeConte 1853 (as *Elater luteolus* LeConte); Dietrich 1945; Downie and Arnett 1996.

Ampedus semicinctus (Randall) (Fig. 36)
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:** LeConte 1853 (as *Elater semicinctus* Randall); Dietrich 1945; Downie and Arnett 1996; Majka and Johnson 2008; Majka et al. 2011.

ENDOMYCHIDAE

Bystus ulkei (Crotch) (Fig. 37)
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:** Crotch 1873 (as *Alexia ulkei* Crotch); Blatchley 1910 (as *Rhymbus ulkei* (Crotch)); Boving and Craighead 1930 (as *R. ulkei)*; Strohecker 1986; Peck and Thomas 1998; Shockley et al. 2009.

EUCINETIDAE

Tohlezkus inexpectus Vit (Fig. 38)
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. (2012a):** 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. 39)
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:** Dury 1888 (as *Deltometopus rufipes* (Melsheimer)); Knull 1947 (as *Del. rufipes*); Downie and Arnett 1996 (as *Dromaeolus rufipes* (Melsheimer)); Muona 2000.

Isorhipis obliqua (Say) (Fig. 40)
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:** Knull 1946; Peterson 1960 (illustrated larva); Downie and Arnett 1996; Peck and Thomas 1998; Muona 2000; Majka 2007b; Majka et al. 2011.

Melasis pectinicornis Melsheimer (Fig. 41)
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:** Dury 1888; Blatchley 1910; Kirk 1922; Hopping 1926; Peterson 1960 (illustrated larva); Downie and Arnett 1996; Peck and Thomas 1998; Muona 2000.

Microrhagus subsinuatus LeConte (Fig. 42)
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:** Dury 1888; Knull 1946 (as *Dirhagus imperfectus* (LeConte)); Downie and Arnett 1996; Muona 2000; Majka 2007b; Majka et al. 2011.

HISTERIDAE

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

Bacanius tantillus LeConte (Fig. 43)
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:** Horn 1873; Casey 1893 (key to most species); Blatchley 1910; Wenzel 1960; Downie and Arnett 1996; Peck and Thomas 1998; Kovarik and Caterino 2002.

LEIODIDAE

Leiodinae

***Agathidium* spp.** (female) (Fig. 44)
Comments. 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. (2012a):** 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); Peck and Thomas 1998; Miller and Wheeler 2005; Wheeler and Miller 2005; Majka et al. 2011.

MELANDRYIDAE

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

Dircaea liturata (LeConte) (Fig. 45)
Range: northeastern 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:** Felt 1906 (as *Phloeotrya liturata* LeConte); Blatchley 1910 (as *Phloeotrya quadrimaculata* Say); Downie and Arnett 1996; Peck and Thomas 1998; Pollock 2002a; Majka et al. 2011.

Hypulus simulator Newman (Fig. 46)
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:** Packard 1890; Downie and Arnett 1996 (as *Mystaxus simulator* Newman); Pollock 2002a; Majka et al. 2011.

PTILIIDAE

Ptiliidae are 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. 47)
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; Dybas 1990; Downie and Arnett 1996; Hall 2001.

Acrotrichinae

***Acrotrichis* spp.** (Fig. 48)
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. (2012a):** 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; Dybas 1990; Downie and Arnett 1996; Peck and Thomas 1998; Hall 2001.

Ptiliinae

***Pteryx* spp.** (Fig. 49)
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. (2012a):** 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; Dybas 1990; Downie and Arnett 1996; Hall 2001; Majka et al. 2011.

PTINIDAE (formerly ANOBIIDAE)
Anobiinae

Oligomerus obtusus LeConte (Fig. 50)
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; White 1962, 1976, 1982; Downie and Arnett 1996.

Priobium sericeum (Say) (Fig. 51)
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)); White 1962 (as *T. sericeus*), 1982; Downie and Arnett 1996; Peck and Thomas 1998; Majka 2007a; Majka et al. 2011.

PYROCHROIDAE

Dendroides canadensis Latreille (Fig. 52)
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:** Payne 1931; Young 1975, 1983, 2002; Downie and Arnett 1996; Peck and Thomas 1998; Majka et al. 2011.

Dendroides concolor (Newman) (Fig. 53)
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:** Packard 1890; MacGillivray and Houghton 1902; Blatchley 1910; Young 1975, 1983, 2002; Downie and Arnett 1996; Majka et al. 2011.

RHYSODIDAE

Clinidium baldufi Bell (Fig. 54)
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; Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2000.

SALPINGIDAE

Rhinosimus viridiaeneus (Randall) (Fig. 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:** Blatchley 1910; Blair 1932; Howden and Howden 1981; Downie and Arnett 1996; Pollock 2002b; Majka et al. 2011.

STAPHYLINIDAE
Aleocharinae

Aleocharinae gen. spp. (Fig. 56)
Comments. These specimens could not be reliably identified to genus. Aleocharinae are the largest subfamily of Staphylinidae with 21 tribes, 183 genera, and 1385 described species known from North America and are 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. (2012a):** 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. 57)
Comments. 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. (2012a):** significantly higher abundance in leaf litter and spring, indifferent to forest type. **Present Study:** not significantly associated with any substrate or forest type. **References:** Seevers 1978; Downie and Arnett 1996; Newton et al. 2001; Gusarov 2002a–e, 2003a–e, 2004a–b; Elven et al. 2010.

Atheta spp. (Fig. 58)
Comments. These specimens could only be reliably identified to the genus *Atheta* Thomson. Gusarov (2003e) 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.); Peck and Thomas 1998; Newton et al. 2001 (as *Xenota* sp.); Gusarov 2003e; Majka et al. 2011.

Leptusa carolinensis Pace (Fig. 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. **Col-**

lection 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:** Pace 1989; Klimaszewski et al. 2004; Gouix and Klimaszewski 2007; Webster et al. 2009; Park et al. 2010.

Leptusa cribratula (Casey) (Fig. 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; Klimaszewski et al. 2004; Gouix and Klimaszewski 2007.

Leptusa pusio (Casey) (Fig. 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. (2012a):** 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. 62)
Comments. 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. (2012a):** 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. 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. (2012a):** significantly higher abundance in CWD5, secondary forest, and spring. **Present Study:** significantly higher abundance in FWD2, CWD3–4, and primary forest. **References:** Horn 1871 (as *Glyptoma costale* Erichson, figure and key to common species in North America); Blatchley 1910; Notman 1920; Irmler 1985; Downie and Arnett 1996 (figure is not *T. costalis*); Peck and Thomas 1998; Ferro and Gimmel 2011; Majka et al. 2011.

Pselaphinae

Adranes lecontei Brendel (Fig. 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. (2012a):** 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:** Wickham 1901; Blatchley 1910; Park 1932a (with notes on life history), 1935, 1964; Akre and Hill 1973; Hill et al. 1976; Downie and Arnett 1996; Newton et al. 2001.

***Batrisodes* spp.** (female) (Fig. 65)
Comments. 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. (2012a):** indifferent to substrate, forest type, and season. **Present Study:** not significantly associated with any substrate or forest type. **References:** Blatchley 1910; Park 1932b, 1947, 1948; Chandler 1990a; Downie and Arnett 1996; Peck and Thomas 1998; Newton et al. 2001; Majka et al. 2011.

Leptoplectus pertenuis (Casey) (Fig. 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:** Wagner 1975; Grigarick and Schuster; Peck and Thomas 1998; Newton et al. 2001.

