Apheloria polychroma, a new species of millipede from the Cumberland Mountains (Polydesmida: Xystodesmidae)

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Abstract

Millipedes of the genus *Apheloria* occur in temperate broadleaf forests throughout eastern North America and west of the Mississippi River in the Ozark and Ouachita Mountains. Chemically defended with toxins made up of cyanide and benzaldehyde, the genus is part of a community of xystodesmid millipedes that compose several Müllerian mimicry rings in the Appalachian Mountains. We describe a model species of these mimicry rings, *Apheloria polychroma* n. sp., one of the most variable in coloration of all species of Diplopoda with more than six color morphs, each associated with a separate mimicry ring.

Keywords: aposematic, Appalachian, Myriapoda, taxonomy, systematics

Introduction

Millipedes in the family Xystodesmidae are most diverse in the Appalachian Mountains where about half of the family's species occur. In the New World, the family is distributed throughout eastern and western North America and south to El Salvador (Marek et al. 2014, Marek et al. 2017). Xystodesmidae occur in the Old World in the Mediterranean, the Russian Far East, Japan, western and eastern China, Taiwan and Vietnam. Taxa include species that are bioluminescent (genus *Motyxia*) and highly gregarious (genera *Parafontaria* and *Pleuroloma*); some form Müllerian mimicry rings. Despite their fascinating biology and critical ecological function as native decomposers in broadleaf deciduous forests in the U.S., their alpha-taxonomy is antiquated, and scores of new species remain undescribed. For example, the genus *Nannaria* includes 18 described species; recent work on the genus in our laboratory indicates that at least 50 additional species await description.

The genus *Apheloria* is ubiquitous in the eastern United States where the taxon *Apheloria virginiensis corrugata* (Wood), popularly known as the Cherry Millipede, is a widespread and colorful inhabitant of deciduous forests. The "cherry" in the common name refers to the aroma of benzaldehyde, released by the millipede following the enzymatic breakdown of mandelonitrile (a cyanogen); the process also releases hydrogen cyanide, and a single millipede can produce 18 times the lethal dose of cyanide for a pigeon (Eisner et al. 1963; Eisner et al. 2005). These cyanogenic millipedes warn avian, amphibian and reptilian predators of their toxicity with aposematic coloration composed of highly contrasting striped or spotted patterns of white, reds, yellows, and oranges against a jet-black background. Some nocturnal taxa, such as *Motyxia*, which are preyed on by colorblind rodents, have aposematic bioluminescence where the exoskeleton emits a green glow in the dark (Marek & Moore, 2015).

Some xystodesmid taxa, such as those in the tribe Apheloriini, assemble into mimicry rings where unrelated toxic species have converged in appearance as a result of the evolution of mutualistic Müllerian mimicry (Marek & Bond, 2009). This evolutionary phenomenon of convergence in appearance of chemically defended animals has been documented in a number of taxa such as butterflies (Flanagan et al. 2004), velvet ants (Wilson et al. 2015), and poison frogs (Symula et al. 2001). In the Cumberland Mountain Thrust Block region of Virginia, Tennessee and Kentucky, the millipede genera *Apheloria*, *Brachoria*, and *Appalachioria* display mimicry rings that center on at least six shared aposematic resemblances—corresponding to separate rings (Marek & Bond 2009). The species of *Apheloria* described here displays all of these six unique phenotypes.

During the latter half of the 20th century, Richard Hoffman had been working on a revision of the genus *Apheloria* (Hoffman 1978). He synonymized several names, mostly those of R. V. Chamberlin, and clarified several old conundrums associated with the taxon (Hoffman 1999) before his death in 2012. While working on the genus, he discovered one of its members from southwestern Virginia and determined that it was a new taxon, assigning the temporary name *Apheloria* "*flavissima*" on the determination label due to its entirely yellow collum and intensely brilliant hue (Latin *flavus* meaning 'yellow'). In conversation with PEM about *Apheloria*, Hoffman commented that the generic revision was pending, but obstacles remained regarding the disposition of several key taxa including *Apheloria virginiensis virginiensis* (Drury), *Apheloria luminosa* (Kenyon), and *Apheloria* "*flavissima*". Several years later, PEM undertook a study of Müllerian mimicry in the Cumberland Mountain Thrust region between species of the genera *Apheloria*, *Brachoria*, and *Appalachioria* and sampled at 29 locations to encapsulate the geographical extent of the observed mimetic radiation (Marek & Bond 2009). Based on molecular phylogenetics, two *Apheloria* species were collected in the study: *Apheloria montana* (Bollman) and a second that formed a monophyletic group encompassing individuals of *Apheloria* "*flavissima*". *Apheloria montana* was less common throughout the study region and possessed two color morphs: two-spotted yellow and three-spotted white. However, *A*. "*flavissima*" was more variable in coloration and over four times more abundant, thereby providing evidence that it is likely a model species in this mutualistic radiation of mimics. *Apheloria* "*flavissima*" as a model is also supported by its widespread distribution and high frequency of mimetic interactions with unrelated species (Marek & Bond 2009). Whenever the other species of *Brachoria* and *Appalachioria* were found to co-occur with *A.* "*flavissima*", their coloration was nearly identical to that of *A. "flavissima."*

