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Abstract. The community within extremely decayed downed coarse woody debris, here referred to as decay class V (CWD5), has never been systematically sampled. The presumption has been that rotten wood is eventually overrun by surrounding soil and litter inhabitants. Leaf litter and CWD5 were sampled for Coleoptera with a sifting/Berlese technique at three primary and three secondary forest sites in Great Smoky Mountains National Park, Tennessee, USA, during fall 2006 and spring 2007. A total of 4261 adult beetle specimens, representing 216 lowest identifiable taxa within 159 genera and 28 families, were collected. Sixty-six species (31%) were represented by single individuals. Many more specimens (3471) and species (170) were collected from leaf litter than from CWD5 (790 and 111, respectively) but species accumulation curves showed that species richness was not significantly different between the two habitats. Eight species were significantly associated with CWD5, and 40 species were significantly associated with leaf litter. Species richness was significantly higher in secondary forest than primary forest, but more species were significantly associated with primary than secondary forest. Species richness was significantly higher in spring than fall. Notes on the biology and photographs of the 59 species represented by 10 or more specimens are given to provide an atlas of common eastern U.S. beetle species found in these habitats. Overall CWD5 is a distinct but overlooked habitat that may harbor numerous undescribed species or species considered rare.

Do not go gentle into that good night,
Old age should burn and rave at close of day;
Rage, rage against the dying of the light.
—Dylan Thomas, *Do not go gentle into that good night*

Behold this compost! behold it well!
—Walt Whitman, *This Compost*

Introduction

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

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

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

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

Very few direct comparisons of the invertebrate community between leaf litter and CWD of any decay class are available. Johnston and Crossley (1996) summarize the literature on studies comparing ground, litter, and CWD mite distribution in North American forests. A study in North Carolina found 10% of mite species used CWD as a preferred habitat.

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

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

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

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

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

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

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

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

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

Ulyshen et al. (2011) studied the effect of ash (*Fraxinus* spp.) CWD on litter dwelling invertebrates in Michigan. They found higher richness of Coleoptera near (immediately next to) ash CWD than 1–3 meters away. Ulyshen et al. (2011) also provide a comprehensive table of previous studies focused on differences in arthropod abundance near and far from CWD.

The above studies are difficult to compare, but some generalities can be highlighted. Pitfall traps may not be appropriate for use in these comparisons because they may bias for large vagile organisms that move on or near the leaf litter surface and against smaller less mobile organisms that stay under leaf litter or within wood. Across all studies "near" CWD was designated as 0–5 cm and "distant" was 1–10 m. Where distant samples were less than 2 m from CWD, few taxa showed differences in density. Studies that identified taxa below order tended to find that taxa within an order responded differently to distance from CWD, implying a direct positive correlation between identification to low taxonomic levels and an accurate understanding of the system. None of the above studies used a control (non-organic, "pseudo-log") to test for the sole effect of habitat heterogeneity on arthropod communities in leaf litter rather than the combined effect of structure and resources.

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

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

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

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

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

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

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

Yee et al. (2006) and Brin et al. (2010) showed that species assemblages in rotten wood differ with log diameter. Generally bigger logs accommodate more species. Old growth forests, with a higher volume of CWD, greater continuity of CWD, and greater diameter of logs are important for saproxylic species conservation (Siitonen et al. 2001; Grove 2002). Great Smoky Mountains National Park contains large tracts of forest that have not been cut since European settlement in North America, while other areas of the park were recently logged (<100 years ago). Comparison of saproxylic species assemblages between old growth and regrowth sites are needed to determine what, if any, species are restricted to old growth forest and may be of conservation concern.

The purpose of this study was to survey the Coleoptera community within CWD5 within GSMNP, compare that community with the Coleoptera found within the surrounding leaf litter, and to see how those communities differ between seasons (fall and spring) and forest types (primary and secondary).

Material and Methods

Study Area. Great Smoky Mountains National Park (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. Most of the area is topographically complex, ranging in elevation from 270–2024 m (875–6643 ft). The Great Smoky Mountains range itself extends from the northeast corner of the park to the southwest. The southeastern corner and the adjacent Cherokee Indian Reservation are part of the Balsam Mountains. Five major forest communities are recognized in the park, though 80% may be broadly classified as eastern deciduous forest (Houk and Collier 1993). Lower and intermediate elevations (1070–1525 m; 3500–5000 ft) are dominated by northern hardwood forests and spruce-fir forests at higher elevations (above 1525 m; 5000 ft). Cove forests are found in sheltered valleys at mid-elevations (1070–1370 m; 3500–4500 ft). This community represents the most diverse habitat in the park with its diversity of tree species, complex understory, and deep, moist litter layer. Some of the old growth cove forest stands are among the most beautiful and best preserved examples of this forest type in existence. The eastern half of the park contains the largest remaining tract of old growth forest in the eastern U.S. (Davis et al. 1996). 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 6 m diameter) provided substrates for diverse communities of subcortical beetles and other insects for many years after falling. Beginning in 1904, chestnut blight rapidly spread throughout the eastern U.S., killing almost every large chestnut tree in the country (Hepting 1974).

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

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

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

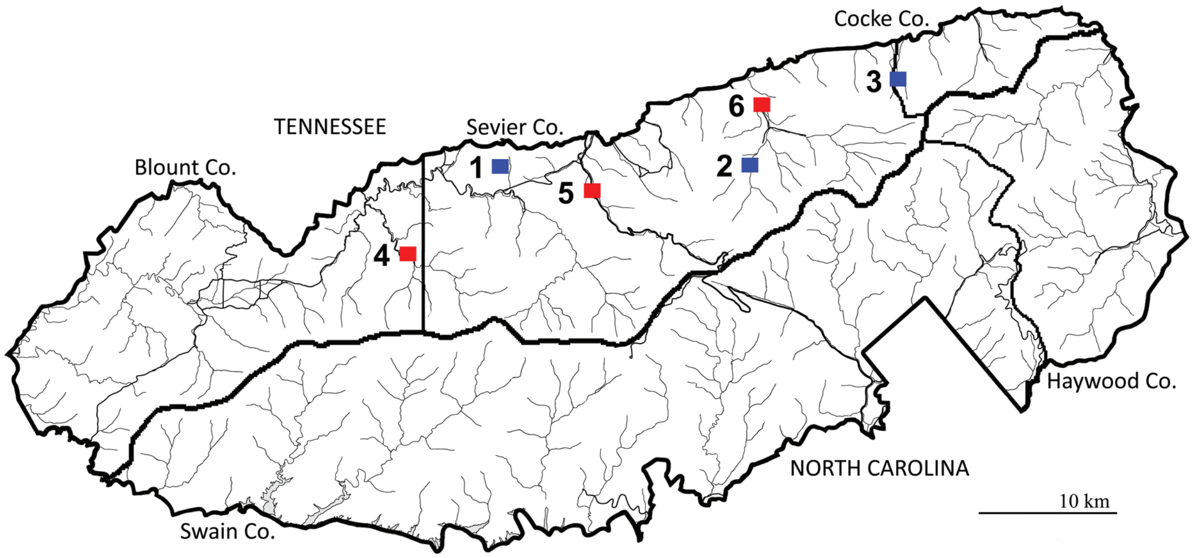


Figure 1. Map of collection locations in Great Smoky Mountains National Park. Primary forest sites: **1)** Laurel Falls; **2)** Porters Creek; **3)** Albright Grove. Secondary forest sites: **4)** Tremont; **5)** Sugarlands Quiet Walkway; **6)** Greenbrier.

selective cut and during a 1938 survey this location was designated as cove hardwood. Coarse woody debris volume was 663 m^3/ha.

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

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

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

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

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

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

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

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

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

Adult Coleoptera were pinned or pointed as needed, and labeled. Identification to the finest level possible (typically species) was performed with the appropriate taxonomic literature (primarily Arnett and Thomas (2001) and Arnett et al. (2002) and references therein, plus additional literature as needed), and/or comparison with authoritatively identified reference specimens. All other macroinvertebrates were sorted from the debris, labeled, and preserved in 90% ethanol. Specimens are deposited in the Louisiana State Arthropod Museum (LSAM), LSU AgCenter, Baton Rouge, Louisiana, and Great Smoky Mountains Natural History Museum (GSNP), Gatlinburg, Tennessee.

These practices are in line with the recommendations given by Gotelli (2004) and Bortolus (2008) concerning appropriate taxonomic practices when conducting community level research. Specifically: 1) specimens were identified in an appropriate manner, not through the use of "gray literature" or previous ecological publications; 2) taxonomic experts were consulted concerning the identification of various taxa and are thanked in the Acknowledgments section; 3) literature used to identify taxa is cited (see above and Discussion); 4) specimens have been deposited in scientific institutions so that further taxonomic confirmations can be made; and 5) taxonomy as a science was supported; two taxonomists were trained, more than 20 new species were described as a result of this research, and keys were provided for their identification (Ferro and Carlton 2010; Park et al. 2010; 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). Chi square goodness of fit testing was performed for 59 species represented by 10 or more specimens (i.e. an expected value of five or more specimens per subset, see Crawley 2007). Tests were performed for a difference in number of specimens of a given species between different substrates, forests, and seasons. For all tests, degrees of freedom = 1 and $\alpha = 0.05$. 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 ~3 comparisons (5% of 59) within each group of tests.

Results

Total. A total of 4261 adult beetle specimens, representing 216 lowest identifiable taxa within 159 genera and 28 families, were collected as part of this research (Appendix 1). Of the 216 lowest identifiable taxa, four were identifiable only to family or tribe, 75 were identifiable only to genus, and 137 were identified to species. Groups only identified to family, tribe, or genus may contain multiple species (see discussion). For the remainder of the results and discussion all 216 lowest identifiable taxa will be referred to as “species” in an attempt to reduce jargon and increase readability.

Staphylinidae were, by a wide margin, the most species rich family with 106 species, followed by Carabidae (25 spp.), Leiodidae (21 spp.), and Curculionidae (20 spp.). Fifteen families were represented by a single species. Seven species were represented by more than 100 specimens, and 66 species (31%) 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 leaf litter (3471 and 170, respectively) than from CWD5 (790 and 111, respectively). However, a comparison of the species accumulation curves for both subsamples (Fig. 3) shows species richness was not significantly different between leaf litter and CWD5 when normalized for number of specimens.

Of the 170 species from leaf litter, 105 (49% of total) were only collected in leaf litter (Fig. 2). Of the 111 species collected from CWD5, 46 (21%) were only collected in CWD5. The remaining 65 species (30%) were collected in both substrates. The Sorensen’s quotient of similarity for these two substrates is 0.46.

Forest. Many more specimens but fewer species were collected from primary forest (2853 and 144, respectively) than from secondary forest (1408 and 146, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 4) shows significantly higher species richness in secondary forest when normalized for number of specimens.

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

Season. More specimens and more species were collected during spring (2271 and 172, respectively) than during fall (1990 and 149, respectively). A comparison of the species accumulation curves for both subsamples (Fig. 5) shows significantly higher species richness during spring.

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

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

Forest x Substrate. Subsets based on a combination of forest and substrate showed that the greatest number of specimens was collected in primary forest leaf litter (2520) and the fewest specimens were collected from primary forest CWD5 (333). The greatest number of species was collected in secondary forest leaf litter (116) and the fewest species were collected in secondary CWD5 (65). Species richness based on species accumulation curve comparisons (Fig. 6) was not significantly different between secondary forest litter and primary forest CWD5. Those two combinations were significantly higher in species richness than primary forest leaf litter and secondary CWD5.

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	4261	28	159	216	/
2	Leaf Litter	3471	25	135	170	a
2	CWD5	790	17	82	111	a
3	Primary	2853	24	105	144	b
3	Secondary	1408	24	115	146	a
4	Spring	2271	23	128	172	a
4	Fall	1990	25	114	149	b
5	Spring, Litter	1777	21	109	136	a
5	Fall, Litter	1694	22	95	117	b
5	Spring, CWD5	494	13	64	84	a
5	Fall, CWD5	296	17	56	71	a
6	Primary, Litter	2520	21	82	107	b
6	Secondary, Litter	951	21	98	116	a
6	Secondary, CWD5	457	11	51	65	b
6	Primary, CWD5	333	17	59	77	a
7	Spring, Primary	1459	17	83	111	b
7	Fall, Primary	1394	20	75	97	c
7	Spring, Secondary	812	18	91	108	a
7	Fall, Secondary	596	16	78	97	a
8	Spring, Primary, Litter	1266	16	65	85	b
8	Fall, Primary, Litter	1254	17	59	74	c
8	Spring, Secondary, Litter	511	17	74	84	a
8	Fall, Secondary, Litter	440	16	64	76	a
8	Spring, Secondary, CWD5	301	10	41	51	b
8	Spring, Primary, CWD5	193	12	44	54	a
8	Fall, Secondary, CWD5	156	9	35	40	b
8	Fall, Primary, CWD5	140	16	38	47	a

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

Season x Forest x Substrate. A comparison of the eight possible combinations of season, forest, and substrate showed that the greatest number of specimens was collected in spring primary forest leaf litter (1266), and the fewest collected in fall primary forest CWD5 (140). The greatest number of spe-

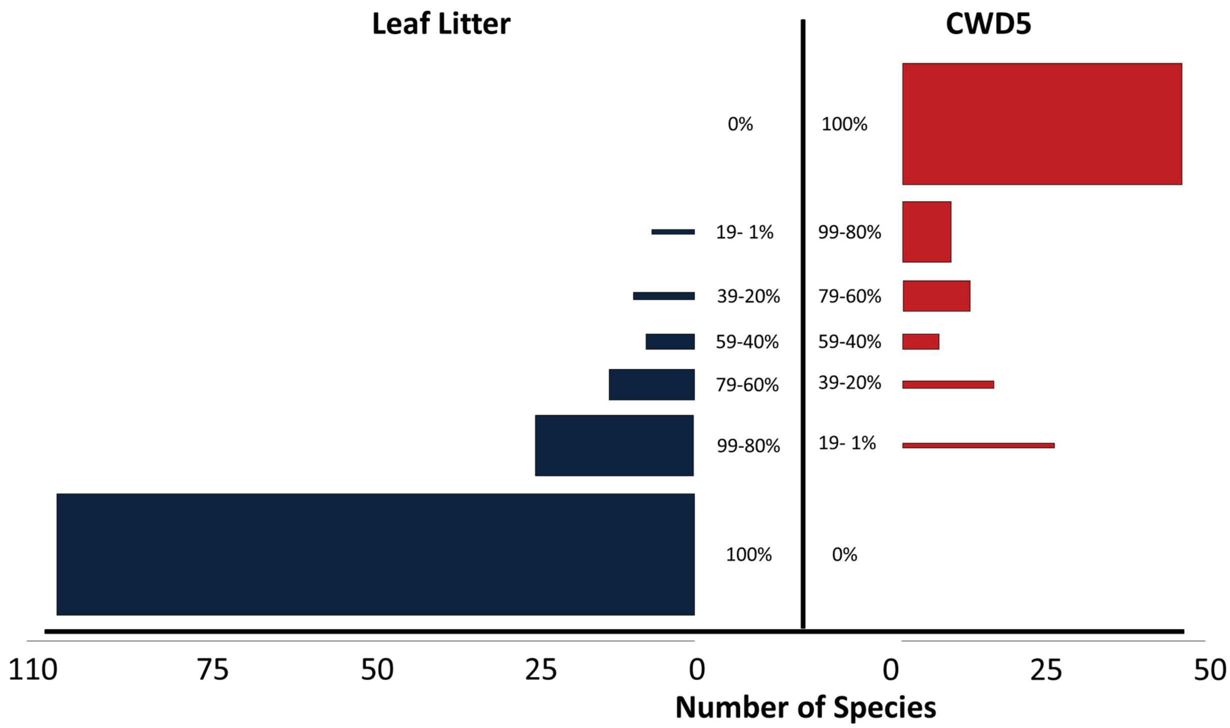


Figure 2. Number of species represented by proportions of specimens in leaf litter and CWD5.

cies was collected in spring primary forest leaf litter (85) and the fewest was collected in fall secondary forest CWD5 (40). Species richness based on species accumulation curve comparisons was highest in, and not significantly different among, spring secondary forest leaf litter, fall secondary forest leaf litter, spring primary forest CWD5, and fall primary forest CWD5. Species richness among spring primary forest leaf litter, spring secondary CWD5, and fall secondary forest CWD5 was not significantly different and intermediate within all combinations. Fall primary forest leaf litter had significantly lower species richness than all other combinations.