***Pycnoplectus* spp**. (female) (Fig. 67)
Comments. 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:** Wagner 1975; Grigarick and Schuster 1980; Chandler 1990a; Peck and Thomas 1998; Newton et al. 2001.

***Sonoma* spp.** (female) (Fig. 68)
Comments. 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. (2012a):** 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; Newton et al. 2001; Ferro and Carlton 2010.

Trimioplectus obsoletus Brendel (Fig. 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:** Brendel and Wickham 1890–1891; Blatchley 1910; Park 1949; Grigarick and Schuster 1980; Chandler 1990b.

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. 70)
***Euconnus* (*Scopophus*) n. sp.** Casey (Fig. 71)
***Euconnus* (*Scopophus*) spp.** Casey (Fig. 72)

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. **Ferro et al. (2012a):** 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); Peck and Thomas 1998; O'Keefe 2001; Grebennikov and Newton 2009; Majka et al. 2011.

Staphylininae

Hesperus apicialis (Say) (Fig. 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:** Horn 1884 (as *Philonthus apicalis* (Say)); Blatchley 1910 (as *Hesperus apicalis* (Say)); Moore 1958; Frank 1983; Smetana 1995; Downie and Arnett 1996 (as *H. apicalis*); Peck and Thomas 1998; Majka et al. 2011.

Tachyporinae

Sepedophilus brachypterus Campbell (Fig. 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; Newton 1984; Downie and Arnett 1996; Majka et al. 2011.

Sepedophilus cinctulus (Erichson) (Fig. 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; Newton 1984; Downie and Arnett 1996; Majka et al. 2011.

Sepedophilus occultus (Casey) (Fig. 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. 77)
Comments. 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:** Packard 1890; Fall 1931; Downie and Arnett 1996; Peck and Thomas 1998; Dunford and Young 2004; Majka et al. 2008, 2011; Steiner 2008.

Strongylium crenatum Mäklin (Fig. 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:** Triplehorn and Spilman 1973; Downie and Arnett 1996; Peck and Thomas 1998.

THROSCIDAE

Aulonothroscus distans Blanchard (Fig. 79)
Comments. 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.

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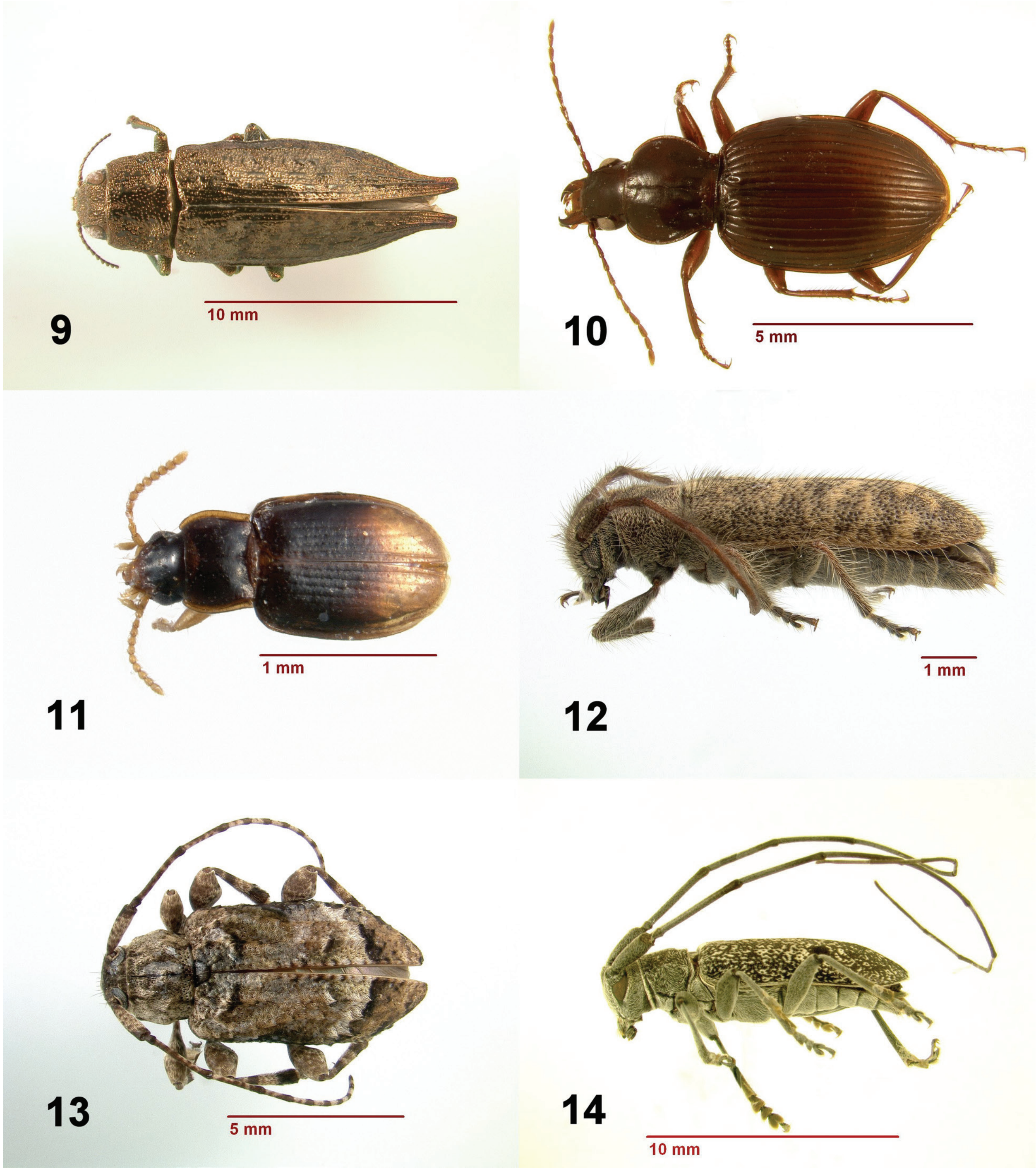

Figures 9–14. Habitus images. **9)** *Dicerca divaricata* (Say) (Buprestidae: Chrysochroinae). **10)** *Gastrellarius honestus* (Say) (Carabidae: Harpalinae). **11)** *Mioptachys flavicauda* (Say) (Carabidae: Trechinae). **12)** *Eupogonius pauper* LeConte (Cerambycidae: Lamiinae). **13)** *Leptostylus transversus* (Gyllenhal) (Cerambycidae: Lamiinae). **14)** *Microgoes oculatus* (LeConte) (Cerambycidae: Lamiinae).