New species of the genus *Brachoria*, part of this system of mimicry, were described recently (Marek 2010); however, *A*. "*flavissima*" remained unnamed. This taxon is currently the subject of co-evolutionary studies of mimicry evolution and has been listed under various names in faunistic surveys (Hobson 2010) and phylogenetic publications (Marek & Bond 2007; Marek &

Bond 2009; Means & Marek 2017). A formal species name is now required. In this paper, we name and describe *A.* “*flavissima*” and document its surprisingly large color variation.

Methods and Results

Live millipedes were found according to Means et al. (2015). Individuals were collected by raking through leaf litter and detritus on the forest floor. Millipede specimens were photographed and their hue, value, and chroma (e.g., 1.25Y 7/14) measured with a Munsell Book of Color using sunlight (cloudless at noon) as an illumination source (Munsell Color Services 2000). Millipede gonopods were photographed using ultraviolet-induced fluorescent imaging as described by Marek (2017). Body dimensions were measured at the following six locations according to Marek (2010): body length (BL), collum width (CW), intergenal width (IW), interantennal socket width (ISW), body ring 10 width (B10W), and body ring 10 height (B10H). Measurements are provided in millimeters. The range, mean, and standard deviation of the measurements are given to assess continuous variation. Total genomic DNA was extracted and purified with a Qiagen DNeasy kit, and DNA of the large subunit ribosomal RNA gene (16S) from the mitochondrion was amplified using polymerase chain reaction and sequenced using a Sanger protocol according to Means and Marek (2017). Chromatograms were trimmed, bases called, and overlapping fragments made into contiguous sequences in Mesquite using phred and phrap in the Chromaseq module (Maddison and Maddison, 2010; Ewing et al., 1998). The program Prank (Probabilistic Alignment Kit, Löytynoja and Goldman 2005) was used to align the sequences using the default gap opening and extension probabilities, and a parsimony guide tree with two iterations, thereby improving the tree on the second iteration. Multiple individuals with a uniform 16S sequence were collapsed into a single terminal (e.g., AlfVLE19IV) in the alignment according to the protocol described in Marek and Bond (2009). Specimens used for molecular phylogenetics are in Table 1. Bayesian phylogenetic inference was used to evaluate alternative tree topologies and models of nucleotide substitution using MrBayes (Ronquist et al. 2012). One-quarter of the trees from the MCMC analysis were discarded as the burn-in phase, and the topologies averaged with the commands “sumt” and “contype=half-compat” to generate a consensus phylogeny with > 50% of the compatible groupings retained in Fig. 1. Millipedes were categorized into six color morphs, each with a unique dorsal color and pattern, following Marek and Bond (2009). Color morph categories underestimate observed variation because some individuals of the same morph may have differently colored legs or variable collum patterns (e.g., an entirely yellow collum versus one with a hourglass shape medially). These characters were mapped onto the phylogeny using a parsimony reconstruction of character history in the program Mesquite. Types were deposited in the Field Museum of Natural History (institutional abbreviation FMNH), Virginia Tech Insect Collection (abbreviation VTEC), and Virginia Museum of Natural History (abbreviation VMNH).

Apheloria **Taxonomy**

Class **Diplopoda** de Blainville in Gervais, 1844
Order **Polydesmida** Pocock, 1887

Family **Xystodesmidae** Cook, 1895
Subfamily **Xystodesminae** Cook, 1895
Tribe **Apheloriini** Hoffman, 1980
Genus ***Apheloria*** Chamberlin, 1921

***Apheloria polychroma*, new species**
Vernacular name: "The Colorful Cherry Millipede"
Figs 1 – 6.

Material examined: Type specimens. ♂ holotype (FMNH-INS60792), 1 ♀ paratype (FMNH-INS71228), 3 ♂, 3 ♀ paratypes (VTEC, MMC0309, 310, 313, 305, 306, 308), 1 ♂, 1 ♀ paratypes (VMNH, MMC0314, 312) from Virginia, Lee County, The Cedars, CR-738 (36.65624°N, -83.20165°W, Elev. 436 m), 28 September 2006, 16:00 (Colls: P. and B. Marek). Non-type material examined listed in Table 1.