Species Data. Of the 216 species collected, 59 (27%) were represented by 10 or more specimens (Appendix 1) and available for statistical evaluation.

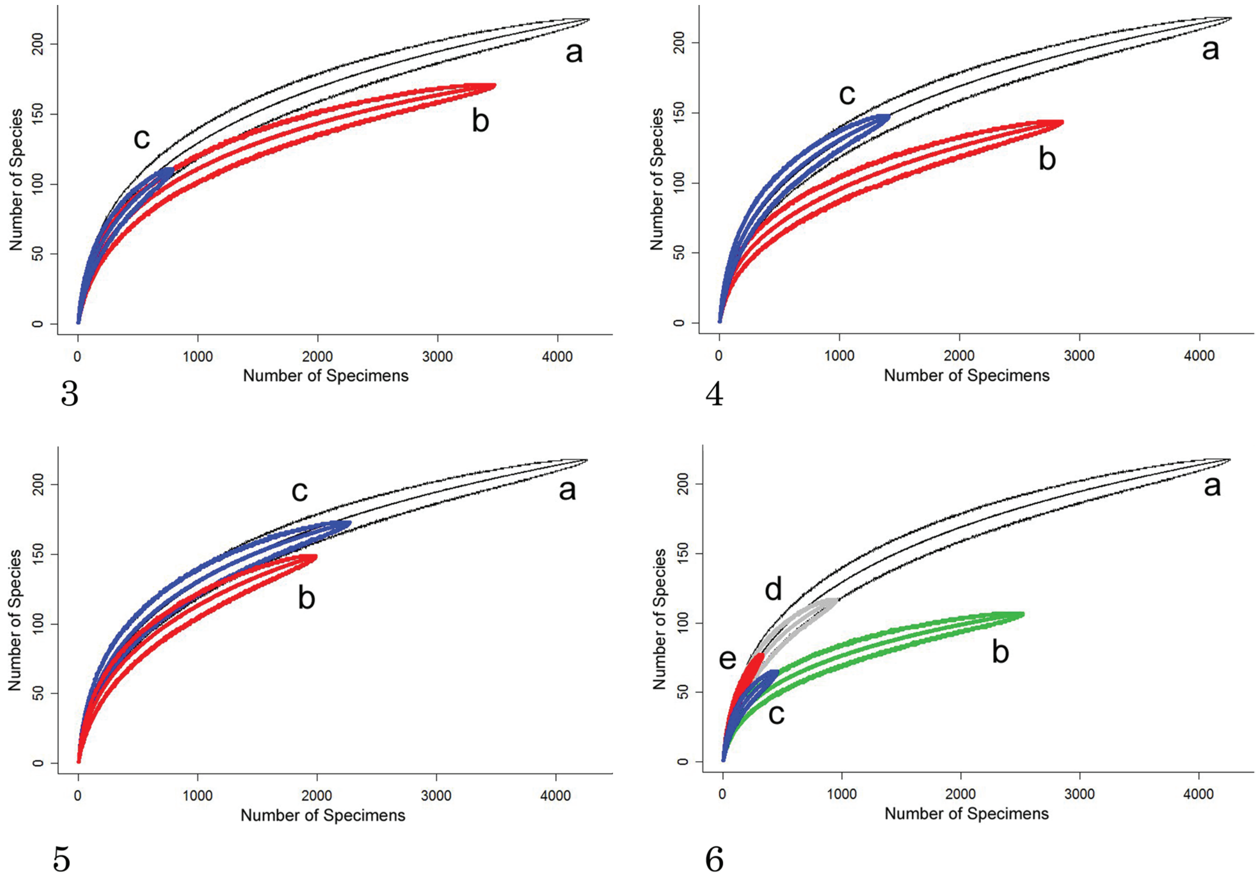
Substrate. Of the 59 species available for testing, 40 species (68%) were represented by significantly more specimens in leaf litter, eight species (13%) were represented by significantly more specimens in CWD5, and 11 species (19%) showed no significant difference between the two habitats.

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

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

Discussion

Coarse woody debris decay class V is a unique habitat with a rich fauna equal to that of leaf litter. However, specimens in CWD5 were much less abundant. With the exception of *Mychocerus striatus* (Sen Gupta and Crowson) no species averaged more than one specimen per two samples. This apparent rarity can be explained for some species that were abundant in leaf litter (vagrants), and some



Figures 3–6. 3) Species accumulation curves for a: total; b: leaf litter; c: CWD5. **4)** Species accumulation curves for a: total; b: primary forest; c: secondary forest. **5)** Species accumulation curves for a: total; b: fall samples; c: spring samples. **6)** Species accumulation curves for a: total; b: leaf litter from primary forest; c: CWD5 from secondary forest; d: leaf litter from secondary forest; e: CWD5 from primary forest.

species that may be holdovers from earlier decay stages (at a habitat edge). However, any species associated only with CWD5 (with the possible exception of *M. striatus*) may truly be represented by few individuals across the landscape. For example *Tohlezkus inexpectus* Vit and *Leptusa pusio* (Casey) are significantly associated with both CWD5 and primary forests. Prior to this research *T. inexpectus* was known from only a few individuals (see below), and *L. pusio* was only known from the type series of two specimens (Gusarov 2003e). *Leptusa pusio* was first collected in Ohio and is winged so it may have a wide distribution. Conversely, *T. inexpectus* is wingless and has only been collected in the Southern Appalachians, making it a possible species of interest in future conservation studies.

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

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

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

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

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

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

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

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

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

Space edge effects. Of the 45 singleton species in CWD5 (species represented by a single specimen within the CWD5 samples), 19 (42%) were also collected in leaf litter. Of the 48 singleton species in leaf litter, 8 (17%) were also collected in CWD5. No singletons of the same species were collected in each substrate. Of the 49 singleton species in secondary forest, 21 (43%) were also collected in primary forest. Of the 53 singleton species in primary forest, 15 (28%) were also collected in secondary forest. Singletons of five species were collected in both forest types.

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

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

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

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

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

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

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

An unknown number of undescribed species were collected during this study (see notes below). However, several undescribed species collected as part of this research were recognizable as such and described. Ferro and Carlton (2010) revised the eastern species of the staphylinid genus *Sonoma* and described 15 new species, three from this study: *S. chouljenkoi* Ferro and Carlton, *S. gilae* Ferro and Carlton, and *S. gimmeli* Ferro and Carlton. Additionally Park and Carlton (Park et al. 2010) described four new species of *Leptusa*, two were collected during this research: *L. gimmeli* Park and Carlton, and *L. pseudosmokyiensis* Park and Carlton. While researching *Thoracophorus*, Ferro and Gimmel (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, where there is a potential to encounter many undescribed or difficult to identify species, special effort should be made to collaborate with taxonomic experts and specific funds should be requested to facilitate taxonomic and/or nomenclatural research.

Related Research. This publication represents a portion of a larger body of research, specifically the Coleoptera component of the All Taxa Biodiversity Inventory at GSMNP (Carlton and Bayless 2007). This effort has resulted in a suite of publications related by collectors, localities, and even specific samples (e.g. specimens collected as part of this research were described as new species in Ferro and Carlton (2010) and Park et al. (2010)). Simultaneous research was conducted by the same authors at the same localities concerning Coleoptera in decay classes I–IV (Ferro et al. 2011a) and flight intercept traps were used to compare their effectiveness at sampling saproxylic Coleoptera with sifting and emergence (Ferro et al. 2011b).

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

Conclusion

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

Species Accounts

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

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

CARABIDAE
Trechinae

Anillinus cherokee Sokolov and Carlton (Fig. 7)
Range: Blount Co., Tennessee; Graham Co., North Carolina. **Habitat:** deciduous hardwood forests at middle altitudes (600–1510 m). **Collection Method:** sifting/Berlese forest litter. **Biology:** blind, flightless, presumed predatory, otherwise unknown. **Present Study: s**ignificantly higher abundance in leaf litter, primary forest, and spring. **References:** Sokolov and Carlton 2008.

Anillinus langdoni Sokolov and Carlton (Fig. 8)
Range: northwest ranges of Great Smoky Mountains: Cocke, Monroe, and Sevier Counties, Tennessee. **Habitat:** litter of hardwood forests at low to middle altitudes (700–1300 m). **Collection Method:** sifting/Berlese forest litter and rotten logs. **Biology:** blind, flightless, presumed predatory, otherwise unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Sokolov et al. 2004, 2007.

Polyderis laevis (Say) (Fig. 9)
Range: eastern North America: Quebec, south to Texas, west to Iowa. **Habitat:** lowlands, pastures, open ground, leaf litter. **Collection Method:** inspecting ant nests, under stones, sifting/Berlese wood chips, light trapping. **Biology:** overwinters as an adult, predacious, frequent flyer. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Lindroth 1966 (as *Tachys laevis* Say); Downie and Arnett 1996; Ciegler 2000; Larochelle and Larivière 2003 (and references therein).

Trechus* (*Microtrechus*) *pisgahensis Barr (Fig. 10)
Range: North Carolina, high altitudes (1400–1600 m). **Habitat:** mountains, coniferous forests, moist areas including leaf litter and moss. **Collection Method:** collection from leaf litter, searching under moss. **Biology:** overwinters as an adult, flightless, presumably predatory. **Present Study:** indifferent

to substrate and season, all specimens taken in primary forest. **References:** Barr 1979 (as *Trechus* (*Microtrechus*) *vandykei pisgahensis* Barr); Bousquet and Larochelle 1993; Larochelle and Larivière 2003.

CERYLONIDAE
Ceryloninae

Mychocerus striatus (Sen Gupta and Crowson) (Fig. 11)
Range: North Carolina, Tennessee. **Habitat:** forests, under and in rotten logs, rarely leaf litter. **Collection Method:** sifting/Berlese litter, rotten wood. **Biology:** larvae and adults possess piercing mouthparts, probably a fungivore, brachypterous. **Present Study:** significantly more abundant in CWD5, secondary forest, in the spring. **References:** Sen Gupta and Crowson 1973 (as *Lapecautomus striatus* (Sen Gupta and Crowson)); Lawrence and Stephan 1975 (as *Lapethus striatus* (Sen Gupta and Crowson)).

CORYLOPHIDAE
Corylophinae

***Holopsis* spp.** (Fig. 12)
Comments. Accurate species identifications cannot be performed until a species level revision is completed. Important higher level work on this family can be found in Bowestead 1999, Leschen and Bowestead 2001, and Slipinski et al. 2009. **Range:** Pennsylvania to Florida, West to Texas and Southern California. **Habitat:** members of the family have been collected on leaves, flowers, in leaf litter, and under bark. **Collection Method:** sifting/Berlese litter, sweep netting. **Biology:** both adults and larvae feed on fungal spores. **Present Study:** significantly more abundant in leaf litter and secondary forest, indifferent to season. **References:** Lawrence 1991; Downie and Arnett 1996 (as *Bathona* Casey and *Corylophodes* Matthews); Bowestead 1999; Leschen and Bowestead 2001; Slipinski et al. 2009.

CURCULIONIDAE
Cossoninae

Caulophilus dubius (Horn) (Fig. 13)
Range: throughout eastern United States: New York to Florida, west to Michigan and Texas. **Habitat:** under bark of dead trees and *Vitis* vine, in leaf litter and tree holes. **Collection Method:** searching under bark and sifting/Berlese leaf litter and rotten wood. **Biology:** unknown. **Present Study:** significantly more abundant in leaf litter and spring, indifferent to forest. **References:** Blatchley and Leng 1916 (as *Allomimus dubius* Horn); Downie and Arnett 1996; Peck and Thomas 1998; Ciegler 2010.

Cryptorhynchinae

Eurhoptus pyriformis LeConte (Fig. 14)
Range: eastern and central United States, North Carolina to Florida, west to Texas, Colorado, and Wisconsin. **Habitat:** in moss, pine litter, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Blatchley and Leng 1916; Downie and Arnett 1996; Peck and Thomas 1998; Anderson 2002; Ciegler 2010.

Eurhoptus n. sp. (R. S. Anderson pers. com.) (Fig. 15)
Comments. This genus contains numerous undescribed species and is in need of revision. **Range:** unknown. **Habitat:** unknown. **Collection Method:** sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Anderson 2002 (key to genus).

Dryophthorinae

Dryophthorus americanus (Bedel) (Fig. 16)
Range: throughout eastern North America. **Habitat:** "very old logs", dead pine, forest litter. **Collection Method:** sifting/Berlese litter, collecting under bark, flight intercept trap, UV light. **Biology:** breeds under bark of dead pines, winged. **Present Study:** significantly higher abundance in CWD5, secondary forest, and spring. **References:** Blatchley and Leng 1916; Downie and Arnett 1996; Peck and Thomas 1998; Anderson 2002; Ciegler 2010.