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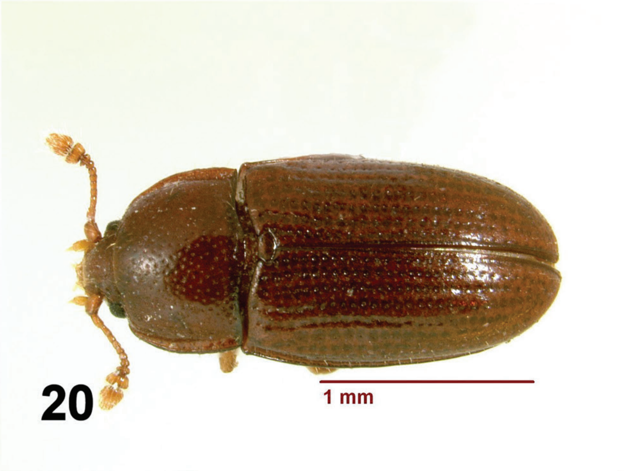
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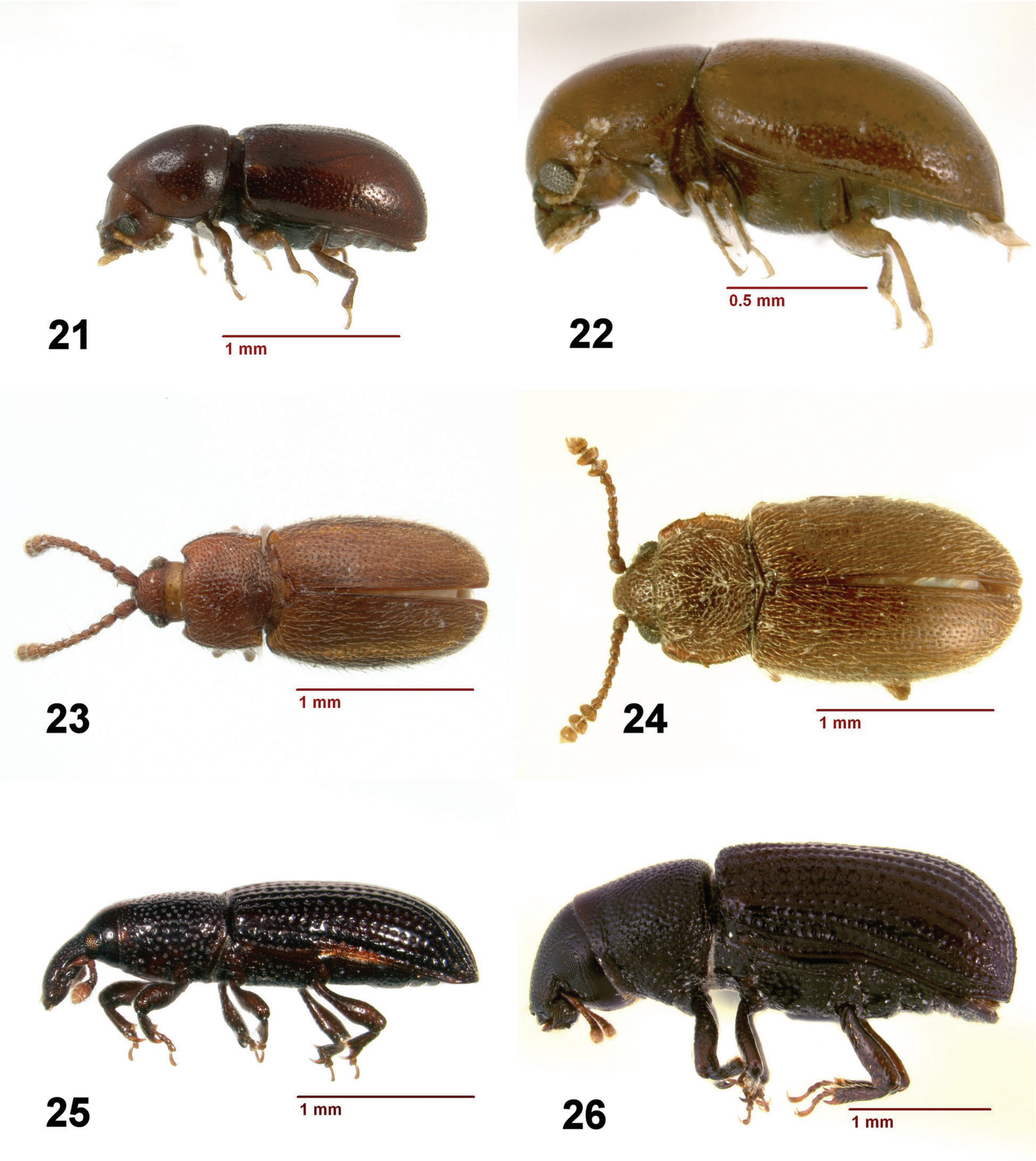
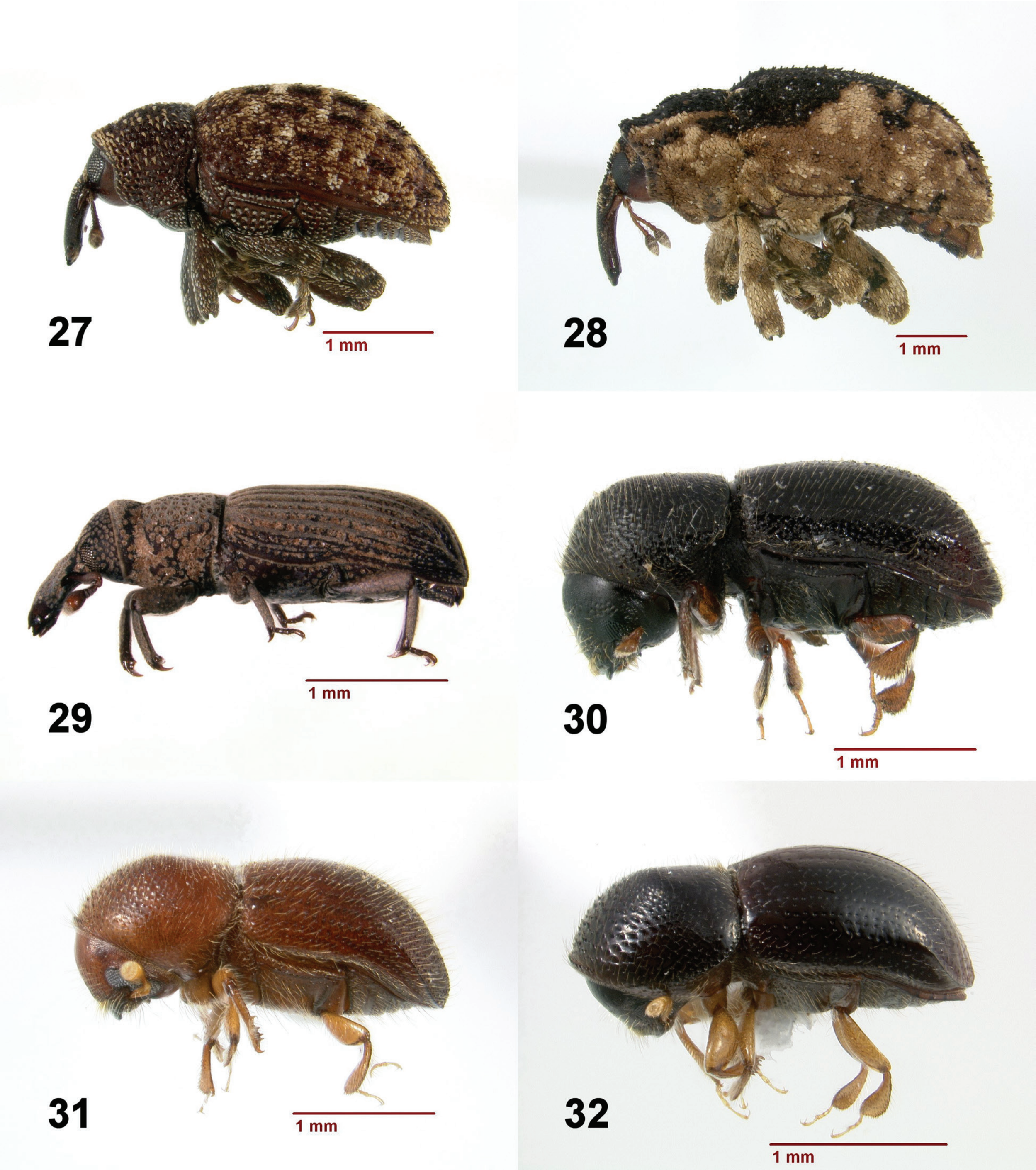
Figures 15–20. Habitus images. **15)** *Urographis fasciatus* (Degeer) (Cerambycidae: Lamiinae). **16)** *Analeptura lineola* Say (Cerambycidae: Lepturinae). **17)** *Trachysida mutabilis* (Newman) (Cerambycidae: Lepturinae). **18)** *Cerylon castaneum* Say (Cerylonidae). **19)** *Mychocerus striatus* (Sen Gupta and Crowson) (Cerylonidae). **20)** *Philothermus glabriculus* (LeConte) (Cerylonidae).