Diagnosis. Adult males of *A. polychroma* are distinct from other apheloriine genera based on the following combination of characters: **Color**. Tergites usually with 4 yellow spots (i.e. 1 metatergal, 1 prozonal, 2 paranotal spots, Fig. 2A – F, M – P). Collum usually uniformly yellow (1.25Y 7/14). Jet-black background (N 0.5 - 0.75). **Gonopods**. Gonopodal acropodite smoothly circular, O-shaped (Fig. 3A, B)—without elbow as in *A. tigana* (Fig. 4C, arrow). Acropodite narrow, half width of tibia on leg pair 9, of uniform width throughout. Acropodite gradually tapered to curved acuminate J-shaped apex, not L-shaped and abruptly twisted as in *A. montana*, *A. tigana*, *A. virginiensis corrugata* (Figs 3C; 4B, D, F). Acropodite shaft without cingulum (midlength transverse groove) or preapical teeth or projections as in *Brachoria*. Prefemur with a thin sharp prefemoral process, one-ninth length of acropodite (Fig. 3A, arrow), not long and scythe-like as in *A. montana*, *A. tigana*, *A. virginiensis corrugata* (Figs 4B, D, F).

Note: The 4-spotted yellow color morph with a uniformly yellow collum unambiguously diagnoses *A. polychroma* (Fig. 2A, C, E). However, there are at least 6 color morphs of the species with a substantial continuum of hues and patterns among them (Figs 2, 5). There are frequently several color morphs of the species at a single locality, and as color varies considerably, it should be used with caution as a diagnostic character for this species.

Description. Holotype (♂) FMNH-INS60792 – **Measurements**: BL = 48.70, CW = 7.50, IW = 4.10, ISW = 1.00, B11W = 9.50, B11H = 5.40. **Head**: Antennae extending posteriorly to anterior margin of 3rd tergite, relative antennomere lengths 2>5>3>4>6>1>7. Antennae with 4 sensillum types, sensillum shafts smooth without barbules. Four apical cones (AS) in square cluster on 7th antennomere. Chaetiform sensilla (CS) on antennomeres 5 - 7. Antennomeres 1 - 4 smooth with sparse vestiture of CS. Trichoid sensilla (TS) on antennomeres 1- 7, coronally encircling apex. Spiniform basiconic sensilla (Bs_2) in clusters of 15 on apical dorsal (retrolateral) surface of antennomeres 5, 6; Bs_2 shaft 1/10 length of CS. **Tergites**: collum with straight cephalic edge, abruptly tapering laterally. Collum with carina present on anterolateral margins, absent medially. Caudolateral corners of paranota rounded cephalically on body rings 1 - 4; acute, projecting caudally on body rings 5 - 19. Caudolateral corners of paranota 7 - 19 with small posterior-projecting nubbin. Paranota dorsal surface loosely wrinkled, appearing leathery. Ozopores oriented dorsolaterally. Pore formula normal: 5, 7, 9, 10, 12, 13, 15 - 19. Paranota with anterodorsal region scooped out. Gonapophyses cylindrical apically. Pleural tubercle absent, with slight swelling between paranotal base and spiracle. Sterna without posteriorly projecting spines, with slightly curved caudal margin. Sterna 2 - 11 sparsely setose (ca. 10 setae), sterna 12 - 18 lacking setae, ventral surface smooth. **Gonopods**: In situ configuration — Acropodite base projected posteroventrally, curved anteromedially in smooth O-shaped form (Fig. 3A, B). Terminal arc of acropodite oriented ventrolaterally. O-shaped arc nearly closed, gap 1/8 length of circumference between prefemoral process and apex (Fig. 3A, B). Right, left acropodites crossed midlength, appearing intertwined. Gonocoxae with conical protuberance apically, telopodites arising subapically. Telopodites — Prefemur with thin sharp prefemoral process, one-ninth length of acropodite, with apex tapered to sharp curved point, sickle-shaped, width at base 1/4 its length (Fig. 3A, arrow). Acropodite bent 90° posteriorly at prefemur (Fig. 3C, arrow), prostatic groove arcs 90° from cannula to acropodite base (Fig. 3B, arrows). Gonopodal acropodite narrow, half width of tibia on leg pair 9, tapered to curved acuminate apex. Acropodite with ventrobasal surface facing anterolaterally. Acropodite base without spines on dorsal surface. Acropodal basal and apical ventral surfaces not coplanar, apical surface facing ventrolaterally; anterior twist absent (Fig. 3C). Acropodal ventral surface flat, not swollen, smooth. Acropodite without midlength transverse groove, or cingulum. Acropodite shaft of uniform width, tapered to acuminate apex distal to region with setae. Acropodite elliptical in cross-section, tapered acuminate apex thinner, transparent. Acropodite margin rounded, lacking sharp edge; marginal teeth absent. Apical 1/9 of acropodite recurved, J-shaped, projecting cephalically (Fig. 3C). Acropodite region with setae about 1/3 its total length (Fig. 3B). Paratype (♀) FMNH-INS71228 – Measurements: BL = 50.30, CW = 8.00, IW = 4.80, ISW = 1.40, B10W = 11.81, B10H = 7.10. **Cyphopods**: Cyphopod receptacle (at its greatest breadth) equal in width to prefemur length. Receptacle heart-shaped, pointed end facing medially. Cyphopodal valves symmetric, anterior valve slightly more convex. Cyphopods with valvular suture facing laterally, without midlength ramp-like swell.