Entiminae

Panscopus impressus Pierce (Fig. 17)
Comments. This genus is in need of revision (Anderson 2002). Buchanan (1936) designated a subspecies, *Panscopus impressus thoracicus*, but in light of the uncertainty of its validity specimens from this study are only identified to the species level. **Range:** central eastern United States, Indiana, North Carolina, South Carolina, Tennessee, Virginia. **Habitat:** swept from weeds in low damp woods, leaf litter. **Collection Method:** sweep netting, sifting/Berlese litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Blatchley and Leng 1916; Buchanan 1936; Anderson 2002; Ciegler 2010.

EUCINETIDAE

Tohlezkus inexpectus Vit (Fig. 18)
Range: Sevier Co., Tennessee, and Macon Co., North Carolina. **Habitat:** rotten wood, very rarely in leaf litter. **Collection Method:** dung trap, sifting/Berlese litter and CWD5. **Biology:** adults have unique suctorial mouthparts, possibly feed on slime molds. **Present Study:** significantly higher abundance in CWD5, primary forest, and spring. **References:** Vit 1995.

LEIODIDAE
Catopocerinae

***Catopocerus* spp.** (female) (Fig. 19)
Comments. Males of *Catopocerus appalachianus* Peck and possibly an undescribed species were collected; however, none were represented by more than 10 specimens. Information provided below applies to the genus in general. **Range:** unglaciated mountain ranges in eastern and western North America. **Habitat:** moist forest litter, soil, well rotten logs, under rocks, in caves. **Collection Method:** sifting/Berlese litter, rotten pig liver bait, carrion pitfall traps. **Biology:** eyeless, wingless, probably feeds on organic debris and fungi, larvae and teneral adults collected in the spring. **Present Study:** significantly higher abundance in leaf litter, indifferent to forest and season. **References:** Peck 1974, 2001; Downie and Arnett 1996.

Cholevinae

Ptomaphagus appalachianus (Peck) (Fig. 20)
Range: northern Georgia and Alabama, eastern Tennessee. **Habitat:** caves, forest floor debris, tree hole, rotten tree roots. **Collection Method:** sifting/Berlese litter, carrion bait traps. **Biology:** probably a scavenger on decaying organic matter, collected from January through September. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Peck 1978 (as *Adelopsis appalachiana* Peck).

***Ptomaphagus* spp.** (female) (Fig. 21)
Comments. The only other member of this genus we collected was *Ptomaphagus appalachianus* (Peck) and many of these specimens are probably females of that species; however, Tishechkin (2007) reported several undescribed species within GSMNP. **Range:** this genus is found eastern North America. **Habitat:** caves, forest floor debris, tree hole, rotten tree roots. **Collection Method:** sifting/Berlese litter, carrion bait traps. **Biology:** probably a scavenger on decaying organic matter. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Blatchley 1910; Peck 1978 (as *Adelopsis*), 2001; Peck and Thomas 1998; Tishechkin 2007.

Leiodinae

***Agathidium* spp.** (female) (Fig. 22)
Comments. This genus was represented in this research by males of six identifiable species and one possibly undescribed species; however, none of the males were represented by more than 10 specimens. Information provided below applies to the genus in general. **Range:** throughout eastern United States and worldwide. **Habitat:** high humidity locations, forests, leaf litter, dead wood. **Collection Method:** collection and dissection of slime molds (warming a slime mold in the laboratory will cause adults to move and become visible), sifting/Berlese leaf litter and dead wood, flight intercept traps. **Biology:** winged and wingless species, strongly associated with slime molds (Myxomycetes), Wheeler and Miller (2005) provide a list of host associations for numerous species. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Blatchley 1910; Downie and Arnett 1996 (key out of date); Peck and Thomas 1998; Peck 2001; Miller and Wheeler 2005; Wheeler and Miller 2005.

NITIDULIDAE
Nitidulinae

Stelidota octomaculata (Say) (Fig. 23)
Range: eastern North America, west to Ontario and Arizona. **Habitat:** sap in spring, fungi, rotten fruit, acorns and seeds of numerous tree species (see Galford et al. 1991). **Collection Method:** hand collection, under bark, sifting/Berlese forest litter, pitfall traps. **Biology:** feeds on acorns in winter, overwinters as an adult, begins breeding March to May, Galford et al. (1991) reared this species from seeds of 40 plant species. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Blatchley 1910; Parsons 1943; Peng et al. 1990 (key to immatures); Galford et al. 1991 (life history); Downie and Arnett 1996; Peck and Thomas 1998.

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.

Acrotrichinae

***Acrotrichis* spp.** (Fig. 24)
Range: throughout North America. **Habitat:** leaf litter, decaying logs, tree holes, fungi, animal dung, under bark, moist decaying organic matter. **Collection Method:** sifting/Berlese organic material, flight intercept trap. **Biology:** De Coninck and Coessens (1981) studied *Acrotrichis intermedia* (Gillmeister): probably general detritivore, adults live about 150 days and produce ~10 eggs each, probably reproduction takes place throughout the year with overlap of generations. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Blatchley 1910 (as *Trichopteryx* Kirby and Spence); De Coninck and Coessens 1981; Dybas 1990; Downie and Arnett 1996; Peck and Thomas 1998; Hall 2001.

Ptiliinae

***Pteryx* spp.** (Fig. 25)
Range: throughout North America. **Habitat:** forest floor debris, tree holes, logs, sphagnum bogs. **Collection Method:** sifting/Berlese organic material. **Biology:** probably general detritivore. **Present Study:** significantly higher abundance in CWD5, indifferent to forest type or season. **References:** Blatchley 1910; Dybas 1990; Downie and Arnett 1996; Hall 2001.

RHYSODIDAE

Clinidium valentinei Bell (Fig. 26)
Range: three regions: north-central Alabama; mountainous Georgia, North Carolina, South Carolina, Tennessee; southwestern Pennsylvania. **Habitat:** humid ravines at low elevations in the southern Appalachians. **Collection Method:** sifting/Berlese forest litter and CWD5 (this study). **Biology:** possibly feeds on slime molds, otherwise unknown. **Present Study:** indifferent to substrate, forest, and season. **References:** Bell 1970; Bell and Bell 1985; Bousquet and Larochelle 1993; Downie and Arnett 1996; Ciegler 2000.

SCARABAEIDAE
Aphodiinae

Dialytellus tragicus (Schmidt) (Fig. 27)
Range: southeastern Canada and northeastern United States, south to North Carolina and Tennessee. **Habitat:** found near deer dung in forested habitats and leaf litter, rarely in CWD5. **Collection Method:** sifting/Berlese leaf litter and rotten wood, presumably this species could also be collected with deer dung baited traps. **Biology:** feeds on deer and sheep dung in shaded locations, cold adapted species, generally active in winter. **Present Study:** significantly higher abundance in leaf litter, primary forests, and spring. **References:** Downie and Arnett 1996 (as *Aphodius humeralis* (LeConte)); Ratcliffe et al. 2002 (as *A. humeralis*); Gordon and Skelley 2007.

STAPHYLINIDAE
Aleocharinae

Aleocharinae gen. spp. (Fig. 28)
Comments. These specimens could not be reliably identified to genus. Aleocharinae is the largest subfamily of the Staphylinidae with 21 tribes, 183 genera, and 1385 described species known from North America and is badly in need of a comprehensive revision. See Newton et al. (2001), and references therein, for further information about this subfamily. **Range:** throughout North America. **Habitat:** ubiquitous in terrestrial habitats. **Collection Method:** sifting/Berlese leaf litter, pitfall traps, bait traps, UV light, etc. **Biology:** virtually every mode of life (many very specialized) is known in this subfamily: free living, parasitic, herbivore, carnivore, fungivore, flier, walker, runner, swimmer, gregarious, solitary, etc., but life history is almost unknown at the species level. **Present Study:** indifferent to substrate, forest type, and season. **References:** Downie and Arnett 1996; Newton et al. 2001.

Aleodorus bilobatus (Say) (Fig. 29)
Range: eastern North America: Ontario to southern New England, south to Georgia, west to Illinois and Iowa. **Habitat:** moist habitats, under bark, sifted vegetable debris, dead grass, moss, and duff. **Collection Method:** sifting/Berlese leaf litter, hand collection. **Biology:** unknown, specimens have been collected from March to November. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Hoebeke 1985; Downie and Arnett 1996; Gouix and Klimaszewski 2007.

Athetini gen. spp. Casey (Fig. 30)
Comments. These specimens could only be reliably identified to Athetini, a large difficult tribe. Seevers (1978) characterization of the tribe and genera is inadequate. Currently 64 genera are recognized within the tribe in North America (Newton et al. 2001) but a complete revision is needed. Gusarov (2002a–e, 2003a–e, 2004a–b) has greatly contributed to our knowledge of many genera and Elven et al. (2010) provided the first molecular phylogeny of the tribe, but more work needs to be done. **Range:** throughout North America. **Habitat:** ubiquitous; decaying plants and animals, dung, bird and mammal nests, riparian areas, ant nests, under bark and logs. **Collection Method:** sifting/Berlese leaf litter. **Biology:** unknown; predators. **Present Study:** significantly higher abundance in leaf litter and spring, indifferent to forest type. **References:** Seevers 1978; Downie and Arnett 1996; Newton et al. 2001; Gusarov 2002a–e, 2003a–e, 2004a–b; Elven et al. 2010.

Leptusa gimmeli Park and Carlton (Fig. 31)
Range: Tennessee. **Habitat:** known only from Albright Grove, GSMNP, old growth forest. **Collection Method:** sifting/Berlese leaf litter, one specimen collected from dead wood with emergence chamber. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Park et al. 2010.

Leptusa pusio (Casey) (Fig. 32)
Range: Ohio, Tennessee. **Habitat:** forest leaf litter. **Collection Method:** sifting/Berlese leaf litter, and collected from dead wood with emergence chamber. **Biology:** unknown. **Present Study:** significantly higher abundance in CWD5, primary forest, and spring. **References:** Downie and Arnett 1996; Gusarov 2003e; Park et al. 2010.

***Leptusa* spp.** (Fig. 33)
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/Berlese leaf litter, and collected from dead wood with emergence chamber. **Biology:** unknown. **Present Study:** indifferent to substrate, forest type and season. This is almost certainly a reflection of the habits of multiple species represented by these specimens. **References:** Blatchley 1910; Downie and Arnett 1996; Newton et al. 2001; Park et al. 2010.

***Myllaena* spp.** (Fig. 34)
Comments. There are 22 species known from North America. Klimaszewski (1982), Klimaszewski and Génier (1986), and Klimaszewski and Frank (1992) provided a key to species and distributional data for this genus. Our specimens could not be identified due to time constraints. **Range:** throughout North America. **Habitat:** riparian habitats. **Collection Method:** sifting/Berlese leaf litter and rotten wood. **Biology:** unknown, adults have been collected year round. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate and season. **References:** Blatchley 1910; Klimaszewski 1982; Klimaszewski and Génier 1986; Klimaszewski and Frank 1992; Downie and Arnett 1996; Newton et al. 2001; Gouix and Klimaszewski 2007.

Dasycerinae

***Dasycerus* spp.** (Fig. 35)
Comments. This genus contains three species known from the Appalachian Mountains. Löbl and Calame (1996) provided a key to species. Our specimens could not be identified due to time constraints and uncertainty about the presence of undescribed species. **Range:** southern Appalachian: Virginia to Georgia. **Habitat:** moist broadleaf forest litter. **Collection Method:** sifting/Berlese forest litter. **Biology:** eastern species are wingless with small eyes, dissected females have only been found with a single egg, known to occur on fruiting fungi, but may not specifically feed on them. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Wheeler and McHugh 1994; Löbl and Calame 1996; Newton et al. 2001.

Osoriinae

Thoracophorus costalis (Erichson) (Fig. 36)
Range: throughout eastern North America: New Jersey to Florida, west to Louisiana and Illinois. **Habitat:** under bark, in dead wood, forest litter. **Collection Method:** sifting/Berlese litter, debris, and dead wood. **Biology:** unknown. **Present Study:** significantly higher abundance in CWD5, secondary forest, and spring. **References:** 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.

Oxytelinae

***Anotylus* spp.** (Fig. 37)
Comments. This genus is in need of revision. Newton et al. (2001) report 18 species, at least 5 of them adventive in North America. Keys may be found in Casey (1893) (as *Oxytelus* Gravenhorst in part), Downie and Arnett (1996), and Hatch (1957), but the accuracy of these keys is unknown. **Range:** throughout North America. **Habitat:** dung, rotting plant and animal matter, forest litter, some reported from mammal and ant nests. **Collection Method:** sifting/Berlese leaf litter. **Biology:** basically unknown at the species level, in general species probably feed on dung or decaying vegetation, see Hammond (1976) for more information. **Present Study:** significantly higher abundance in litter, primary forest, and spring. **References:** Casey 1893 (as *Oxytelus* Gravenhorst in part); Hatch 1957; Hammond 1976; Downie and Arnett 1996; Newton et al. 2001.

***Carpelimus* spp.** (Fig. 38)
Comments. This genus was redefined by Herman (1970) but is badly in need of revision. About 79 species are known in North America North of Mexico. Casey (1889), Downie and Arnett (1996), and Hatch (1957) provide keys to some species, but the accuracy of these keys is unknown. **Range:** throughout North America. **Habitat:** moist habitats such as wet debris near streams and ponds, others in leaf litter. **Collection Method:** sifting/Berlese forest litter. **Biology:** unknown. **Present Study:** significantly higher abundance in leaf litter, primary forest, and fall. **References:** Casey 1889 (as *Trogophloeus* Mannerheim); Hatch 1957; Herman 1970; Downie and Arnett 1996; Newton et al. 2001.

Paederinae

Sunius rufipes (Casey) (Fig. 39)
Range: North Carolina, Tennessee, Virginia. **Habitat:** damp litter, under bark. **Collection Method:** sifting/Berlese litter, UV light. **Biology:** unknown, Paederinae are considered predators. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Casey 1905 (as *Hemimedon rufipes* Casey).

Pselaphinae

Actiastes fundatum Grigarick and Schuster (Fig. 40)
Range: Tennessee. **Habitat:** sycamore tree hole, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predatory. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Grigarick and Schuster 1971.

***Actiastes* spp.** (female) (Fig. 41)
Comments. Female *Actiastes* Casey cannot be identified to species. These specimens probably represent *Actiastes fundatum* Grigarick and Schuster and/or *Actiastes suteri* (Park), both of which are known from GSMNP. **Range:** Alabama, Georgia, North Carolina, Tennessee. **Habitat:** rhododendron duff, tree holes, leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predatory. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Grigarick and Schuster 1971; Chandler 1990b.