Figures 21–26. Habitus images. **21)** *Ceracis singularis* (Dury) (Ciidae). **22)** *Octotemnus laevis* Casey (Ciidae). **23)** *Atomaria* sp. (Cryptophagidae). **24)** *Cryptophagus* sp. (Cryptophagidae). **25)** *Caulophilus dubius* (Horn) (Curculionidae: Cossoninae). **26)** *Stenoscelis brevis* (Boheman) (Curculionidae: Cossoninae).



Figures 27–32. Habitus images. **27)** *Apteromechus ferratus* (Say) (Curculionidae: Cryptorhynchinae). **28)** *Cophes fallax* (LeConte) (Curculionidae: Cryptorhynchinae). **29)** *Dryophthorus americanus* (Bedel) (Curculionidae: Dryophthorinae). **30)** *Xyleborus atratus* Eichhoff (Curculionidae: Scolytinae). **31)** *Xylosandrus crassiusculus* (Motschulsky) (Curculionidae: Scolytinae). **32)** *Xylosandrus germanus* (Blandford) (Curculionidae: Scolytinae).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Figures 33–38. Habitus images. **33)** *Xyloterinus politus* (Say) (Curculionidae: Scolytinae). **34)** *Ampedus areolatus* (Say) (Elateridae). **35)** *Ampedus luteolus* (LeConte) (Elateridae). **36)** *Ampedus semicinctus* (Randall) (Elateridae). **37)** *Bystus ulkei* (Crotch) (Endomychidae). **38)** *Tohlezkus inexpectus* Vit (Eucinetidae).

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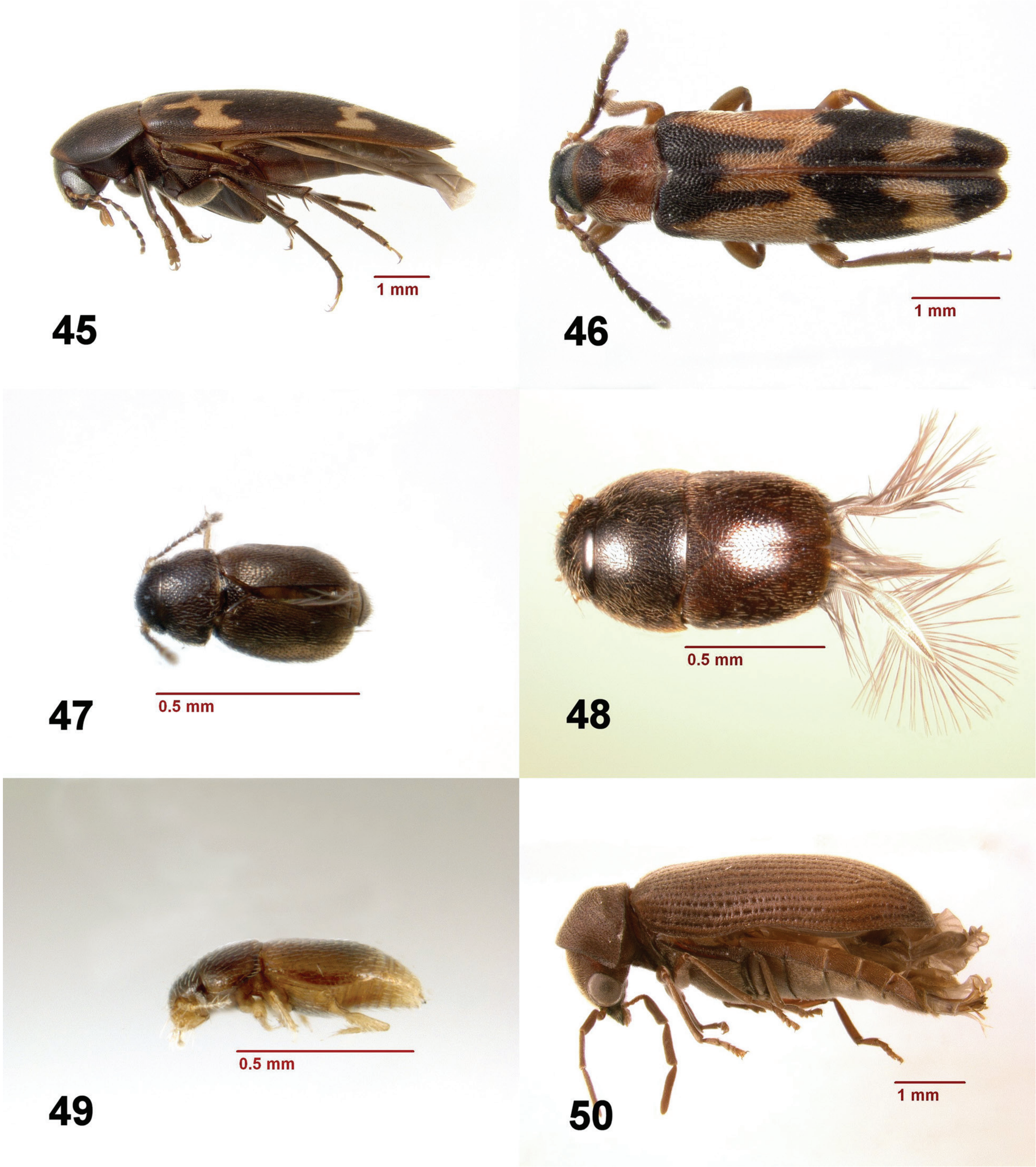
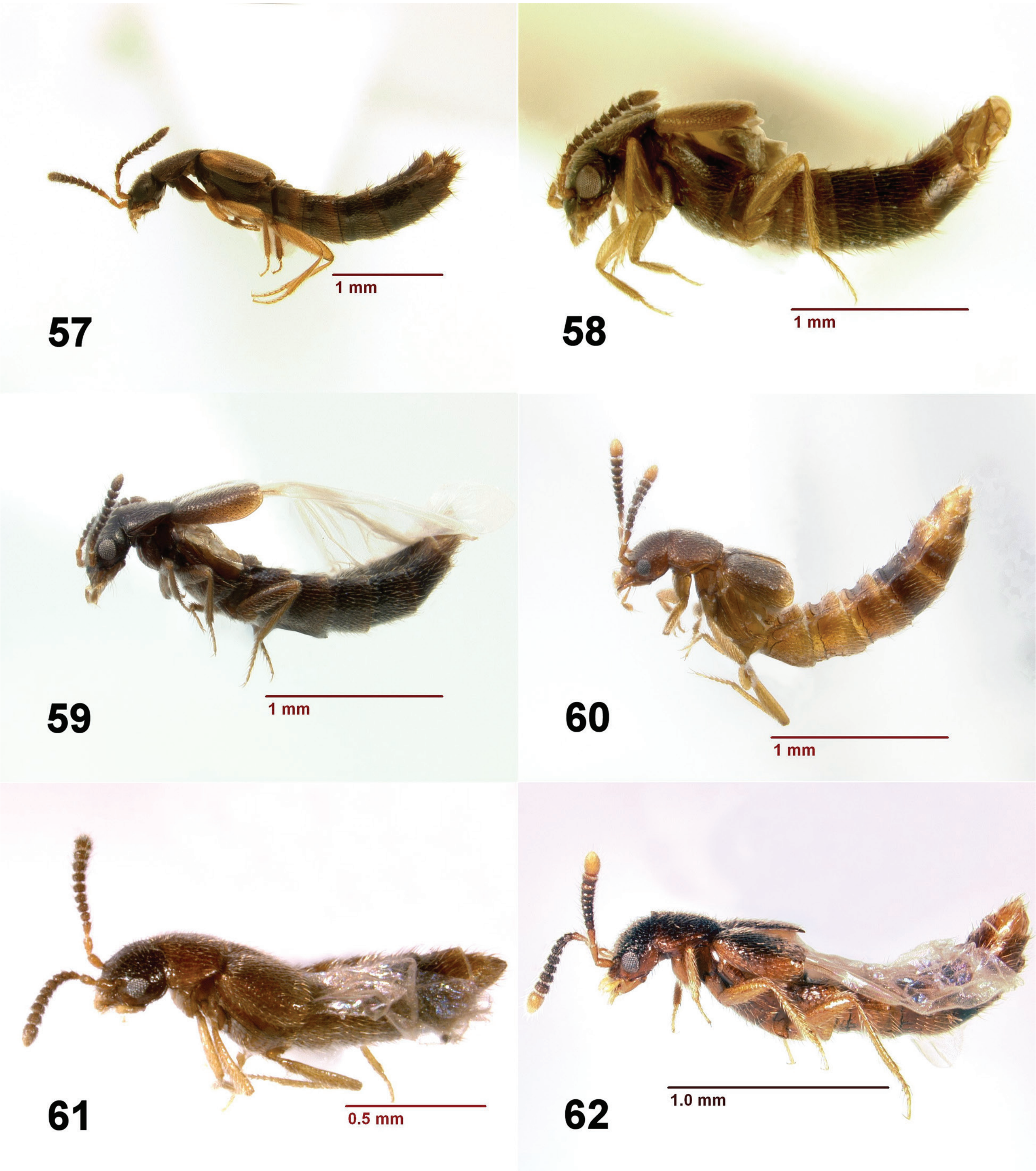
Figures 39–44. Habitus images. **39)** *Isarthrus rufipes* (Melsheimer) (Eucnemidae). **40)** *Isorhipis obliqua* (Say) (Eucnemidae). **41)** *Melasis pectinicornis* Melsheimer (Eucnemidae). **42)** *Microrhagus subsinuatus* LeConte (Eucnemidae). **43)** *Bacanius tantillus* LeConte (Histeridae). **44)** *Agathidium* sp. (female) (Leiodidae: Leiodinae).