Variation. *Apheloria polychroma* is known from the Cumberland Mountain Thrust Block region at the confluence of southwestern Virginia, northeastern Tennessee, and southeastern Kentucky (Fig. 6). There are at least six color morphs with substantial variation in coloration between them: (1) four-spotted, with yellow to orange paranotal, metatergal, prozonal and collum spots, and legs and collum often completely yellow and sometimes with red legs (Fig. 2A – F, M – O); (2) striped, with yellow metatergal, paranotal, anterior collum stripes, and legs (Fig. 2G, H); (3) three-spotted, with creamy white paranotal, metatergal and collum spots, and red legs (Fig. 2I, J); (4) three-spotted, with yellow paranotal, metatergal and collum spots, and red or yellow legs (Figs 2K, L; 5A, B); (5) striped/four-spotted mix, superimposition of striped and four-spotted yellow morphs (Fig. 2M, N); and (6) two-spotted, with yellow paranotal spots, and red or yellow legs (Fig. 2Q – T). Some three-spotted yellow individuals possess faint metatergal spots, appearing nearly two-spotted (Fig. 2S). The dorsal color of *A. polychroma* is always yellow and black; however, the pattern varies from two, three, or four maculae, to metatergal stripes. The hue consists of variations of yellow: from light cream-white to brilliantly saturated yellow. Based on the molecular phylogeny of populations of *A. polychroma* (Fig. 1), some individuals that share a uniform mitochondrial 16S sequence possess three distinct color morphs (morphs 1, 2 and 5 from above). The color morphs lack phylogenetic conservation, whereby individuals sharing the same aposematic appearance are not monophyletic (Fig. 1). Evolutionary shifts between colors, based on reconstructing color morphs on a phylogeny using parsimony, occurred frequently with ca. 29 changes (Fig. 1). *Brachoria dentata* Keeton mimics *A. polychroma* in color and pattern at six of the seven localities where they were found to co-occur. The other five species of *Brachoria* co-occur at fewer localities. There is typical sexual size dimorphism between males and females, and negligible variation of measurements within sex. Measurements: ♂ (n = 10) BL = 37.80 – 49.45 (45.68/3.45). CW = 6.90 – 8.80 (7.58/0.63). IW = 4.10 – 5.00 (4.63/0.30). ISW = 1.00 – 1.40 (1.20/0.13). B10W = 8.80 – 10.79 (10.11/0.82). B10H = 4.60 – 6.10 (5.66/0.65). ♀ (n = 7) BL = 41.60 – 50.30 (46.67/3.07). CW = 6.60 – 8.30 (7.63/0.59). IW = 4.70 – 5.40 (5.01/0.29). ISW = 1.20 – 1.40 (1.31/0.09). B10W = 9.10 – 11.81 (10.64/0.96). B10H = 6.10 – 7.10 (6.4/0.37).

Ecology. *Apheloria polychroma* individuals were collected in mesic broadleaf deciduous forests and occasionally in more xeric glades, for example The Cedars Natural Area Preserve in Lee County, Virginia that consists of karst overlain with a mixed deciduous and Eastern Red Cedar forest (*Juniperus virginiana* L.). Individuals were encountered beneath decomposing leaves and walking atop detritus on the forest floor. Individuals of *A. polychroma* were more often exposed to view than other apheloriines, bolder in behavior, and were more likely to thrash when disturbed. When handled, individuals would emit copious amounts of defense secretions. Due to similarity in color patterns and overlap in distribution, *A. polychroma* may be confused in the field with six species of *Brachoria*, which include *B. dentata*, *Brachoria cedra* Keeton, *Brachoria hoffmani* Keeton, *Brachoria insolita* Keeton, *Brachoria mendota* Keeton, and *Brachoria sheari* Marek. Mimetic resemblance between individuals of *A. polychroma* and *B. mendota* at Natural Tunnel State Park (Scott County, Virginia) is one of the most accurate in the mimicry system (Fig. 5). *Apheloria polychroma* can be distinguished from these taxa by the absence of a cingulum, or a midlength transverse groove on the acropodite, and presence of an O-shaped telopodite (Fig. 3A, B).