Adranes lecontei Brendel (Fig. 42)
Range: Kentucky, Mississippi, New York, Pennsylvania, Tennessee. **Habitat:** lives in nests of *Lasius* spp. ants (Hymenoptera: Formicidae); nests have been found in beech logs in advanced stages of decay. **Collection Method:** sifting *Lasius* spp. ant nests, rarely sifting/Berlese forest litter. **Biology:** obligate myrmecophile on *Lasius* spp. ants; adults feed on fluids obtained from their adult and immature hosts; possibly feed on dead immature ants; see Park (1932a) and Akre and Hill (1973) for interesting behavioral observations of the genus. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate or season, probably heavily influenced by their host. **References:** 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 beyeri Schaeffer (Fig. 43)
Range: North Carolina. **Habitat:** forest leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown; some members of this genus are associated with ants, others are litter dwellers, members of this subfamily are predatory, see Park (1932b) about feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte). **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Schaeffer 1906; Park 1932b (as *B. globosus* LeConte), 1947, 1948.

***Batrisodes* spp.** (female) (Fig. 44)
Comments. Female *Batrisodes* Reitter cannot be reliably identified. These female specimens are probably representative of the twelve described and five known but undescribed species that have been collected in GSMNP. **Range:** Eastern North America. **Habitat:** within this genus some members are found in leaf litter, mosses, and rotten wood, others are associated with ants or caves. **Collection Method:** sifting/Berlese litter. **Biology:** poorly known, but see Park (1932b) about feeding behavior of *Batrisodes lineaticollis* Aubé (as *B. globosus* LeConte). **Present Study:** indifferent to substrate, forest type, and season. **References:** Blatchley 1910; Park 1932b, 1947, 1948; Chandler 1990b; Downie and Arnett 1996; Newton et al. 2001.

Conoplectus canaliculatus (LeConte) (Fig. 45)
Range: eastern United States, New York to Florida, west to Texas and Ohio. **Habitat:** moist habitats (sphagnum bogs, swamps), hardwood duff, rotten logs, pine floor duff, tree holes. **Collection Method:** sifting/Berlese litter. **Biology:** one of the most abundant pselaphines in eastern North America, predacious, occasionally collected with ants. **Present Study:** significantly higher abundance in CWD5 and secondary forest, indifferent to season. **References:** Park et al. 1950 (as *Rhexidius canaliculatus* (LeConte)); Reichle 1966 (as *R. canaliculatus*); Carlton 1983; Downie and Arnett 1996 (as *R. canaliculatus*).

***Ctenisodes* spp.** (female) (Fig. 46)
Comments. This genus was last treated by Casey (1897) (as *Pilopius* Casey) and is in need of revision. **Range:** throughout North America. **Habitat:** western species are known from arid habitats, one species associated with ants, eastern species are found in leaf litter and rotten wood. **Collection Method:** sifting/Berlese litter. **Biology:** predacious, overwinters as adults in Illinois prairie. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and fall. **References:** Casey 1897 (as *Pilopius*); Park et al. 1949, 1953 (as *Pilopius*); Mickey and Park 1956 (as *Pilopius*); Park 1964 (as *Pilopius*); Chandler 1990b (as *Pilopius*); Downie and Arnett 1996 (as *Pilopius*); Newton et al. 2001 (as *Pilopius*).

Euboarhexius perscitus (Fletcher) (Fig. 47)
Range: southern Appalachian: Georgia, North Carolina, Tennessee. **Habitat:** leaf litter, rhododendron litter, under rock. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Fletcher 1932 (as *Rhexidius perscitus* Fletcher); Carlton and Allen 1986.

Eutyphlus dybasi Park (Fig. 48)
Range: southern Appalachian: Tennessee. **Habitat:** leaf litter, rhododendron litter. **Collection Method:**

sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Park 1956.

***Eutyphlus* spp.** (female) (Fig. 49)
Comments. *Eutyphlus* females cannot be reliably identified. These female specimens are probably representative of the four species that have been collected in GSMNP. The vast majority are probably *Eutyphlus similis* LeConte. **Range:** eastern North America, particulary southern Appalachians. **Habitat:** leaf litter, rhododendron litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Park 1956; Chandler 1990b; Downie and Arnett 1996; Newton et al. 2001.

Machaerodes carinatus (Brendel) (Fig. 50)
Range: eastern North America: Pennsylvania to Georgia, west to Ohio. **Habitat:** pine, oak, rhododendron, and beech leaf litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and primary forest, indifferent to season. **References:** Park 1953; Chandler 1990b, 1994; Downie and Arnett 1996; Newton et al. 2001.

Mipseltyrus nicolayi Park (Fig. 51)
Range: North Carolina, Tennessee. **Habitat:** deep leaf mold in rhododendron thickets. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, wingless, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Park 1953.

Pseudactium arcuatum (LeConte) (Fig. 52)
Range: Alabama, Florida, Georgia, South Carolina, Tennessee. **Habitat:** forest floor debris, hardwood litter. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, wingless, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and fall. **References:** Carlton and Chandler 1994.

Rhexius schmitti Brendel (Fig. 53)
Range: eastern North America west to Oklahoma. **Habitat:** rotten wood, leaf litter. **Collection Method:** sifting/Berlese litter, UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Chandler 1990a; Downie and Arnett 1996.

***Rhexius* spp.** (female) (Fig. 54)
Comments. Female *Rhexius* LeConte cannot be reliably identified. These female specimens are probably representative of the two described and two undescribed species that have been collected in GSMNP. **Range:** eastern North America west to Oklahoma. **Habitat:** rotten wood, leaf litter, flood debris. **Collection Method:** sifting/Berlese litter, grass roots, flight intercept trap, UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter and secondary forest, indifferent to season. **References:** Blatchley 1910, Chandler 1990a, b; Downie and Arnett 1996; Newton et al. 2001.

***Sonoma* spp.** (female) (Fig. 55)
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/Berlese litter and rotten wood, Lindgren funnel, Malaise trap, flight intercept trap, rarely at UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:**

significantly higher abundance in CWD5, indifferent to forest type and season. **References:** Chandler 1990b; Downie and Arnett 1996; Newton et al. 2001; Ferro and Carlton 2010.

Trimiomelba dubia (LeConte) (Fig. 56)
Range: eastern United States west to Texas. **Habitat:** leaf litter, rotten logs. **Collection Method:** sifting/Berlese litter and rotten wood, at UV light. **Biology:** unknown, members of this subfamily are predacious. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Blatchley 1910; Chandler 1990b, 1999; Downie and Arnett 1996 (as *T. laevis* Casey, and *T. convexula* (LeConte)); Newton et al. 2001.

Scaphidiinae

Baeocera pallida Casey (Fig. 57)
Range: eastern North America west to Ontario and Texas. **Habitat:** forest litter, on spring edge, sifted chestnut oak litter, humus, rotten wood. **Collection Method:** sifting/Berlese litter. **Biology:** unknown, some species in this genus feed on slime molds (see Lawrence and Newton 1980), adults collected April to October. **Present Study:** significantly higher abundance in secondary forest, indifferent to substrate and season. **References:** Lawrence and Newton 1980; Löbl and Stephan 1993.

Scydmaeninae

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

***Euconnus* spp.** (Fig. 58)
***Euconnus* (*Napochus*) spp.** (Fig. 59)
***Euconnus* (*Scopophus*) spp.** (Fig. 60)
Range: mostly midwest, northeast, and southeastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** only *Euconnus* (*Napochus*) sp. was found in significantly higher abundance in leaf litter and secondary forest. **References:** Blatchley 1910; Downie and Arnett 1996 (usefulness of keys uncertain); Peck and Thomas 1998; O'Keefe 2001; Grebennikov and Newton 2009.

***Parascydmus* spp.** (Fig. 61)
Range: eastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** significantly higher abundance in primary forest in spring, indifferent to substrate. **References:** O'Keefe 2001.

***Scydmaenus* spp.** (Fig. 62)
Range: southwestern, central, and eastern United States. **Habitat:** forest floor litter, moss, tree holes, rotting logs, and other moist habitats. **Collection method:** sifting/Berlese litter, pitfalls, flight intercept traps, UV lights, looking under stones. **Biology:** adults and immatures feed on oribatid mites. **Present study:** significantly higher abundance in leaf litter, indifferent to forest type and season. **References:** Blatchley 1910; Downie and Arnett 1996 (usefulness of keys uncertain); Peck and Thomas 1998; O'Keefe 2001.

Steninae

***Stenus* spp.** (Fig. 63)
Comments. *Stenus* is one of the largest beetle genera with 167 species known from North America and

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

Tachyporinae

Ischnosoma lecontei Campbell (Fig. 64)
Range: Appalachian Mountains from Virginia to Georgia at 600–2020 m elevation, one questionable record from Ohio. **Habitat:** leaf litter of various hardwoods, edge of streams, rotting logs and stumps, tree holes. **Collection Method:** sifting/Berlese litter and debris. **Biology:** unknown, adults have been collected year round. **Present Study:** significantly higher abundance in leaf litter, primary forest, and spring. **References:** Campbell 1991.

TENEBRIONIDAE
Lagriinae

Anaedus brunneus (Ziegler) (Fig. 65)
Range: eastern United States: New York to Florida, west to Indiana. **Habitat:** sandy localities beneath bark and stones, forest litter. **Collection Method:** sifting/Berlese litter, searching under bark. **Biology:** overwinters as an adult, otherwise unknown. **Present Study:** significantly higher abundance in leaf litter, secondary forest, and spring. **References:** Blatchley 1910; Downie and Arnett 1996.