Figures 45–50. Habitus images. **45)** *Dircaea liturata* (LeConte) (Melandryidae). **46)** *Hypulus simulator* Newman (Melandryidae). **47)** Ptiliidae gen. sp. (Ptiliidae). **48)** *Acrotrichis* sp. (Ptiliidae: Acrotrichinae). **49)** *Pteryx* sp. (Ptiliidae: Ptiliinae). **50)** *Oligomerus obtusus* LeConte (Ptinidae: Anobiinae).

Figures 51–56. Habitus images. **51)** *Priobium sericeum* (Say) (Ptinidae: Anobiinae). **52)** *Dendroides canadensis* Latreille (Pyrochroidae). **53)** *Dendroides concolor* (Newman) (Pyrochroidae). **54)** *Clinidium baldufi* Bell (Rhysodidae). **55)** *Rhinosimus viridiaeneus* (Randall) (Salpingidae). **56)** Aleocharinae gen. sp. (Staphylinidae: Aleocharinae).



Figures 57–62. Habitus images. **57)** Athetini sp. (Staphylinidae: Aleocharinae). **58)** *Atheta* sp. (Staphylinidae: Aleocharinae). **59)** *Leptusa carolinensis* Pace (Staphylinidae: Aleocharinae). **60)** *Leptusa cribratula* (Casey) (Staphylinidae: Aleocharinae). **61)** *Leptusa pusio* (Casey) (Staphylinidae: Aleocharinae). **62)** *Leptusa* sp. (Staphylinidae: Aleocharinae).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Figures 63–68. Habitus images. **63)** *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae). **64)** *Adranes lecontei* Brendel (Staphylinidae: Pselaphinae). **65)** *Batrisodes* sp. (female) (Staphylinidae: Pselaphinae). **66)** *Leptoplectus pertenuis* (Casey) (Staphylinidae: Pselaphinae). **67)** *Pycnoplectus* sp. (female) (Staphylinidae: Pselaphinae). **68)** *Sonoma* sp. (female) (Staphylinidae: Pselaphinae).

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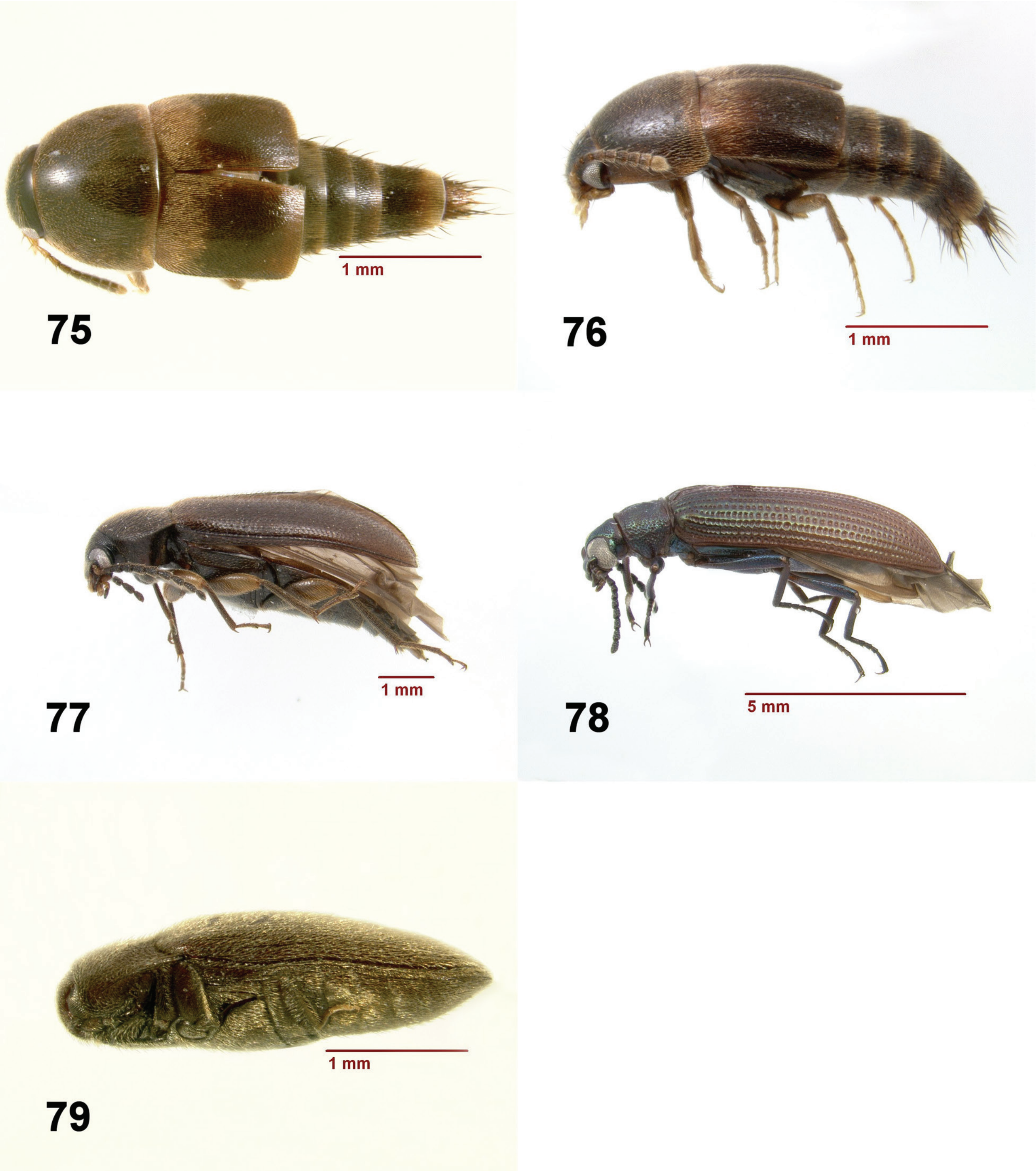
Figures 69–74. Habitus images. **69)** *Trimioplectus obsoletus* Brendel (Staphylinidae: Pselaphinae). **70**) *Euconnus* (*Napochus*) sp. (Staphylinidae: Scydmaeninae). **71)** *Euconnus* (*Scopophus*) n. sp. (Staphylinidae: Scydmaeninae). **72)** *Euconnus* (*Scopophus*) sp. (Staphylinidae: Scydmaeninae). **73)** *Hesperus apicialis* (Say) (Staphylinidae: Staphylininae). **74)** *Sepedophilus brachypterus* Campbell (Staphylinidae: Tachyporinae).