Distribution. Known from southwestern Virginia (Lee, Scott, Norton, and Wise Counties), southeastern Kentucky (Bell and Harlan Counties), and northeastern Tennessee (Campbell, Claiborne, and Hancock Counties, Fig. 6). The distribution of *A. polychroma* is coincident with the boundaries of the High Knob Landform, and more broadly the Cumberland Mountain Thrust Block (Rich 1934; Browning 2009).

Notes. *Apheloria polychroma* was previously known by the informal names *Apheloria* "*flavissima*" (Hobson, 2010), *Apheloria* "Stone" (Marek & Bond 2007; Means & Marek 2017), and *Apheloria* "Clade A" (Marek & Bond 2009).

Etymology. This species is named for its extremely variable coloration. The specific name is a noun in apposition derived from the Greek *polu*-, 'many', and *khrōma*, 'color.

Discussion

The genus *Apheloria* currently consists of six species: *Apheloria luminosa*, *Apheloria montana*, *Apheloria polychroma*, *Apheloria tigana* Chamberlin, *Apheloria whiteheadi* (Shelley), and *Apheloria virginiensis*. *Apheloria virginiensis* comprises an assemblage of five subspecies: *virginiensis*, *butleriana*, *corrugata*, *iowa*, and *reducta*. Based on molecular phylogenetics, the subspecies *butleriana*, *corrugata*, and *reducta* are monophyletic (Means & Marek 2017). (The subspecies *virginiensis* and *iowa* have not yet been sampled for DNA analysis.) The taxa *A. montana*, *A. polychroma*, *A. tigana*, and *A. whiteheadi* are a sister group to the *virginiensis* clade (Fig. 1). Millipedes collected from near the type locality of *Apheloria virginiensis virginiensis* were recently described and a neotype of the genus established based on these collections (Shelley et al., 2017). In the study, *A. tigana* was made a synonym of *A. virginiensis virginiensis* based on the morphological similarity of the telopodites. However, this inferred close affiliation based solely on gonopodal similarity appears to be a result of homoplasy, specifically convergent shape similarities between distantly related species in the acropodite of the gonopod (Means and Marek 2017). The telopodite morphology and molecular phylogenetics do not indicate a close relationship between *A. tigana* and the *A. virginiensis* group (Fig. 4C, D versus 4E, F). As a result, *A. tigana* is hereby removed from synonymy with *A. virginiensis virginiensis*.

The combination of rampant color variation within *A. polychroma* and relatively constrained morphological variation in the O-shaped telopodite amongst *Apheloria* species has made confidently distinguishing the species solely on phenotypic variation challenging. Even though the four-spotted "*flavissima*" morph with its uniformly yellow collum appears to be a distinct taxon (Fig. 2A, C, E), a naturalist may encounter up to three morphs of the species in a single 10 m^2 patch of forest. To the casual observer, the individuals are so divergent in appearance as to certainly be different species. However, as a result of mimicry, there are instances where two mimicry rings co-exist in a single 10 m^2 area, for instance *A. polychroma* and *B. sheari* possess two morphs, each mimicking one another (the Honey Tree Trail, Cumberland Gap National Historic Park, Virginia: "site 20" from Marek and Bond (2009)). Albeit fascinating from an evolutionary perspective, color variation in this region of Appalachia has confounded taxonomy of its apheloriine millipedes. In other parts of the range of *Apheloria* beyond this region of mimicry, color generally appears to be consistent with species and with distinct gonopodal forms that have traditionally been used in millipede taxonomy. *Apheloria tigana* is generally two-spotted yellow, *Apheloria montana* is three-spotted yellow, and the former species has a distinct elbow mid-length on the acropodite (Fig. 4C versus Fig. 4A). In this mimicry region, there are numerous instances of two-spotted and three-spotted yellow *Apheloria* individuals (in addition to the four other color morphs) that traditionally may have presented a challenge to previous workers overly reliant on color. Color variation also presents a significant challenge for identification of photographs of millipede taxa on citizen science websites, and there are at least a dozen polydesmidan species that are two-spotted yellow as a result of evolutionary convergence on a common aposematic appearance that have been misidentified with one another based exclusively on coloration (e.g. *Harpaphe haydeniana haydeniana* (Wood), *Chondrodesmus cairoensis* Loomis, *Orthomorpha coarctata* (DeSaussure), and *Apheloria tigana* Chamberlin).