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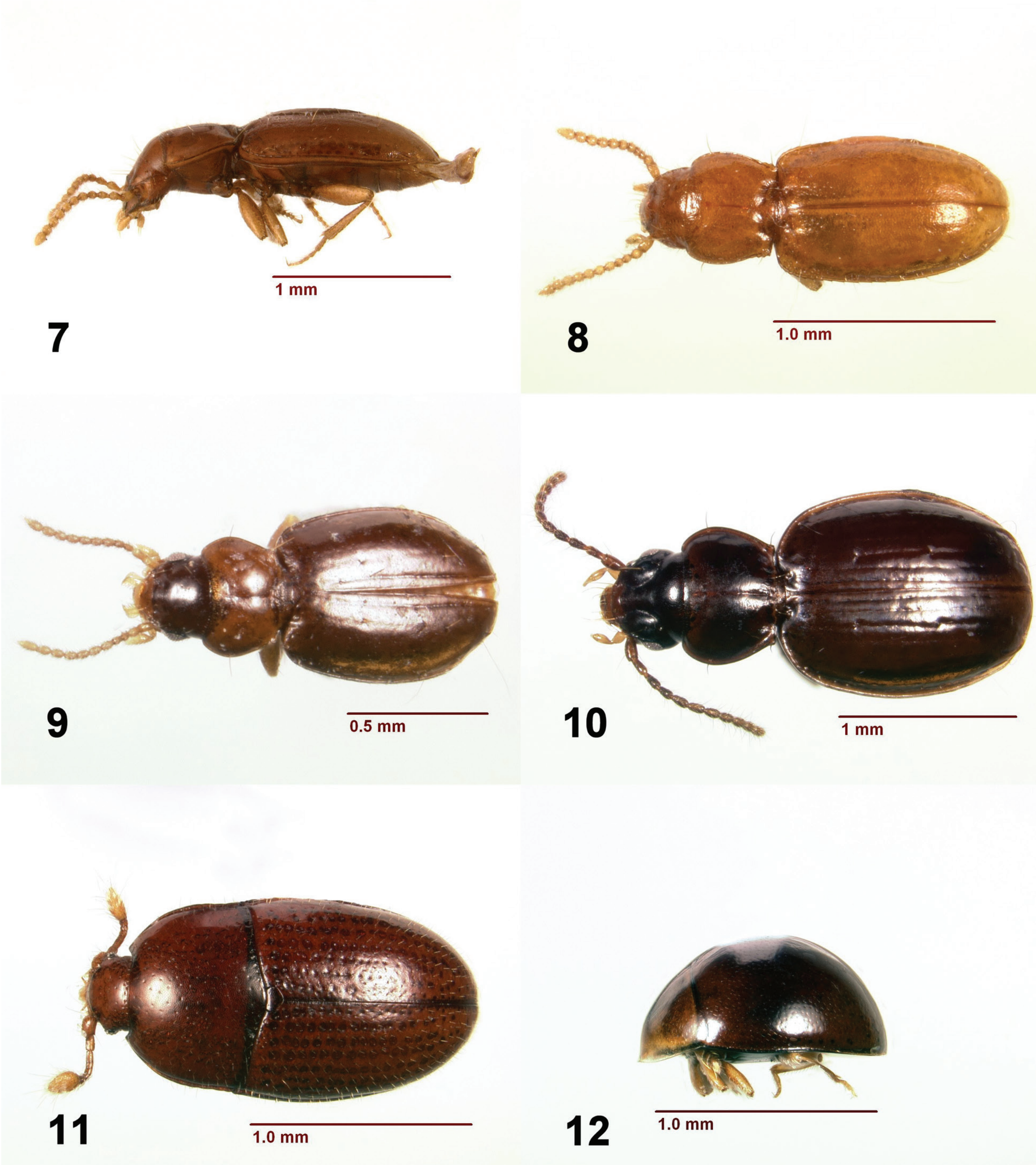
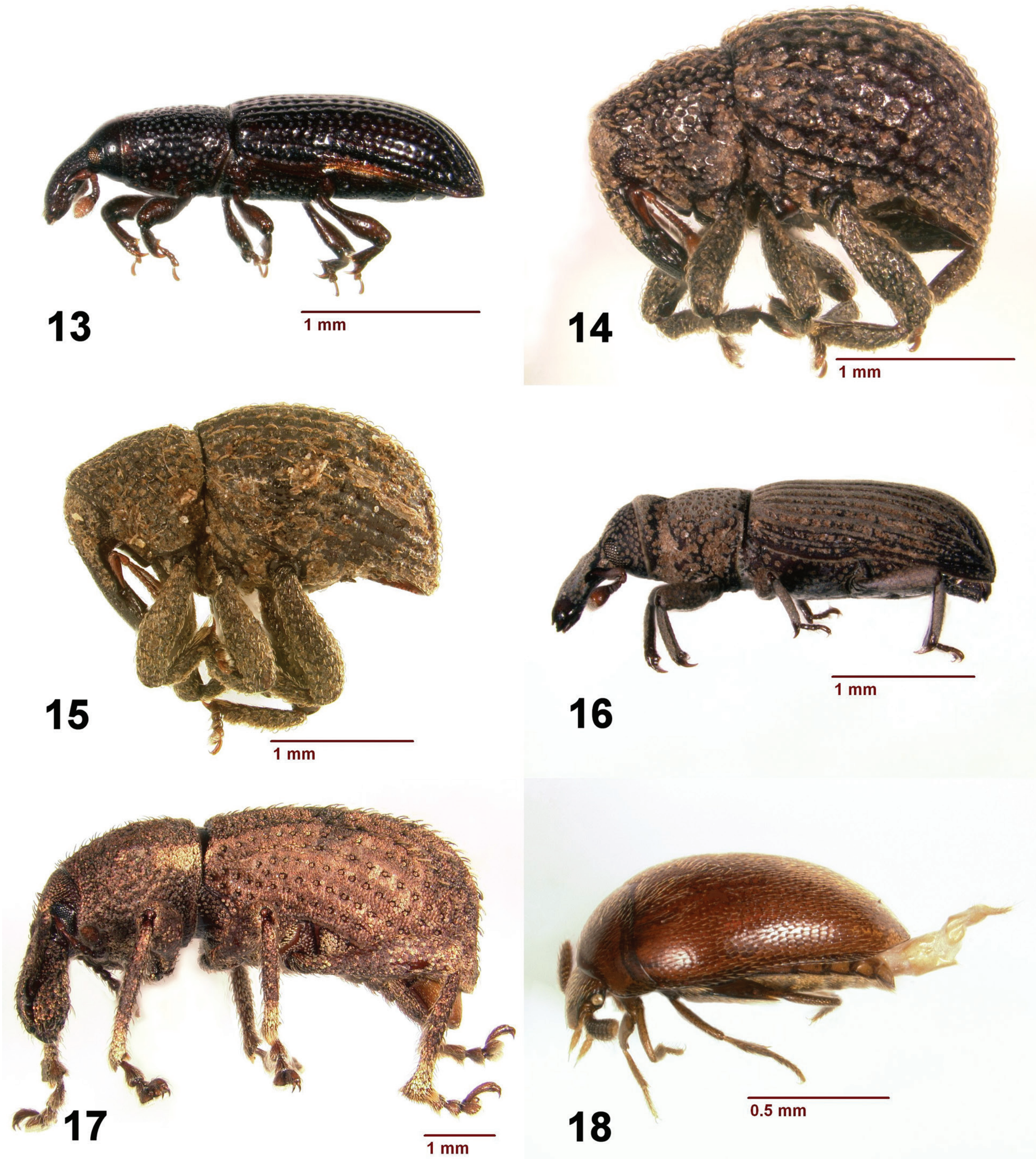
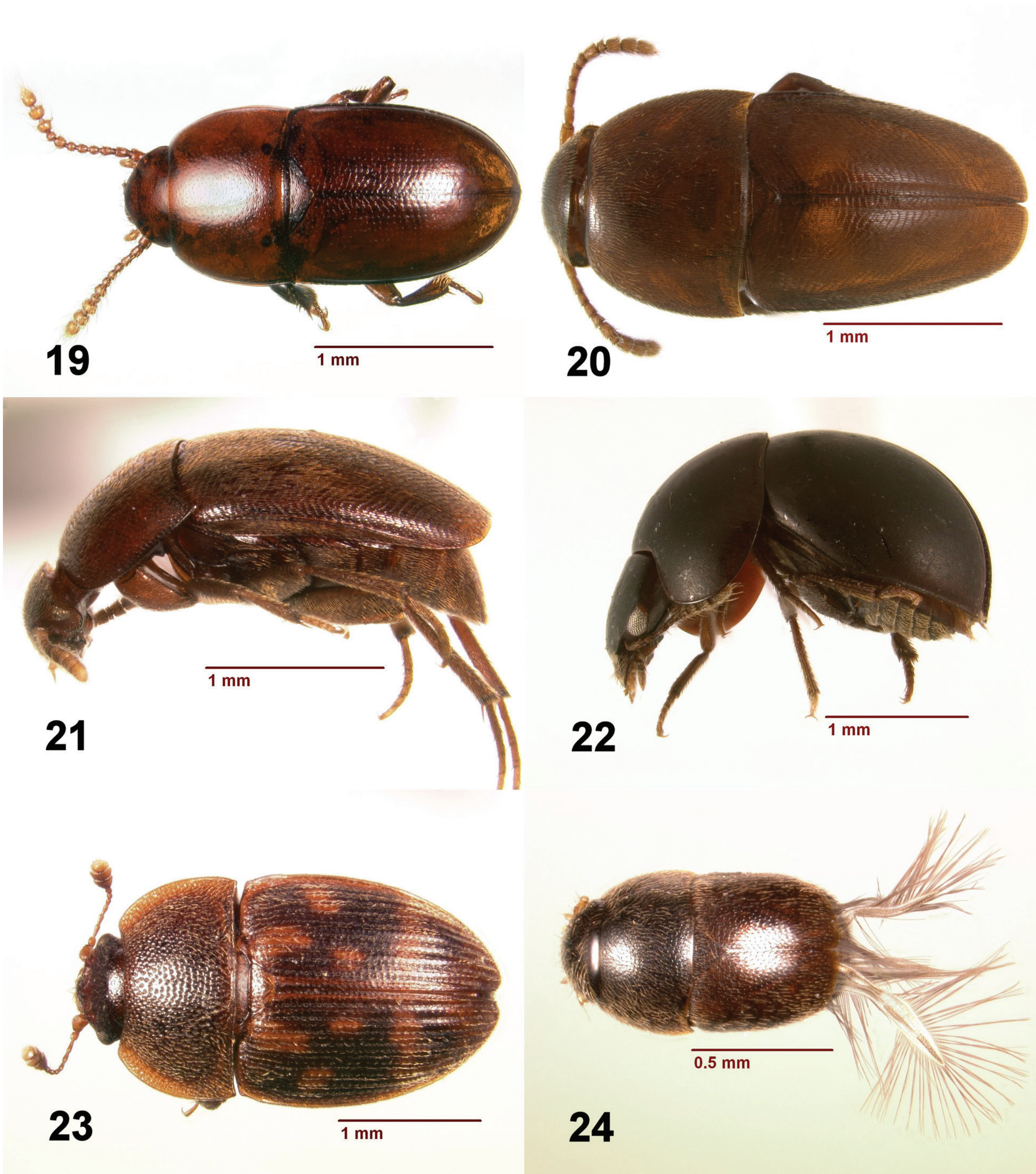


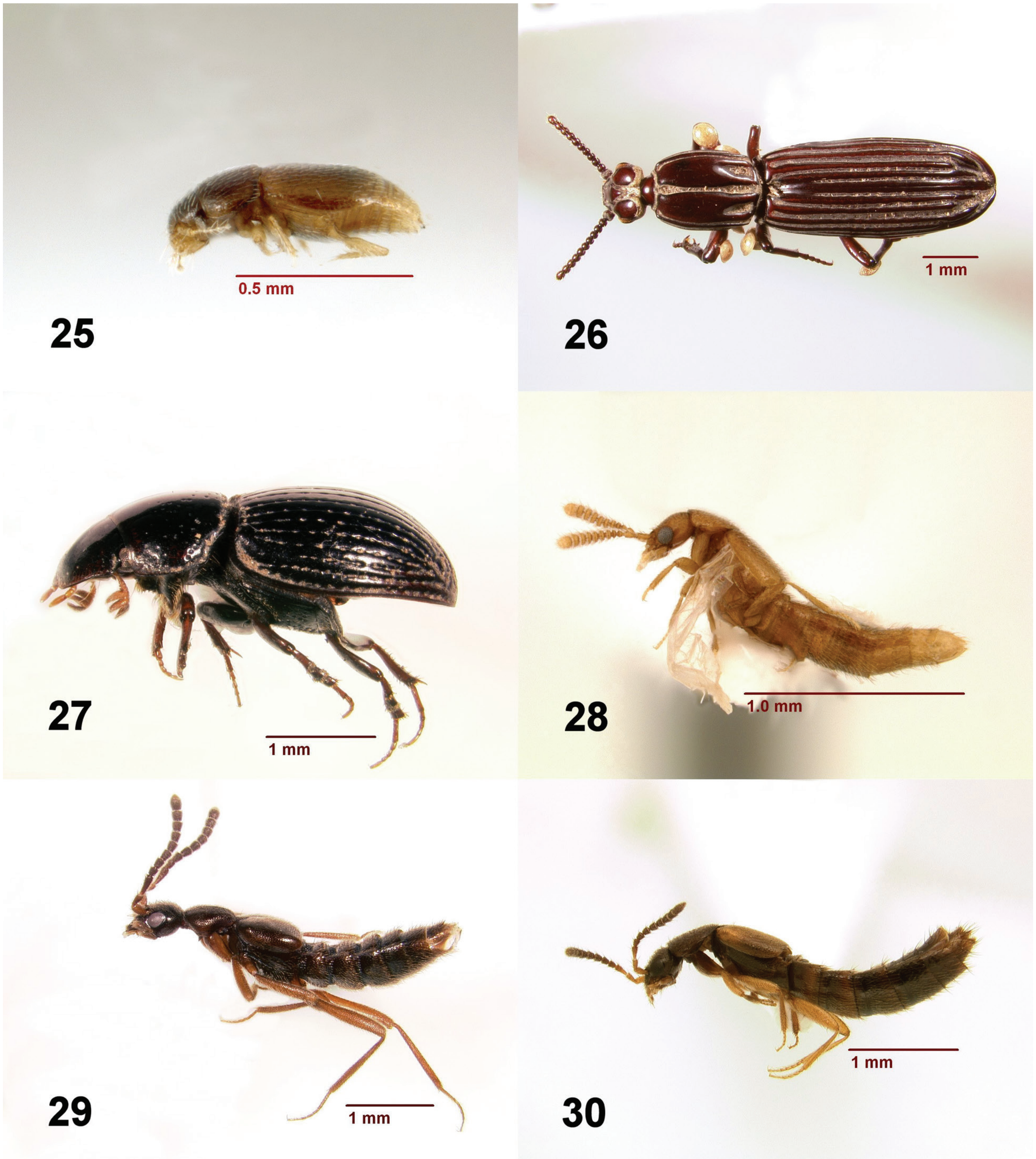
Figures 7–12. Habitus images. **7)** *Anillinus cherokee* Sokolov and Carlton (Carabidae: Trechinae). **8)** *Anillinus langdoni* Sokolov and Carlton (Carabidae: Trechinae). **9)** *Polyderis laevis* (Say) (Carabidae: Trechinae). **10)** *Trechus* (*Microtrechus*) *pisgahensis* Barr (Carabidae: Trechinae). **11)** *Mychocerus striatus* (Sen Gupta and Crowson) (Cerylonidae: Ceryloninae). **12)** *Holopsis* sp. (Corylophidae: Corylophinae).



Figures 13–18. Habitus images. **13)** *Caulophilus dubius* (Horn) (Curculionidae: Cossoninae). **14)** *Eurhoptus pyriformis* LeConte (Curculionidae: Cryptorhynchinae). **15)** *Eurhoptus* n. sp. (Curculionidae: Cryptorhynchinae). **16)** *Dryophthorus americanus* (Bedel) (Curculionidae: Dryophthorinae). **17)** *Panscopus impressus* Pierce (Curculionidae: Entiminae). **18)** *Tohlezkus inexpectus* Vit (Eucinetidae).

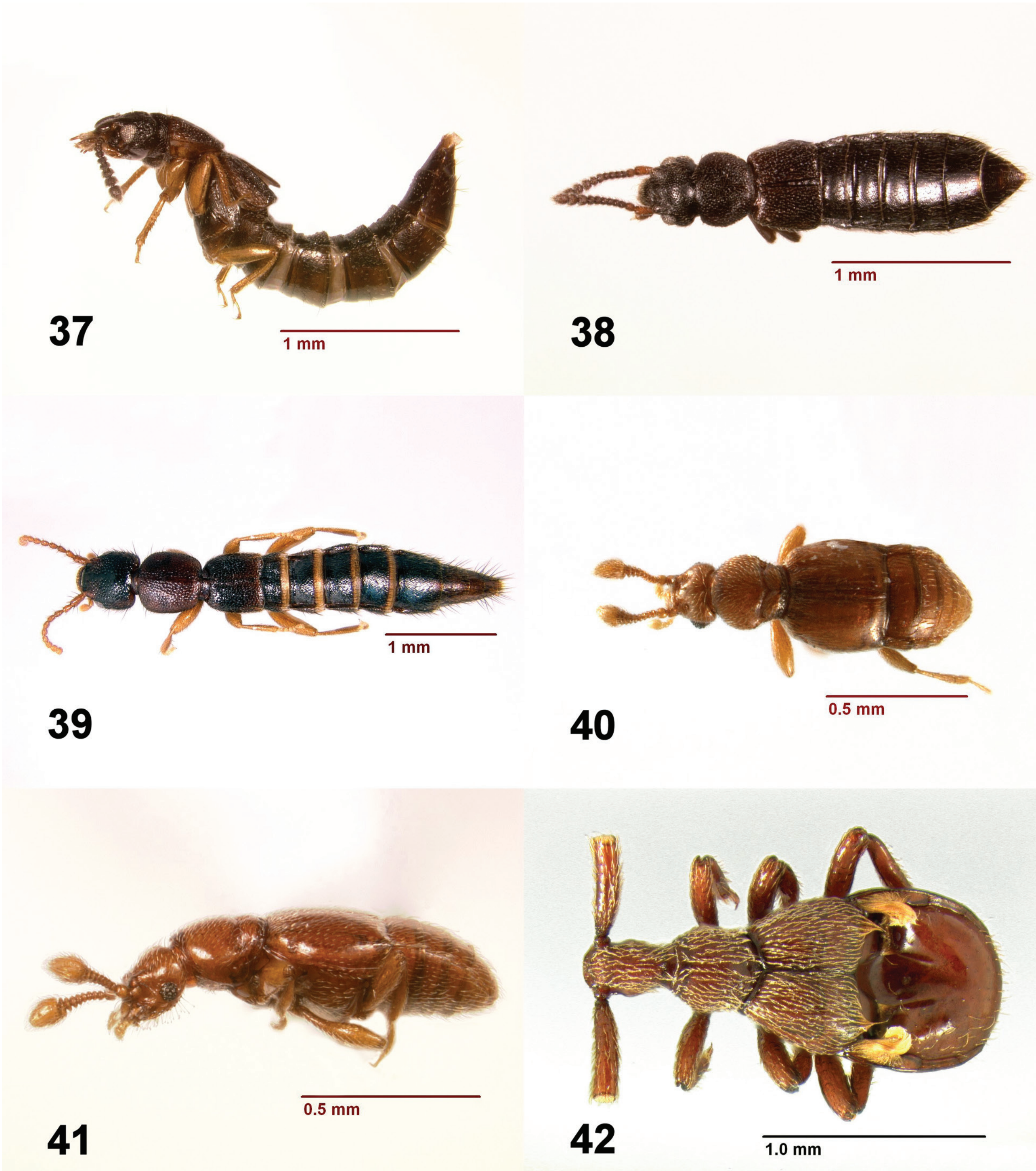


Figures 19–24. Habitus images. **19)** *Catopocerus* sp. (female) (Leiodidae: Catopocerinae). **20)** *Ptomaphagus appalachianus* (Peck) (Leiodidae: Cholevinae). **21)** *Ptomaphagus* sp. (female) (Leiodidae: Cholevinae). **22)** *Agathidium* sp. (female) (Leiodidae: Leiodinae). **23)** *Stelidota octomaculata* (Say) (Nitidulidae: Nitidulinae). **24)** *Acrotrichis* sp. (Ptiliidae: Acrotrichinae).