Figures 75–79. Habitus images. **75)** *Sepedophilus cinctulus* (Erichson) (Staphylinidae: Tachyporinae). **76)** *Sepedophilus occultus* (Casey) (Staphylinidae: Tachyporinae). **77)** *Hymenorus* sp. (female) (Tenebrionidae). **78)** *Strongylium crenatum* Mäklin (Tenebrionidae). **79)** *Aulonothroscus distans* Blanchard (Throscidae).

Appendix 1. List of taxa and number of specimens collected as part of this research. 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. (2012a), 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	–
ANTHRIBIDAE										
2	*Eurymycter tricarinatus* Pierce	0	1	0	0	1	1	1	2	
3	*Ormiscus* spp.	1	0	0	1	0	2	0	2	–
BUPRESTIDAE										
4	*Agrilus masculinus* Horn	2	0	0	0	0	2	0	2	–
5	*Agrilus* spp.	3	0	0	0	0	3	0	3	–
6	*Dicerca divaricata* (Say)	0	3	5	2	0	6	4	10	–
							X=0.40	***P*=0.5271**		
CARABIDAE										
7	*Agonum ferreum* Haldeman	1	0	0	0	0	0	1	1	–
8	*Anillinus loweae* Sokolov and Carlton	0	0	0	0	1	0	1	1	–
9	Carabidae gen. sp. (teneral specimen)	0	0	0	1	0	1	0	1	–
10	*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**		
11	*Harpalus spadiceus* Dejean	0	0	0	0	1	0	1	1	1
12	*Mioptachys flavicauda* (Say)	0	1	2	8	0	8	3	11	–
							X=2.27	***P*=0.1317**		
13	*Polyderis laevis* (Say)	0	0	0	0	1	1	0	1	3
14	*Pterostichus tristis* (Dejean)	0	0	0	1	0	0	1	1	–
15	*Trechus* (*Microtrechus*) *pisgahensis* Barr	0	0	0	0	2	0	2	2	23

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
CERAMBYCIDAE										
16	*Aegomorphus modestus* (Gyllenhal)	0	1	0	4	0	5	0	5	–
17	*Aegomorphus quadrigibbus* (Say)	0	2	0	0	0	0	2	2	–
18	*Analeptura lineola* Say	0	25****	0	0	1	4	22***	26	–
		X=25.00	***P*<0.0001**				**X=12.46**	***P*=0.0004**		
19	*Anoplodera pubera* (Say)	0	0	0	1	0	0	1	1	–
20	*Astylopsis maculata* (Say)	3	1	0	1	0	4	1	5	–
21	*Bellamira scalaris* (Say)	0	0	0	3	0	3	0	3	–
22	*Clytus ruricola* (Olivier)	1	1	0	0	1	0	3	3	–
23	*Cyrtophorus verrucosus* (Olivier)	0	1	0	1	0	1	1	2	–
24	*Elaphidion mucronatum* (Say)	0	0	4	0	0	4	0	4	–
25	*Eupogonius pauper* LeConte	27****	0	0	0	0	27****	0	27	–
		X=27.00	***P*<0.0001**				**X=27.00**	***P*<0.0001**		
26	*Grammoptera exigua* (Newman)	0	1	0	0	0	1	0	1	–
27	*Hyperplatys aspersa* (Say)	0	2	0	0	0	2	0	2	–
28	*Leptorhabdium pictum* (Haldeman)	0	0	2	0	0	0	2	2	–
29	*Leptostylus transversus* (Gyllenhal)	2	0	7	4	1	14***	0	14	–
							X=14.00	***P*=0.0002**		
30	*Lepturges confluens* (Haldeman)	0	1	0	0	0	1	0	1	–
31	*Microgoes oculatus* (LeConte)	13	8	8	2	0	9	22*	31	–
		X=1.19	***P*=0.2752**				**X=5.45**	***P*=0.0196**		
32	*Molorchus b. bimaculatus* Say	4	0	0	0	0	4	0	4	–
33	*Neandra brunnea* (Fabricius)	1	0	1	3	0	1	4	5	–
34	*Oplosia nubila* (LeConte)	2	0	0	5	0	5	2	7	–
35	*Pidonia ruficollis* (Say)	0	1	1	1	0	0	3	3	–
36	*Saperda vestita* Say	0	0	0	1	0	1	0	1	–
37	*Strangalepta abbreviata* (Germar)	0	1	0	0	0	1	0	1	–
38	*Strangalia luteicornis* (Fabricius)	0	2	0	0	0	2	0	2	–

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
39	*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**		
40	*Typocerus velutinus* (Olivier)	0	2	0	0	3	4	1	5	–
41	*Urgleptes foveatocollis* (Hamilton)	0	1	0	0	0	1	0	1	–
42	*Urgleptes querci* (Fitch)	2	1	0	0	0	2	1	3	–
43	*Urographis fasciatus* (DeGeer)	0	0	13	0	0	0	13***	13	–
							X=13.00	***P*=0.0003**		
44	*Xylotrechus nitidus* (Horn)	1	0	0	0	0	1	0	1	–
CERYLONIDAE										
45	*Cerylon castaneum* Say	0	0	4	8	0	0	12***	12	–
							X=12	***P*=0.0005**		
46	*Cerylon unicolor* Ziegler	0	0	1	0	0	1	0	1	–
47	*Hypodacne punctata* LeConte	0	1	0	0	0	1	0	1	–
48	*Mychocerus striatus* (Sen Gupta and Crowson)	0	0	0	0	15****	14***	1	15	246 (a)
				***P*=0.0820**	***P*=0.0820**	***P*<0.0001**	**X=11.27**	***P*=0.0008**		
49	*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										
50	*Cryptocephalus quadruplex* Newman	0	1	0	0	0	0	1	1	–
51	*Tymnes* sp.	0	0	0	1	0	0	1	1	–
CIIDAE										
52	*Ceracis sallei* Mellie	0	0	0	4	0	4	0	4	–
53	*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**		
54	*Ceracis* spp.	0	0	0	7	0	7	0	7	1