The similarity in coloration with co-occurring species is a consequence of Müllerian mimicry. However, why there is intraspecific geographical variation of coloration in *A. polychroma* in several mimicry rings is uncertain. *Apheloria polychroma* color morphs are generally partitioned geographically with the two-spotted-yellow morph west of Cumberland Mountain in Kentucky, four-spotted-yellow east of Cumberland Mountain in Virginia and Tennessee, three-spotted-white in Clinch Mountain and the Tennessee side of Powell Mountain, and three-spotted-yellow with red legs around Natural Tunnel State Park, between Clinch and Powell Mountains, Virginia. Aposematic theory predicts conservation of warning signals because novel morphs (especially at low frequencies) that deviate from the memorized signal of the predator will experience increased predation and be removed from the population, thus making the population appear more like the toxic prey (Choteau and Angers, 2012). This phenomenon exists in millipedes (Marek & Bond 2009), frogs (Twomey et al. 2013), butterflies (Mallet and Joron 1999), velvet ants (Wilson et al. 2015), and other Müllerian systems. Some variation may be a function of geographical variation of avian predators and therefore predator visual preferences; however, the bulk of the variation is within small areas easily traversed by flying predators. The mechanisms of convergence are well-known; however, what drives the variation of Müllerian rings is still poorly understood. Primary documentation of millipede color into an atlas would provide the raw observations and materials required to understand the mechanisms of this spectacular color variation, and is a current project of JCM.

Several taxa of the *Apheloria virginiensis* species group including *A. virginiensis corrugata* possess intraspecific variation in coloration, but not to the extreme degree seen in *A. polychroma*. *Apheloria virginiensis corrugata* and *A. virginiensis virginiensis* are members of a Müllerian mimicry ring with those of the *Appalachioria separanda* species group in areas of the New River and Roanoke Valleys, Virginia. Furthermore, several new taxa of *Apheloria* have been discovered in Virginia and North Carolina that participate in mimicry with other apheloriine species. In addition to these, several new examples of mimicry occur elsewhere in Appalachia, including new taxa and those known but previously undescribed.

The diplopod family Xystodesmidae includes taxa with interesting biological traits including colorful Müllerian mimicry, bioluminescence, and synthesis of 600 μg of cyanide per individual, to which the millipedes have been found to tolerate (Eisner et al. 2005; Hall et al. 1971; Marek & Bond 2009; Marek & Moore 2015). These colorful millipedes are widespread in Appalachian forests, but are among the least known alpha-taxonomically of all U.S. fauna. While deforestation and habitat loss imminently threaten their ecological integrity, by describing and understanding the diversity of these organisms, studies about mimicry, color evolution, and Appalachian ecology can be investigated before it is too late.

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Supplementary data

Uncompressed image files of the gonopod figures and a CSV text file of the material examined are available for download from VTechData (https://data.lib.vt.edu/).

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Figure legends

Figure 1. Population phylogeny of *Apheloria polychroma* n. sp. Colored circles denote color morphs. Legend (bottom right) illustrates the millipede's ninth body ring for each color morph. Tree rooted with *Apheloria tigana* and *Apheloria montana* (their branches omitted). Scale bar: 0.2 expected substitutions per site. Asterisks indicate posterior probability ≥ 0.95. Inset, *Apheloria* species tree from Means and Marek (2017).

Figure 2. *Apheloria polychroma* n. sp. color morphs. Four-spotted yellow morph with red (A: dorsal, B: lateral) and yellow (C: dorsal, D: lateral) legs and entirely yellow collum. Four-spotted orange morph with orange legs and entirely orange collum (E: dorsal, F: lateral). Striped yellow morph (G: dorsal, H: lateral). Three-spotted white morph with red legs (I: dorsal, J: lateral). Three-spotted light yellow morph with orange/yellow legs (K: dorsal, L: lateral). Striped/four-spotted yellow mixed morph (A: dorsal, B: lateral). Four-spotted yellow morph with a hourglass shape medially on the collum (O: dorsal, P: lateral). Two-spotted yellow morph (Q: dorsal, R: lateral). Two-spotted yellow morph, with small median spots (S: dorsal, T: lateral).

Figure 3. *Apheloria polychroma* n. sp. holotype ♂ left gonopod (FMNH-INS60792). Anterior view (A), arrow: prefemoral process. Posterior view (B), bottom arrow: cannula, top arrow: prostatic groove at acropodite base. Medial view (C), arrow: point at prefemur where acropodite bends 90° posteriorly. Scale bar, 0.5 mm.

Figure 4. *Apheloria montana* (VTEC SPC000134), *Apheloria tigana* (VTEC SPC000312), and *Apheloria virginiensis corrugata* (VTEC MPE00770) left gonopod. *Apheloria montana* anterior (A) and medial (B) views. *Apheloria tigana* anterior (C), arrow: acropodite elbow, and medial (D) views. *Apheloria virginiensis corrugata* anterior (E) and medial (F) views, arrow: prefemoral process. Scale bar, 0.5 mm.

Figure 5. Müllerian mimicry between *Apheloria polychroma* n. sp. and *Brachoria mendota* at Natural Tunnel State Park, Scott County, Virginia. The resemblance between the model species (*A. polychroma* n. sp.) and the mimic species (*B. mendota*) is one of the most accurate instances of 'impressionistic' imitation in the Appalachian xystodesmid mimicry system.