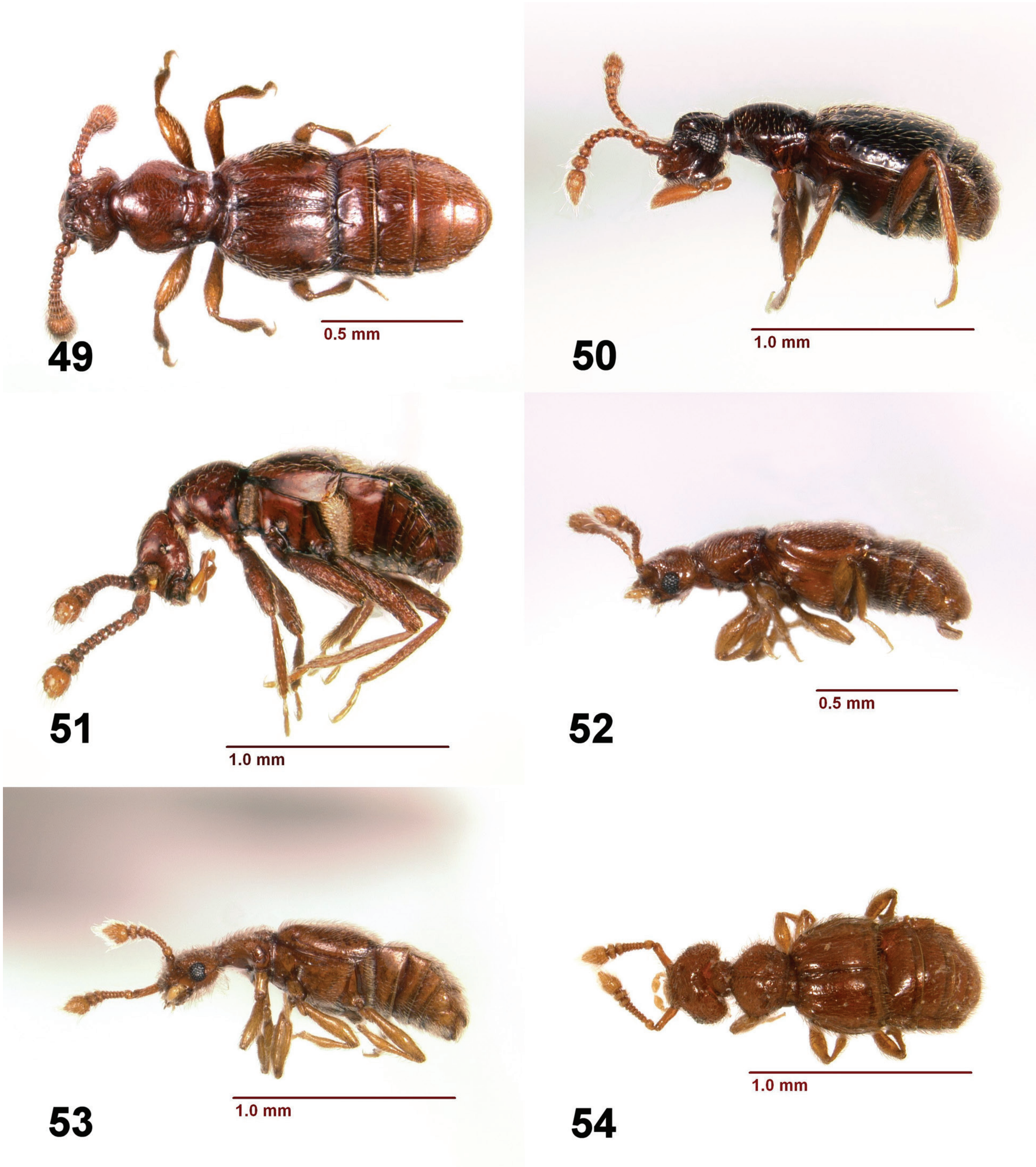
Figures 25–30. Habitus images. **25)** *Pteryx* sp. (Ptiliidae: Ptiliinae). **26)** *Clinidium valentinei* Bell (Rhysodidae). **27)** *Dialytellus tragicus* (Schmidt) (Scarabaeidae: Aphodiinae). **28)** Aleocharinae gen. sp. (Staphylinidae), representative of the specimens that could not be identified to genus. **29)** *Aleodorus bilobatus* (Say) (Staphylinidae: Aleocharinae). **30)** Athetini gen. sp. (Staphylinidae: Aleocharinae) representative of the specimens that could not be identified to genus.

Figures 31–36. Habitus images. **31)** *Leptusa gimmeli* Park and Carlton (Staphylinidae: Aleocharinae). **32)** *Leptusa pusio* (Casey) (Staphylinidae: Aleocharinae). **33)** *Leptusa* sp. (Casey) (Staphylinidae: Aleocharinae). **34)** *Myllaena* sp. (Staphylinidae: Aleocharinae). **35)** *Dasycerus* sp. (Staphylinidae: Dasycerinae). **36)** *Thoracophorus costalis* (Erichson) (Staphylinidae: Osoriinae).

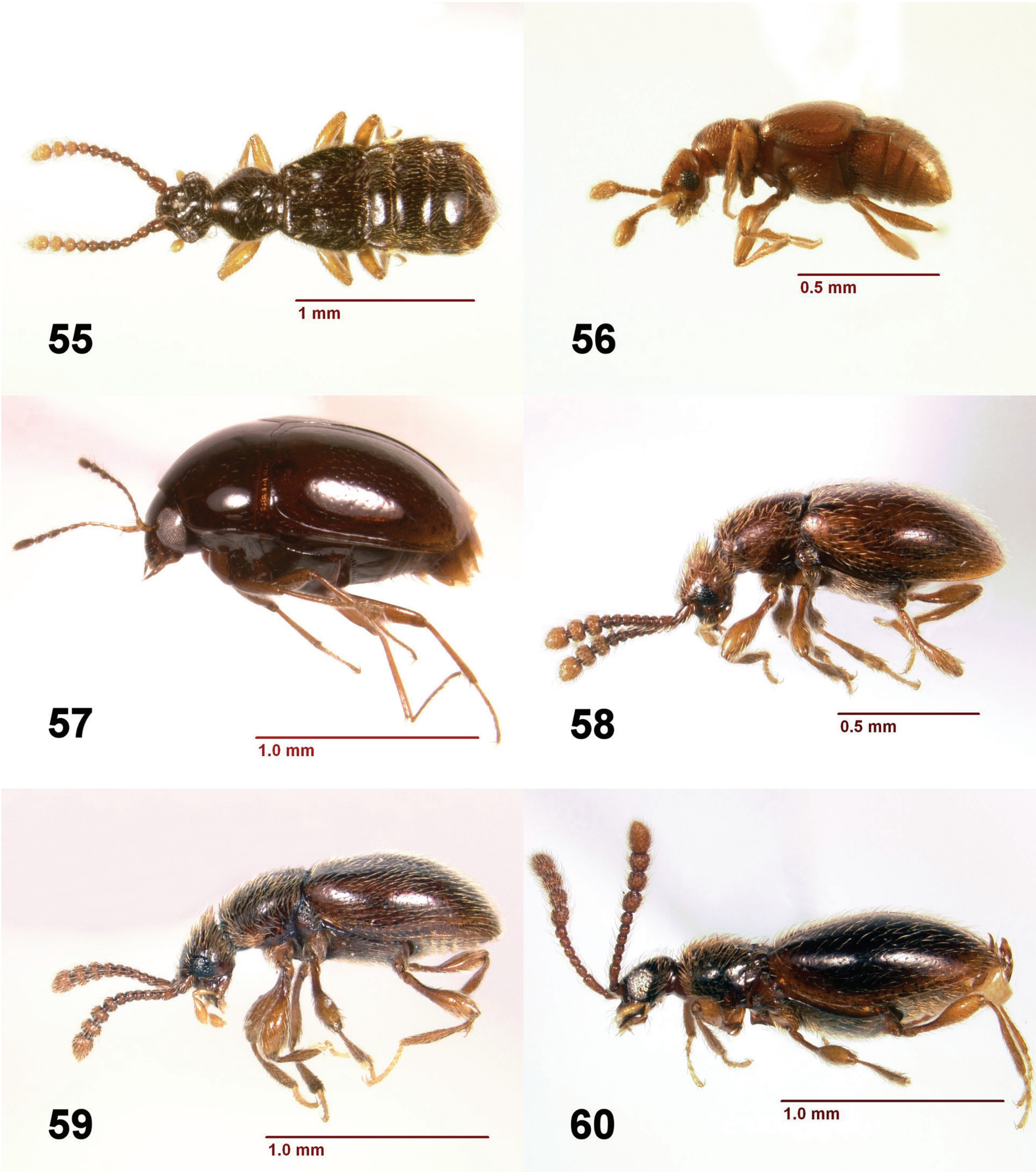


Figures 37–42. Habitus images. **37)** *Anotylus* sp. (Staphylinidae: Oxytelinae). **38)** *Carpelimus* sp. (Staphylinidae: Oxytelinae). **39)** *Sunius rufipes* (Casey) (Staphylinidae: Paederinae). **40)** *Actiastes fundatum* Grigarick and Schuster (Staphylinidae: Pselaphinae). **41)** *Actiastes* sp. (female) (Staphylinidae: Pselaphinae). **42)** *Adranes lecontei* Brendel (Staphylinidae: Pselaphinae).

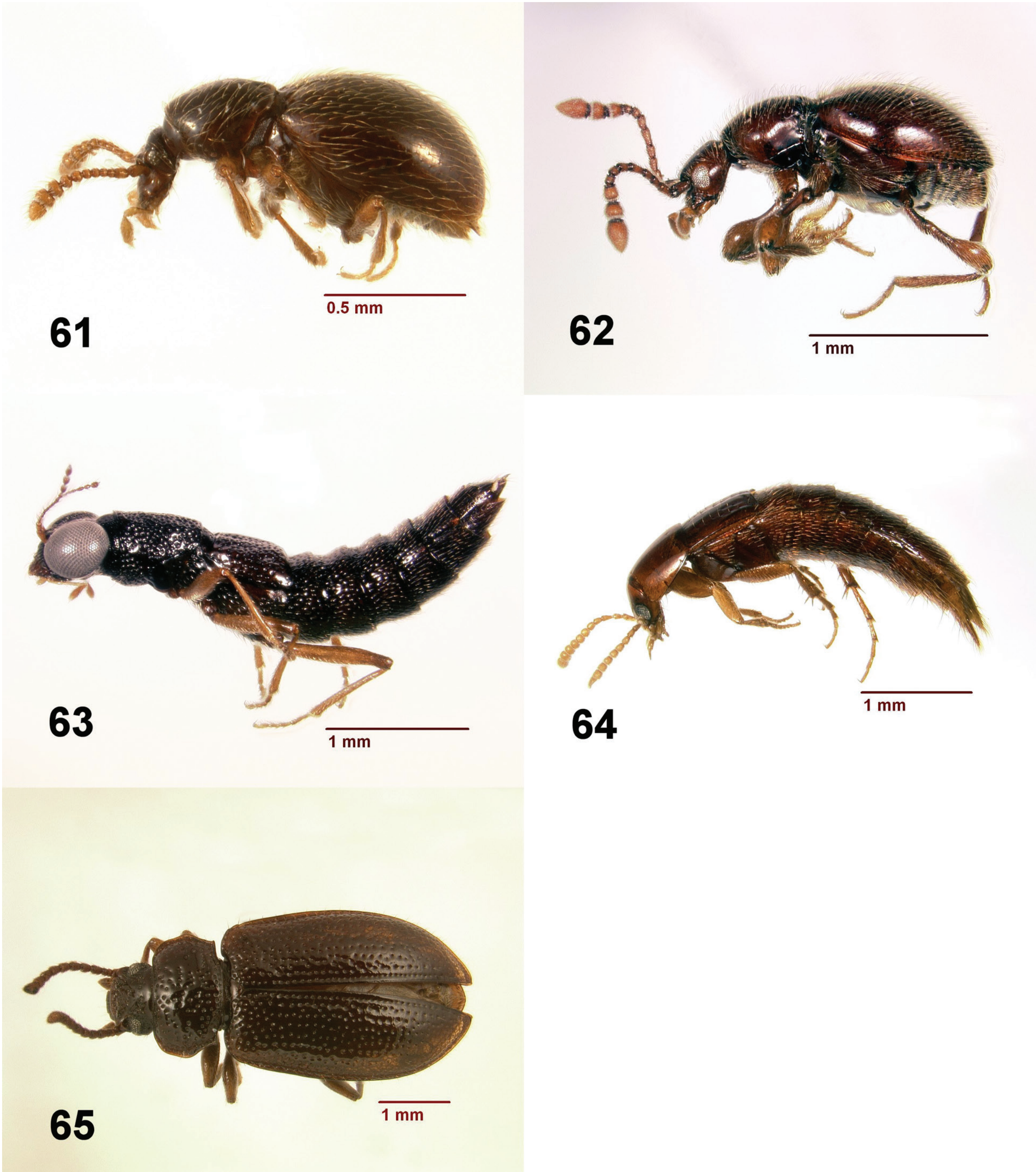
Figures 43–48. Habitus images. **43)** *Batrisodes beyeri* Schaeffer (Staphylinidae: Pselaphinae). **44)** *Batrisodes* sp. (Staphylinidae: Pselaphinae). **45)** *Conoplectus canaliculatus* (LeConte) (Staphylinidae: Pselaphinae). **46)** *Ctenisodes* sp. (Staphylinidae: Pselaphinae). **47)** *Euboarhexius perscitus* (Fletcher) (Staphylinidae: Pselaphinae). **48)** *Eutyphlus dybasi* Park (Staphylinidae: Pselaphinae).