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
55 *Ceracis thoracicornis* Ziegler	0	0	0	3	0	3	0	3	–
56 Ciidae gen. spp.	1	1	0	1	1	1	3	4	–
57 *Cis fuscipes* Mellie	0	0	4	0	2	0	6	6	–
58 *Cis miles* (Casey)	0	0	0	0	1	1	0	1	–
59 *Octotemnus laevis* Casey	42****	0	0	1	3	2	44****	46	–
	X=42.00	***P*<0.0001**				**X=38.35**	***P*<0.0001**		
60 *Rhopalodontus* sp.	1	0	0	0	0	0	1	1	–
CLERIDAE									
61 *Cymatodera bicolor* (Say)	0	0	0	0	1	1	0	1	–
COLYDIIDAE									
62 *Paha laticollis* (LeConte)	0	1	0	0	0	1	0	1	–
63 *Synchita fuliginosa* Melsheimer	0	0	0	2	0	0	2	2	–
CORYLOPHIDAE									
64 Corylophidae gen. sp.	0	0	0	1	0	0	1	1	–
65 *Sericoderus* spp.	0	0	1	1	0	1	1	2	–
CRYPTOPHAGIDAE									
66 *Atomaria* spp.	2	11*	6	4	3	13	13	26	–
	X=6.23	***P*=0.0125**				**X=0.00**	**P=1**		
67 *Caenoscelis* spp.	0	0	0	2	0	0	2	2	–
68 *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									
69 *Cucujus clavipes* Fabricius	0	0	0	1	0	1	0	1	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
CUPEDIDAE									
70 *Cupes capitatus* Fabricius	0	1	1	1	0	1	2	3	–
CURCULIONIDAE									
71 *Acalles carinatus* LeConte	2	1	0	0	0	1	2	3	–
72 *Acoptus suturalis* LeConte	1	0	0	1	0	1	1	2	–
73 *Apteromechus ferratus* (Say)	2	1	10	0	0	13***	0	13	–
						X=13.00	***P*=0.0003**		
74 *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**		
75 *Cercopeus* sp.	0	0	1	0	0	0	1	1	–
76 *Cophes fallax* (LeConte)	19****	0	0	0	0	19****	0	19	–
	X=19.00	***P*<0.0001**				**X=19.00**	***P*<0.0001**		
77 *Cophes obtentus* (Herbst)	1	0	0	0	0	0	1	1	–
78 *Cossonus impressifrons* Boheman	0	0	0	3	0	3	0	3	–
79 Curculionidae gen. spp.	0	0	2	0	2	3	1	4	–
80 *Cyrtepistomus castaneus* (Roelofs)	0	0	0	1	0	0	1	1	–
81 *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**		
82 *Eurhoptus* n. sp.	0	2	0	0	0	0	2	2	1
83 *Hylesinus pruniosus* Eichhoff	0	0	3	0	0	0	3	3	–
84 *Hylesinus* sp.	1	0	0	0	0	0	1	1	–
85 *Hypothenemus* spp.	5	1	0	3	0	9	0	9	–
86 *Micromimus corticalis* Boheman	1	0	0	1	0	2	0	2	–
87 *Myosides seriehispidus* Roelofs	0	1	0	1	0	2	0	2	2
88 *Pityophthorus annectens* LeConte	9	0	0	0	0	9	0	9	–
89 *Pseudopentarthrum* sp.	1	1	0	0	0	2	0	2	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
90 *Pseudopityophthorus asperulus* (LeConte)	0	0	0	0	1	0	1	1	–
91 *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**		
92 *Xyleborus affinis* Eichhoff	0	0	1	0	0	0	1	1	–
93 *Xyleborus atratus* Eichhoff	1	1	9	0	0	4	7	11	–
						X=0.82	***P*=0.3657**		
94 *Xyleborus californicus* Wood	0	0	1	0	0	0	1	1	–
95 *Xyleborus ferrugineus* (Fabricius)	0	0	1	0	0	0	1	1	–
96 *Xyleborus pulliculosus* Eichhoff	1	0	0	0	0	1	0	1	–
97 *Xylosandrus crassiusculus* (Motschulsky)	1	0	1	12	0	14***	0	14	1
						X=14.00	***P*=0.0002**		
98 *Xylosandrus germanus* (Blandford)	14***	0	2	6	0	5	17*	22	–
	X=14.00	***P*=0.0002**				**X=6.55**	***P*=0.0105**		
99 *Xylosandrus* spp.	0	0	0	2	0	2	0	2	–
100 *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									
101 *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**		
102 *Ampedus luteolus* (LeConte)	0	0	0	0	13	9	4	13	–
						X=1.92	***P*=0.1655**		
103 *Ampedus rubricus* (Say)	0	0	0	0	1	1	0	1	1
104 *Ampedus semicinctus* (Randall)	1	2	3	1	3	8	2	10	–
						X=3.60	***P*=0.0577**		
105 *Ampedus* sp.	0	0	0	0	1	0	1	1	1
106 *Athous cucullatus* (Say)	0	1	0	0	5	6	0	6	–
107 *Athous rufifrons* (Randall)	0	0	0	1	0	0	1	1	–

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
108	*Athous scapularis* (Say)	0	1	2	3	0	2	4	6	–
109	*Denticollis denticornis* (Kirby)	0	0	0	0	1	0	1	1	–
110	*Lacon discoideus* (Weber)	0	0	1	1	1	2	1	3	–
111	*Melanotus decumanus* (Erichson)	1	0	0	0	0	0	1	1	–
	ENDOMYCHIDAE									
112	*Bystus ulkei* (Crotch)	3	4	7	0	1	4	11	15	–
							X=3.27	***P*=0.0707**		
113	*Endomychus biguttatus* Say	0	0	2	0	0	0	2	2	–
114	*Micropsephodes lundgreni* Leschen and Carlton	0	0	1	0	0	1	0	1	–
115	*Mycetina perpulchra* (Newman)	0	0	1	0	0	1	0	1	–
116	*Phymaphora pulchella* Newman	0	0	0	0	1	0	1	1	–
	EROTYLIDAE									
117	*Microsternus ulkei* (Crotch)	0	0	0	0	3	3	0	3	–
	EUCINETIDAE									
118	*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									
119	*Dirrhagofarsus lewisi* (Fleutiaux)	0	0	0	1	0	0	1	1	–
120	*Dromaeolus cylindricollis* (Say)	2	0	1	0	0	1	2	3	–
121	*Entomophthalmus rufiolus* (LeConte)	0	0	0	3	3	6	0	6	–
122	*Isarthrus rufipes* (Melsheimer)	0	3	0	1	10	0	14***	14	–
							X=14.00	***P*=0.0002**		
123	*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**		