Figure 6. Distribution map of *Apheloria polychroma* n. sp. collection localities in the Cumberland Mountain Thrust region. Inset: continental location of the distribution of *A. polychroma* n. sp. (black-filled outline) in the eastern U.S. encompassed by the Central Appalachians (green fill) and Ridge and Valley Ecoregions (yellow fill) (Level III, Omernik (1987)).

Table 1. Material examined. Asterisks denote type specimens. NCBI refers to GenBank accession numbers.

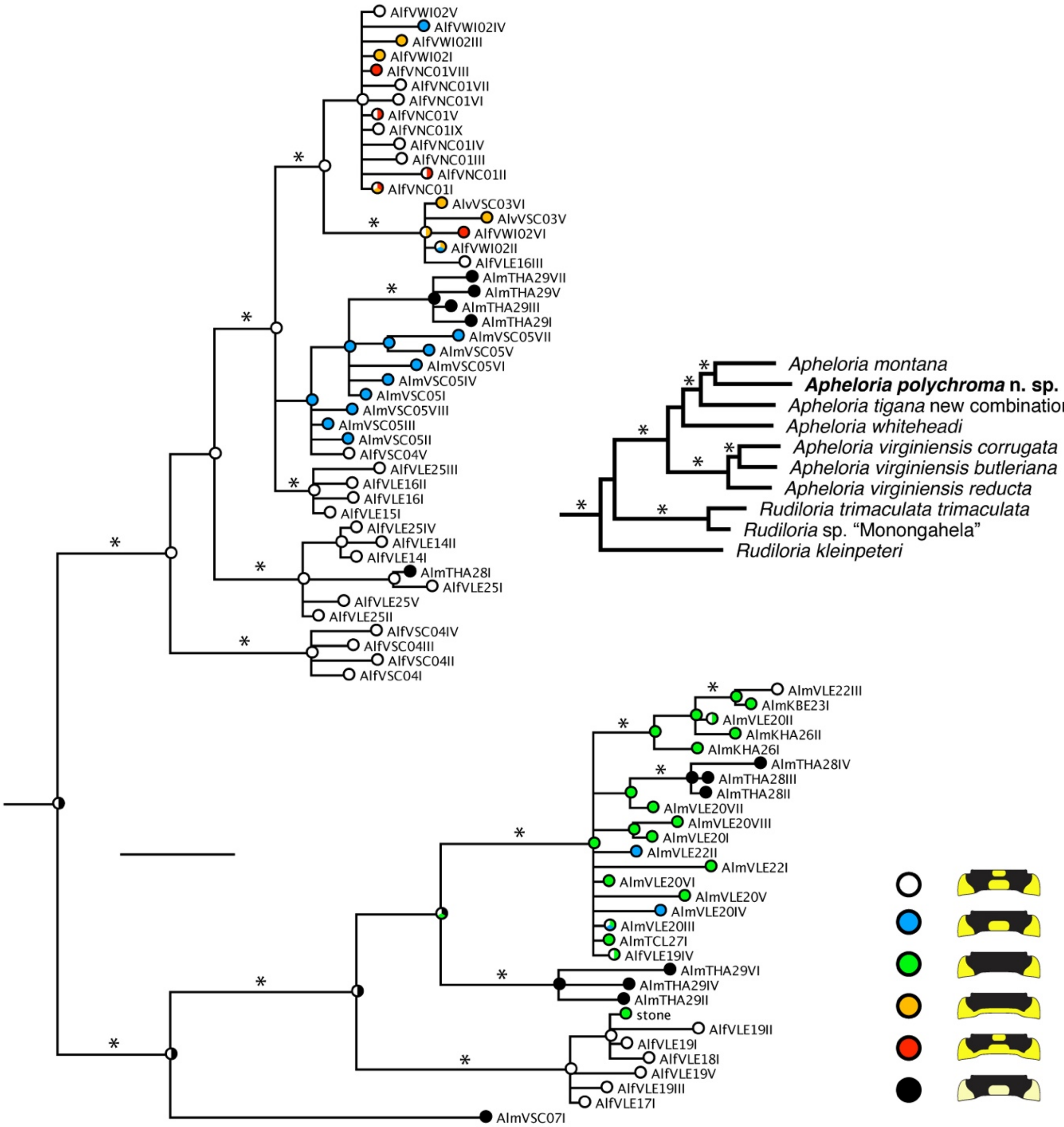
State	County	Specimen Code	Specimen	Haplotype	Latitude	Longitude	NCBI
Virginia	Lee	MMC0267	1M	AlfVLE14I	36.73846	-82.87839	FJ667003
Virginia	Lee	MMC0268	1M	AlfVLE14II	36.73846	-82.87839	FJ667004
Virginia	Lee	MMC0276	1M	AlfVLE15I	36.76366	-82.88194	FJ667005
Virginia	Lee	MMC0282	1M	AlfVLE16I	36.77681	-83.01574	FJ667006
Virginia	Lee	MMC0285	1M	AlfVLE16III	36.77681	-83.01574	FJ667008
Virginia	Lee	MMC0288	1M	AlfVLE16I	36.77681	-83.01574	FJ667006
Virginia	Lee	MMC0309*	1M	AlfVLE19IV	36.65624	-83.20165	FJ667014
Virginia	Lee	MMC0310*	1M	AlfVLE19V	36.65624	-83.20165	FJ667015
Virginia	Lee	INS60792*	1M	AlfVLE17I	36.65624	-83.20165	FJ667009
Virginia	Lee	MMC0313*	1M	AlfVLE17I	36.65624	-83.20165	FJ667009
Virginia	Lee	MMC0314*	1M	AlfVLE17I	36.65624	-83.20165	FJ667009
Virginia	Lee	MMC0321	1M	AlmVLE20I	36.60780	-83.63220	FJ667056
Virginia	Lee	MMC0323	1M	AlmVLE20I	36.60780	-83.63220	FJ667056
Virginia	Lee	MMC0324	1M	AlmVLE20V	36.60780	-83.63220	FJ667060
Virginia	Lee	MMC0327	1M	AlmVLE20IV	36.60780	-83.63220	FJ667059
Virginia	Lee	MMC0329	1M	AlmVLE20VI	36.60780	-83.63220	FJ667061
Virginia	Lee	MMC0330	1M	AlmVLE20II	36.60780	-83.63220	FJ667057
Virginia	Lee	MMC0331	1M	AlmVLE20III	36.60780	-83.63220	FJ667058
Virginia	Lee	MMC0358	1M	AlmVLE20III	36.65277	-83.43590	FJ667058
Virginia	Lee	MMC0359	1M	AlmVLE22II	36.65277	-83.43590	FJ667065
Virginia	Lee	MMC0362	1M	AlmVLE20III	36.65277	-83.43590	FJ667058
Virginia	Lee	MMC0364	1M	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0365	1M	AlmVLE20III	36.65277	-83.43590	FJ667058
Virginia	Lee	MMC0366	1M	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0367	1M	AlmVLE22III	36.65277	-83.43590	FJ667066