Figures 49–54. Habitus images. **49)** *Eutyphlus* sp. (female) (Staphylinidae: Pselaphinae). **50)** *Machaerodes carinatus* (Brendel) (Staphylinidae: Pselaphinae). **51)** *Mipseltyrus nicolayi* Park (Staphylinidae: Pselaphinae). **52)** *Pseudactium arcuatum* (LeConte) (Staphylinidae: Pselaphinae). **53)** *Rhexius schmitti* Brendel (Staphylinidae: Pselaphinae). **54)** *Rhexius* sp. (female) (Staphylinidae: Pselaphinae).



Figures 55–60. Habitus images. **55)** *Sonoma* sp. (female) (Staphylinidae: Pselaphinae). **56)** *Trimiomelba dubia* (LeConte) (Staphylinidae: Pselaphinae). **57)** *Baeocera pallida* Casey (Staphylinidae: Scaphidiinae). **58)** *Euconnus* sp. (Staphylinidae: Scydmaeninae). **59)** *Euconnus* (*Napochus*) sp. (Staphylinidae: Scydmaeninae). **60)** *Euconnus* (*Scopophus*) sp. (Staphylinidae: Scydmaeninae).



Figures 61–65. Habitus images. **61)** *Parascydmus* sp. (Staphylinidae: Scydmaeninae). **62)** *Scydmaenus* sp. (Staphylinidae: Scydmaeninae). **63)** *Stenus* sp. (Staphylinidae: Steninae). **64)** *Ischnosoma lecontei* Campbell (Staphylinidae: Tachyporinae). **65)** *Anaedus brunneus* (Ziegler) (Tenebrionidae: Lagriinae).

Appendix 1. List of taxa and number of specimens collected as part of this research. Chi-square goodness of fit testing (CWD5 vs. leaf litter, primary vs. secondary, spring vs. fall) was performed for all taxa represented by 10 or more specimens. (F) = unidentified female specimens. For all tests degrees of freedom = 1 and α = 0.05. X = chi-square value. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, **** = $P < 0.0001$

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
AGYRTIDAE								
1	*Necrophilus pettitii* Horn	1	0	1	0	0	1	1
BRENTIDAE								
2	*Apion* spp.	0	3	1	2	0	3	3
CANTHARIDAE								
3	*Rhagonycha* sp.	0	1	0	1	1	0	1
CARABIDAE								
4	*Acupalpus testaceus* Dejean	0	1	1	0	1	0	1
5	*Amphasia interstitialis* (Say)	0	6	0	6	4	2	6
6	*Anillinus cherokee* Sokolov and Carlton	2	14**	16****	0	13*	3	16
		X = 9	***P = 0.0027***	**X = 16**	**P < 0.0001**	**X = 6.25**	**P = 0.0124**	
7	*Anillinus langdoni* Sokolov and Carlton	13	543****	467****	89	252	304*	556
		X = 505.2158	***P < 0.0001***	**X = 256.9856**	**P < 0.0001**	**X = 4.8633**	**P = 0.0274**	
8	*Anillinus loweae* Sokolov and Carlton	0	2	2	0	0	2	2
9	*Apenes lucidulus* (Dejean)	0	2	0	2	2	0	2
10	*Carabus* (*s.str.*) *goryi* Dejean	0	1	1	0	1	0	1
11	*Cyclotrachelus freitagi* Bousquet	0	2	0	2	2	0	2
12	*Dicaelus* (*Paradicaelus*) *dilatatus* Say	0	1	0	1	0	1	1
13	*Gastrellarius blanchardi* (Horn)	0	8	7	1	5	3	8
14	*Gastrellarius honestus* (Say)	4	0	1	3	3	1	4
15	*Harpalus spadiceus* Dejean	1	6	7	0	7	0	7
16	*Lebia viridis* Say	0	2	1	1	0	2	2
17	*Olisthopus parmatus* (Say)	1	2	0	3	2	1	3

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
18	*Polyderis laevis* (Say)	3	34****	2	35****	27**	10	37
		X = 25.973	***P < 0.0001***	**X = 29.4324**	**P < 0.0001**	**X = 7.8108**	**P = 0.0051**	
19	*Pterostichus* (*Steropus*) *moestus* (Say)	1	0	1	0	1	0	1
20	*Scaphinotus* (*Maronetus*) spp.	0	3	3	0	3	0	3
21	*Serranillus dunavani* (Jeannel)	2	0	1	1	2	0	2
22	*Serranillus* sp.	1	0	0	1	1	0	1
23	*Sphaeroderus bicarinatus* (LeConte)	0	1	1	0	0	1	1
24	*Sphaeroderus canadensis lengi* Darlington	0	1	1	0	1	0	1
25	*Sphaeroderus stenostomus lecontei* Dejean	0	2	0	2	2	0	2
26	*Trechus* (*Microtrechus*) *pisgahensis* Barr	23	33	56****	0	28	28	56
		X = 1.7857	***P = 0.1814***	**X = 56**	**P < 0.0001**	**X = 0**	**P = 1**	
27	*Trichotichnus autumnalis* (Say)	0	1	0	1	1	0	1
	CERYLONIDAE							
28	*Mychocerus striatus* (Sen Gupta and Crowson)	246****	4	68	182****	153***	97	250
		X = 234.256	***P < 0.0001***	**X = 51.984**	**P < 0.0001**	**X = 12.544**	**P = 0.0004**	
29	*Philothermus glabriculus* LeConte	4	2	4	2	6	0	6
30	*Philothermus stephani* Gimmel and Slipinski	4	0	4	0	0	4	4
	CHRYSOMELIDAE							
31	*Altica* spp.	1	3	4	0	2	2	4
32	*Capraita subvittata* (Horn)	0	3	3	0	1	2	3
33	*Disonycha leptolineata* Blatchley	0	1	1	0	0	1	1
34	*Disonycha xanthomelas* (Dalman)	0	1	1	0	0	1	1
35	*Odontota dorsalis* (Thunberg)	1	8	3	6	4	5	9
36	*Psylliodes appalachianus* Konstantinov and Tishechkin	0	6	6	0	3	3	6

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
CIIDAE							
37 *Ceracis* sp.	1	0	0	1	0	1	1
38 *Strigocis opalescens* (Casey)	1	0	1	0	1	0	1
CLAMBIDAE							
39 *Clambus* sp.	0	1	1	0	0	1	1
CORYLOPHIDAE							
40 *Holopsis* spp.	2	21****	2	21****	13	10	23
	X = 15.6957	***P < 0.0001***	**X = 15.6957**	**P < 0.0001**	**X = 0.3913**	**P = 0.5316**	
CRYPTOPHAGIDAE							
41 *Cryptophagus* sp.	0	1	1	0	1	0	1
42 *Henoticus serratus* (Gyllenhal)	0	1	1	0	0	1	1
CURCULIONIDAE							
43 *Acalles* spp.	0	9	5	4	9	0	9
44 *Anthonomus* sp.	0	1	1	0	1	0	1
45 *Caulophilus dubius* (Horn)	4	45****	30	19	38***	11	49
	X = 34.3061	***P < 0.0001***	**X = 2.4694**	**P = 0.1161**	**X = 14.8776**	**P = 0.0001**	
46 *Conotrachelus* spp.	0	7	7	0	6	1	7
47 *Craponius inaequalis* (Say)	0	1	0	1	1	0	1
48 Curculionidae gen. spp.	1	3	3	1	2	2	4
49 *Cyrtepistomus castaneus* (Roelofs)	0	1	0	1	1	0	1
50 *Dryophthorus americanus* (Bedel)	20****	0	0	20****	17**	3	20
	X = 20	***P < 0.0001***	**X = 20**	**P < 0.0001**	**X = 9.8**	**P = 0.0017**	
51 *Epacalles* spp.	0	4	1	3	0	4	4

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
52 *Eurhoptus* n. sp.	1	38****	4	35****	24	15	39
	X = 35.1026	***P < 0.0001***	**X = 24.641**	**P < 0.0001**	**X = 2.0769**	**P = 0.1495**	
53 *Eurhoptus pyriformis* LeConte	0	55****	44****	11	34	21	55
	X = 55	***P < 0.0001***	**X = 19.8**	**P < 0.0001**	**X = 3.0727**	**P = 0.0796**	
54 *Lechriops oculatus* (Say)	1	0	1	0	1	0	1
55 *Microhyus* n.sp.	0	2	2	0	1	1	2
56 *Microhyus setiger* LeConte	2	0	2	0	2	0	2
57 *Myosides seriehispidus* Roelofs	2	7	0	9	8	1	9
58 *Odontopus calceatus* (Say)	0	1	1	0	0	1	1
59 *Panscopus impressus* Pierce	0	12***	10*	2	2	10*	12
	X = 12	***P = 0.0005***	**X = 5.3333**	**P = 0.0209**	**X = 5.3333**	**P = 0.0209**	
60 *Pseudanthonomus* spp.	0	3	2	1	2	1	3
61 *Xylosandrus crassiusculus* (Motschulsky)	1	0	0	1	0	1	1
62 *Xyloterinus politus* (Say)	0	1	1	0	1	0	1
ELATERIDAE							
63 *Ampedus rubicus* (Say)	1	0	1	0	0	1	1
64 *Ampedus* sp.	1	0	1	0	0	1	1
65 *Dalopius* sp.	0	1	1	0	0	1	1
66 *Limonius nimbatus* (Say)	0	1	0	1	1	0	1
EROTYLIDAE							
67 *Tritoma unicolor* Say	0	1	0	1	1	0	1
EUCINETIDAE							
68 *Tohlezkus inexpectus* Vit	34****	1	31****	4	30****	5	35
	X = 31.1143	***P < 0.0001***	**X = 20.8286**	**P < 0.0001**	**X = 17.8571**	**P < 0.0001**	

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
HISTERIDAE							
69 *Bacanius tantillus* LeConte	2	1	2	1	2	1	3
HYDROPHILIDAE							
70 *Cercyon occallatus* (Say)	0	4	4	0	2	2	4
LATRIDIIDAE							
71 *Dienerella costulata* (Reitter)	2	2	3	1	0	4	4
LEIODIDAE							
72 *Agathidium compressidens* Fall	1	0	1	0	0	1	1
73 *Agathidium divaricatum* Miller and Wheeler	0	2	2	0	1	1	2
74 *Agathidium gallititillo* Miller and Wheeler	0	2	2	0	0	2	2
75 *Agathidium kimberlae* Miller and Wheeler	0	3	2	1	2	1	3
76 *Agathidium* n.sp.	0	5	4	1	3	2	5
77 *Agathidium oniscoides* Beauvois	4	0	4	0	4	0	4
78 *Agathidium rubellum* Fall	2	0	1	1	1	1	2
79 *Agathidium* spp. (F)	7	18*	18*	7	13	12	25
	X = 4.84	***P = 0.0278***	**X = 4.84**	**P = 0.0278**	**X = 0.04**	**P = 0.8415**	
80 *Aglyptinus laevis* (LeConte)	3	0	0	3	1	2	3
81 *Cainosternum imbricatum* Notman	0	1	1	0	0	1	1
82 *Catopocerus appalachianus* Peck	0	5	3	2	3	2	5
83 *Catopocerus* n.sp.	0	4	3	1	2	2	4
84 *Catopocerus* spp. (F)	0	16****	11	5	11	5	16
	X = 16	***P < 0.0001***	**X = 2.25**	**P = 0.1336**	**X = 2.25**	**P = 0.1336**	
85 *Catops paramericanus* Peck and Cook	0	1	1	0	1	0	1
86 *Colenis impunctata* LeConte	0	7	0	7	7	0	7
87 *Colon megasetosum* Peck and Stephan	0	4	0	4	0	4	4

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
88 *Gelae* spp. (F)	1	0	1	0	1	0	1
89 *Hydnobius substriatus* LeConte	0	2	0	2	0	2	2
90 *Ptomaphagus appalachianus* (Peck)	9	25**	31****	3	6	28***	34
	X = 7.5294	***P = 0.0061***	**X = 23.0588**	**P < 0.0001**	**X = 14.2353**	**P = 0.0002**	
91 *Ptomaphagus* spp. (F)	9	32***	36****	5	16	25	41
	X = 12.9024	***P = 0.0003***	**X = 23.439**	**P < 0.0001**	**X = 1.9756**	**P = 0.1599**	
92 *Sciodrepoides watsoni* (Spence)	1	0	1	0	1	0	1
LUCANIDAE							
93 *Platycerus virescens* (Fabricius)	0	1	1	0	1	0	1
MONOTOMIDAE							
94 *Bactridium* sp.	0	1	0	1	0	1	1
NITIDULIDAE							
95 *Epuraea* sp.	0	1	0	1	1	0	1
96 *Pallodes pallidus* (Beauvois)	0	2	2	0	1	1	2
97 *Stelidota geminata* (Say)	0	2	0	2	2	0	2
98 *Stelidota octomaculata* (Say)	0	41****	13	28*	26	15	41
	X = 41	***P < 0.0001***	**X = 5.4878**	**P = 0.0191**	**X = 2.9512**	**P = 0.0858**	
PHALACRIDAE							
99 *Acylomus* n.sp.	0	1	0	1	0	1	1
PTILIIDAE							
100 *Acrotrichis* spp.	17	460****	470****	7	207	270**	477
	X = 411.4235	***P < 0.0001***	**X = 449.4109**	**P < 0.0001**	**X = 8.3208**	**P = 0.0039**	

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
101 *Micridium* sp.	0	1	0	1	0	1	1
102 *Nossidium* spp.	4	1	5	0	5	0	5
103 *Pteryx* spp.	15**	2	8	9	9	8	17
	X = 9.9412	***P = 0.0016***	**X = 0.0588**	**P = 0.8084**	**X = 0.0588**	**P = 0.8084**	
104 Ptiliidae gen. spp.	2	0	1	1	2	0	2
RHYSODIDAE							
105 *Clinidium valentinei* Bell	7	3	2	8	5	5	10
	X = 1.6	***P = 0.2059***	**X = 3.6**	**P = 0.0577**	**X = 0**	**P = 1**	
SCARABAEIDAE							
106 *Dialytellus tragicus* (Schmidt)	2	37****	38****	1	30***	9	39
	X = 31.4103	***P < 0.0001***	**X = 35.1026**	**P < 0.0001**	**X = 11.3077**	**P = 0.0007**	
107 *Serica* spp.	0	6	3	3	6	0	6
STAPHYLINIDAE							
Aleocharinae							
108 *Aleodorus bilobatus* (Say)	0	28****	28****	0	3	25****	28
	X = 28	***P < 0.0001***	**X = 28**	**P < 0.0001**	**X = 17.2857**	**P < 0.0001**	
109 Athetini gen. spp.	0	13***	9	4	11*	2	13
	X = 13	***P = 0.0003***	**X = 1.9231**	**P = 0.1655**	**X = 6.2308**	**P = 0.0125**	
110 *Euvira* spp.	0	5	2	3	3	2	5
111 *Gyrophaena* sp.	0	1	0	1	0	1	1
112 *Hoplandria laeviventris* Casey	0	2	0	2	0	2	2
113 *Leptusa carolinensis* Pace	1	0	1	0	0	1	1
114 *Leptusa cribratula* (Casey)	7	0	0	7	5	2	7
115 *Leptusa gimmeli* Park and Carlton	0	101****	101****	0	37	64**	101
	X = 101	***P < 0.0001***	**X = 101**	**P < 0.0001**	**X = 7.2178**	**P = 0.0072**	