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
124 *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**		
125 *Microrhagus subsinuatus* LeConte	0	0	0	2	14	10	6	16	–
						X=1	***P*=0.3173**		
HISTERIDAE									
126 *Aeletes floridae* (Marseul)	0	0	0	1	0	0	1	1	–
127 *Bacanius tantillus* LeConte	2	3	1	6	4	5	11	16	2
						X=2.25	***P*=0.1336**		
128 *Caerosternus americanus* (LeConte)	0	0	0	0	1	0	1	1	–
129 *Paromalus bistriatus* Erichson	0	0	1	4	1	4	2	6	–
HYDROPHILIDAE									
130 *Cercyon assecla* Smetana	0	1	1	1	1	4	0	4	–
131 *Cercyon occallatus* (Say)	1	0	0	0	0	0	1	1	–
132 *Cercyon versicolor* Smetana	0	0	0	1	0	0	1	1	–
LAEMOPHLOEIDAE									
133 *Charaphloeus adustus* (LeConte)	0	0	0	2	0	2	0	2	–
134 *Laemophloeus biguttatus* (Say)	0	0	0	1	0	1	0	1	–
135 *Laemophloeus megacephalus* Grouvelle	0	0	0	9	0	9	0	9	–
136 *Placonotus zimmermanni* (LeConte)	2	0	0	0	0	2	0	2	–
LAMPYRIDAE									
137 *Lucidota* spp.	0	0	1	5	0	0	6	6	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
LEIODIDAE									
138 *Agathidium atronitens* Fall	0	0	0	0	4	0	4	4	–
139 *Agathidium exiguum* Melsheimer	0	0	0	0	1	0	1	1	–
140 *Agathidium oniscoides* Beauvois	1	2	1	4	0	1	7	8	4
141 *Agathidium rubellum* Fall	0	0	0	0	1	1	0	1	2
142 *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**		
143 *Anisotoma* n. sp.	0	0	0	1	0	0	1	1	–
144 *Catopocerus appalachianus* Peck	0	0	0	1	0	0	1	1	–
145 *Catopocerus* spp. (female)	0	0	0	0	2	1	1	2	–
146 *Catops davidsoni* Salgado	0	0	1	0	0	0	1	1	–
147 *Nemadus triangulum* Jeannel	0	2	0	1	1	2	2	4	–
148 *Sciodrepoides latinotum* Peck and Cook	1	0	3	2	0	1	5	6	–
LUCANIDAE									
149 *Platycerus virescens* (Fabricius)	0	3	0	0	0	0	3	3	–
LYCIDAE									
150 *Plateros* sp.	0	1	0	0	0	1	0	1	–
LYMEXYLIDAE									
151 *Elateroides lugubris* (Say)	0	0	0	1	0	0	1	1	–
MELANDRYIDAE									
152 *Dircaea liturata* (LeConte)	0	0	0	13	0	12**	1	13	–
						X=9.31	***P*=0.0022**		
153 *Emmesa connectens* (Newman)	0	3	0	1	2	1	5	6	–

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
154	*Hypulus simulator* Newman	0	0	0	8	2	8	2	10	–
							X=3.60	***P*=0.0577**		
155	*Microtonus sericans* LeConte	0	1	2	0	2	1	4	5	–
156	*Orchesia castanea* (Melsheimer)	0	0	2	0	0	0	2	2	–
157	*Phloeotrya vaudoueri* Mulsant	0	2	0	0	0	0	2	2	–
158	*Prothalpia undata* (LeConte)	0	2	0	0	0	0	2	2	–
159	*Symphora rugosa* (Haldeman)	0	1	0	1	0	0	2	2	–
MELYRIDAE										
160	*Hypebaeus apicalis* Say	0	0	2	0	0	2	0	2	–
161	*Melyrodes cribratus* (LeConte)	0	0	0	1	0	1	0	1	–
MONOTOMIDAE										
162	*Rhizophagus dimidiatus* Mannerheim	0	0	0	1	0	0	1	1	–
MORDELLIDAE										
163	*Falsomordellistena bihamata* (Melsheimer)	0	3	0	0	0	3	0	3	–
164	*Glipostenoda ambusta* (LeConte)	0	0	0	1	2	1	2	3	–
165	*Mordella* sp.	0	0	0	0	1	1	0	1	–
166	*Mordellaria serval* (Say)	0	0	0	2	0	0	2	2	–
167	*Mordellistena* spp.	0	0	0	0	8	0	8	8	–
168	*Mordellochroa scapularis* (Say)	0	0	1	0	0	0	1	1	–
169	*Paramordellaria triloba* (Say)	0	1	0	0	0	0	1	1	–
MYCETOPHAGIDAE										
170	*Mycetophagus flexuosus* Say	0	0	0	0	1	0	1	1	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
NITIDULIDAE									
171 *Carpophilus* spp.	1	0	3	0	1	5	0	5	–
172 *Epuraea* spp.	1	1	1	2	0	4	1	5	–
173 *Glischrochilus confluentus* (Say)	0	1	0	0	0	1	0	1	–
OEDEMERIDAE									
174 *Asclera ruficollis* (Say)	0	0	2	0	0	0	2	2	–
PTILIIDAE									
175 *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**		
176 *Micridium* sp.	1	0	0	0	0	0	1	1	–
177 *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**		
178 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									
179 *Ptilodactyla carinata* Johnson and Freytag	0	0	0	0	4	3	1	4	–
180 *Ptilodactyla* spp. (female)	1	0	0	1	0	0	2	2	–
PTINIDAE (formerly Anobiidae)									
181 *Hadrobregmus notatus* (Say)	0	0	3	0	1	4	0	4	–
182 *Lasioderma semirufum* Fall	1	0	0	0	0	1	0	1	–
183 *Oligomerus obtusus* LeConte	2	12**	0	0	0	13**	1	14	–
	X=7.14	***P*=0.0075**				**X=10.29**	***P*=0.0013**		
184 *Petalium incisum* Ford	0	2	0	0	0	2	0	2	–

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
185	*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**		
186	*Sculptotheca puberula* (LeConte)	1	4	1	1	1	8	0	8	–
187	*Trichodesma klagesi* Fall	5	2	0	1	1	6	3	9	–
188	*Vrilletta laurentina* Fall	0	1	0	0	0	1	0	1	–
189	*Xyletinus* spp.	0	1	0	1	0	0	2	2	–
PYROCHROIDAE										
190	*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**		
191	*Dendroides concolor* (Newman)	0	8	0	2	0	0	10**	10	–
							X=10.00	***P*=0.0015**		
192	*Neopyrochroa flabellata* (Fabricius)	0	0	0	2	4	0	6	6	–
RHYSODIDAE										
193	*Clinidium baldufi* Bell	0	4	0	2	7	4	9	13	–
							X=1.92	***P*=0.1655**		
194	*Clinidium rosenbergi* Bell	0	1	0	0	0	0	1	1	–
195	*Clinidium sculptile* (Newman)	0	0	0	0	1	1	0	1	–
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	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
SCRAPTIIDAE									
198 *Canifa* sp.	1	0	0	0	0	1	0	1	–
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**		

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
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	–
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**		

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
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	–
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

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
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**		
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. sp.	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	–

SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
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	–
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	–

	SPECIES	FWD1	FWD2	CWD1	CWD2	CWD3–4	SECONDARY	PRIMARY	TOTAL	CWD5†
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**		
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	–
TROGOSTIIDAE										
304	*Airora cylindrica* (Serville)	0	0	1	0	0	1	0	1	–
305	*Thymalus marginicollis* Chevrolat	0	0	0	1	0	1	0	1	–
	ASSOCIATIONS	**10**	**11**	**4**	**14**	**8**	**16**	**27**	**5673**	**8**