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
116	*Leptusa pseudosmokyiensis* Park and Carlton	0	2	2	0	2	0	2
117	*Leptusa pusio* (Casey)	11*	2	13***	0	11*	2	13
		X = 6.2308	***P = 0.0125***	**X = 13**	**P = 0.0003**	**X = 6.2308**	**P = 0.0125**	
118	*Leptusa* spp.	24	16	18	22	21	19	40
		X = 1.6	***P = 0.2059***	**X = 0.4**	**P = 0.5271**	**X = 0.1**	**P = 0.7518**	
119	*Myllaena* spp.	13	11	4	20**	14	10	24
		X = 0.1667	***P = 0.6831***	**X = 10.6667**	**P = 0.0011**	**X = 0.6667**	**P = 0.4142**	
120	*Oxypoda* spp.	0	4	1	3	0	4	4
121	*Phanerota* sp.	0	1	0	1	1	0	1
122	Aleocharinae gen. spp.	4	8	7	5	8	4	12
		X = 1.3333	***P = 0.2482***	**X = 0.3333**	**P = 0.5637**	**X = 1.3333**	**P = 0.2482**	
Dasycerinae								
123	*Dasycerus* spp.	0	20****	0	20****	17**	3	20
		X = 20	***P < 0.0001***	**X = 20**	**P < 0.0001**	**X = 9.8**	**P = 0.0017**	
Euaesthetinae								
124	*Edaphus americanus* Puthz	5	1	2	4	2	4	6
125	*Stictocranius puncticeps* LeConte	1	3	0	4	1	3	4
Osoriinae								
126	*Thoracophorus costalis* (Erichson)	17*	5	2	20***	21****	1	22
		X = 6.5455	***P = 0.0105***	**X = 14.7273**	**P = 0.0001**	**X = 18.1818**	**P < 0.0001**	
Oxytelinae								
127	*Anotylus* spp.	0	86****	83****	3	80****	6	86
		X = 86	***P < 0.0001***	**X = 74.4186**	**P < 0.0001**	**X = 63.6744**	**P < 0.0001**	
128	*Carpelimus* sp. 1	0	12***	11**	1	1	11**	12
		X = 12	***P = 0.0005***	**X = 8.3333**	**P = 0.0038**	**X = 8.3333**	**P = 0.0038**	
129	*Carpelimus* sp. 2	1	0	1	0	1	0	1
130	*Oxytelus convergens* LeConte	0	1	1	0	1	0	1

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
131	*Oxytelus* spp. (F)	0	2	2	0	2	0	2
Paederinae								
132	*Achenomorphus corticinus* (Gravenhorst)	0	3	0	3	1	2	3
133	*Homaeotarsus* sp.	0	1	0	1	0	1	1
134	*Lathrobium* spp.	0	3	0	3	1	2	3
135	*Ochthephilum* sp.	0	1	0	1	0	1	1
136	*Palaminus fraternus* Casey	0	3	0	3	0	3	3
137	*Palaminus* spp. (F)	0	6	0	6	4	2	6
138	*Palaminus testaceus* Erichson	0	1	0	1	0	1	1
139	*Stilicopsis paradoxa* Sachse	0	2	0	2	2	0	2
140	*Sunius confluentus* (Say)	2	0	0	2	2	0	2
141	*Sunius rufipes* (Casey)	9	602****	375****	236	282	329	611
		X = 575.5303	***P < 0.0001***	**X = 31.6219**	**P < 0.0001**	**X = 3.6154**	**P = 0.0572**	
Pselaphinae								
142	*Actiastes fundatum* Grigarick and Schuster	1	41****	42****	0	16	26	42
		X = 38.0952	***P < 0.0001***	**X = 42**	**P < 0.0001**	**X = 2.381**	**P = 0.1228**	
143	*Actiastes* spp. (F)	1	98****	97****	2	59	40	99
		X = 95.0404	***P < 0.0001***	**X = 91.1616**	**P < 0.0001**	**X = 3.6465**	**P = 0.0561**	
144	*Actiastes suteri* (Park)	0	7	6	1	5	2	7
145	*Adranes lecontei* Brendel	8	7	0	15***	10	5	15
		X = 0.0667	***P = 0.7963***	**X = 15**	**P = 0.0001**	**X = 1.6667**	**P = 0.1967**	
146	*Arianops digitata* Barr	1	0	1	0	0	1	1
147	*Batrisodes auerbachi* Park	3	1	2	2	2	2	4
148	*Batrisodes beyeri* Schaeffer	1	11**	11**	1	4	8	12
		X = 8.3333	***P = 0.0038***	**X = 8.3333**	**P = 0.0038**	**X = 1.3333**	**P = 0.2482**	
149	*Batrisodes denticollis* (Casey)	0	3	0	3	3	0	3
150	*Batrisodes lineaticollis* (Aubé)	3	1	3	1	2	2	4

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
151	*Batrisodes* spp. (F)	11	12	13	10	15	8	23
		X = 0.0435	***P = 0.8348***	**X = 0.3913**	**P = 0.5316**	**X = 2.1304**	**P = 0.1444**	
152	*Bibloplectus ruficeps* (Motschulsky)	3	0	0	3	3	0	3
153	*Bibloplectus* spp. (F)	2	0	0	2	2	0	2
154	*Conoplectus canaliculatus* (LeConte)	20***	3	1	22****	9	14	23
		X = 12.5652	***P = 0.0003***	**X = 19.1739**	**P < 0.0001**	**X = 1.087**	**P = 0.2971**	
155	*Ctenisodes* spp.	1	29****	1	29****	8	22*	30
		X = 26.1333	***P < 0.0001***	**X = 26.1333**	**P < 0.0001**	**X = 6.5333**	**P = 0.0105**	
156	*Custotychus daggyi* (Park)	0	1	0	1	0	1	1
157	*Custotychus spiculifer* (Casey)	0	2	0	2	1	1	2
158	*Custotychus* spp. (F)	1	3	0	4	3	1	4
159	*Decarthron nigrocavum* Park	0	2	0	2	2	0	2
160	*Euboarhexius perscitus* (Fletcher)	0	56****	55****	1	24	32	56
		X = 56	***P < 0.0001***	**X = 52.0714**	**P < 0.0001**	**X = 1.1429**	**P = 0.2850**	
161	*Euboarhexius trogasteroides* (Brendel)	0	4	3	1	4	0	4
162	*Euplectus* sp. (F)	1	0	0	1	1	0	1
163	*Eutyphlus dybasi* Park	1	14***	15***	0	4	11	15
		X = 11.2667	***P = 0.0007***	**X = 15**	**P = 0.0001**	**X = 3.2667**	**P = 0.0707**	
164	*Eutyphlus* spp. (F)	3	176****	162****	17	94	85	179
		X = 167.2011	***P < 0.0001***	**X = 117.4581**	**P < 0.0001**	**X = 0.4525**	**P = 0.5011**	
165	*Eutyphlus thoracicus* Park	0	1	1	0	1	0	1
166	*Leptoplectus pertenuis* (Casey)	6	2	0	8	6	2	8
167	*Machaerodes carinatus* (Brendel)	3	50****	53****	0	27	26	53
		X = 41.6792	***P < 0.0001***	**X = 53**	**P < 0.0001**	**X = 0.0189**	**P = 0.8907**	
168	*Mipseltyrus nicolayi* Park	1	33****	34****	0	27***	7	34
		X = 30.1176	***P < 0.0001***	**X = 34**	**P < 0.0001**	**X = 11.7647**	**P = 0.0006**	
169	*Prespelea copelandi* Park	0	1	1	0	1	0	1
170	*Prespelea quirsfeldi* Park	0	4	4	0	2	2	4

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
171	*Pseudactium arcuatum* (LeConte)	2	16***	3	15**	1	17***	18
		X = 10.8889	***P = 0.0009***	**X = 8**	**P = 0.0046**	**X = 14.2222**	**P = 0.0002**	
172	*Pycnoplectus infossus* (Raffray)	1	0	0	1	0	1	1
173	*Pycnoplectus interruptus* (LeConte)	1	0	1	0	1	0	1
174	*Pycnoplectus* spp. (F)	2	0	1	1	2	0	2
175	*Rhexius schmitti* Brendel	0	10**	0	10**	9*	1	10
		X = 10	***P = 0.0015***	**X = 10**	**P = 0.0015**	**X = 6.4**	**P = 0.0114**	
176	*Rhexius* spp. (F)	2	11*	0	13***	9	4	13
		X = 6.2308	***P = 0.0125***	**X = 13**	**P = 0.0003**	**X = 1.9231**	**P = 0.1655**	
177	*Sonoma chouljenkoi* Ferro and Carlton	2	1	1	2	2	1	3
178	*Sonoma gilae* Ferro and Carlton	5	0	5	0	4	1	5
179	*Sonoma gimmeli* Ferro and Carlton	1	2	0	3	2	1	3
180	*Sonoma* spp. (F)	22**	6	10	18	13	15	28
		X = 9.1429	***P = 0.0024***	**X = 2.2857**	**P = 0.1306**	**X = 0.1429**	**P = 0.7055**	
181	*Tmesiphorus* sp.	1	0	0	1	1	0	1
182	*Trimiomelba dubia* (LeConte)	1	11**	0	12***	12***	0	12
		X = 8.3333	***P = 0.0038***	**X = 12**	**P = 0.0005**	**X = 12**	**P = 0.0005**	
Scaphidiinae								
183	*Baeocera pallida* Casey	2	8	0	10**	6	4	10
		X = 3.6	***P = 0.0577***	**X = 10**	**P = 0.0015**	**X = 0.4**	**P = 0.5271**	
184	*Baeocera* spp.	2	0	0	2	2	0	2
185	*Scaphisoma suturale* LeConte	0	3	1	2	3	0	3
186	*Toxidium gammaroides* LeConte	1	2	0	3	2	1	3
Scydmaeninae								
187	*Brachycepsis* sp.	0	1	0	1	1	0	1
188	*Euconnus* (*Napochus*) spp.	22	116****	27	111****	68	70	138
		X = 64.029	***P < 0.0001***	**X = 51.1304**	**P < 0.0001**	**X = 0.029**	**P = 0.8648**	
189	*Euconnus* (*Napoconnus*) sp.	1	0	0	1	0	1	1

SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
190 *Euconnus* (*Scopophus*) spp.	38	25	34	29	35	28	63
	X = 2.6825	***P = 0.1015***	**X = 0.3968**	**P = 0.5287**	**X = 0.7778**	**P = 0.3778**	
191 *Euconnus* spp.	15	12	11	16	13	14	27
	X = 0.3333	***P = 0.5637***	**X = 0.9259**	**P = 0.3359**	**X = 0.037**	**P = 0.8474**	
192 *Leptoscydmus* spp.	6	1	1	6	4	3	7
193 *Microscydmus* (*Delius*) sp.	1	0	0	1	0	1	1
194 *Microscydmus* (*Neladius*) sp.	1	0	1	0	0	1	1
195 *Microscydmus* (*s. str.*) spp.	3	0	0	3	2	1	3
196 *Parascydmus* spp.	3	10	12**	1	13***	0	13
	X = 3.7692	***P = 0.0522***	**X = 9.3077**	**P = 0.0022**	**X = 13**	**P = 0.0003**	
197 *Scydmaenus* spp.	0	15***	6	9	5	10	15
	X = 15	***P = 0.0001***	**X = 0.6**	**P = 0.4386**	**X = 1.6667**	**P = 0.1967**	
198 *Stenichnus* sp.	0	1	1	0	1	0	1
Staphylininae							
199 *Atrecus americanus* (Casey)	1	0	1	0	0	1	1
200 *Erichsonius patella* (Horn)	0	3	0	3	2	1	3
201 *Gabrius fallaciosus* (Horn)	1	0	1	0	1	0	1
202 *Philonthus* spp.	0	2	2	0	0	2	2
203 *Platydracus cinnamopterus* (Gravenhorst)	0	3	0	3	3	0	3
Steninae							
204 *Stenus* spp.	2	38****	40****	0	30**	10	40
	X = 32.4	***P < 0.0001***	**X = 40**	**P < 0.0001**	**X = 10**	**P = 0.0015**	
Tachyporinae							
205 *Bryoporus rufescens* LeConte	0	8	0	8	6	2	8
206 *Ischnosoma lecontei* Campbell	1	29****	25***	5	27****	3	30
	X = 26.1333	***P < 0.0001***	**X = 13.3333**	**P = 0.0002**	**X = 19.2**	**P < 0.0001**	
207 *Mycetoporus americanus* Erichson	0	1	1	0	1	0	1
208 *Sepedophilus basalis* (Erichson)	1	2	0	3	3	0	3

	SPECIES	CWD5	LEAF LITTER	PRIMARY	SECONDARY	SPRING	FALL	TOTAL
209	*Sepedophilus brachypterus* Campbell	7	0	4	3	5	2	7
210	*Sepedophilus cinctulus* (Erichson)	1	0	0	1	1	0	1
211	*Sepedophilus crassus* (Gravenhorst)	1	0	1	0	1	0	1
212	*Sepedophilus occultus* (Casey)	2	0	2	0	0	2	2
213	*Sepedophilus versicolor* (Casey)	4	0	0	4	3	1	4
TENEBRIONIDAE								
214	*Anaedus brunneus* (Ziegler)	0	10**	0	10**	9*	1	10
		X = 10	***P = 0.0015***	**X = 10**	**P = 0.0015**	**X = 6.4**	**P = 0.0114**	
215	*Paratenetus* spp.	0	7	1	6	1	6	7
THROSCIDAE								
216	*Aulonothroscus punctatus* (Bonvouloir)	0	1	0	1	1	0	1
	Significant Associations	**8**	**40**	**28**	**19**	**19**	**9**	