Virginia	Lee	MMC0371	1M	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0372	1M	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0401	1M	AlfVLE25I	36.63716	-83.13682	FJ667016
Virginia	Lee	MMC0402	1M	AlfVLE25II	36.63716	-83.13682	FJ667017
Virginia	Lee	MPE03103	1M	-	36.60314	-83.29407	-
Virginia	Lee	SPC000308	1M	-	36.66032	-83.18390	-
Virginia	Lee	SPC000309	1M	-	36.66032	-83.18390	-
Virginia	Lee	SPC000331	1M	-	36.80174	-82.92245	-
Virginia	Lee	SPC000537	1M	-	36.77681	-83.01574	-
Virginia	Lee	SPC000549	1M	-	36.77681	-83.01574	-
Virginia	Lee	SPC000851	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000861	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000862	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000863	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000866	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000867	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000868	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000870	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000872	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000874	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000875	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000877	1M	-	36.78492	-82.98290	-
Virginia	Lee	SPC000879	1M	-	36.78492	-82.98290	-
Virginia	Lee	MMC0281	1F	AlfVLE15I	36.76366	-82.88194	FJ667005
Virginia	Lee	MMC0283	1F	AlfVLE16II	36.77681	-83.01574	FJ667007
Virginia	Lee	MMC0284	1F	AlfVLE16I	36.77681	-83.01574	FJ667006
Virginia	Lee	MMC0287	1F	AlfVWI02II	36.77681	-83.01574	FJ667036
Virginia	Lee	MMC0293	1F	AlfVLE17I	36.71513	-83.04494	FJ667009
Virginia	Lee	MMC0296	1F	AlfVLE18I	36.74871	-83.07695	FJ667010

State	County	Specimen Code	Specimen	Haplotype	Latitude	Longitude	NCBI
Virginia	Lee	MMC0305*	1F	AlfVLE19II	36.65624	-83.20165	FJ667012
Virginia	Lee	MMC0306*	1F	AlfVLE19I	36.65624	-83.20165	FJ667011
Virginia	Lee	MMC0308*	1F	AlfVLE19III	36.65624	-83.20165	FJ667013
Virginia	Lee	MMC0312*	1F	AlfVLE19I	36.65624	-83.20165	FJ667011
Virginia	Lee	INS71228*	1F	AlfVLE17I	36.65624	-83.20165	FJ667009
Virginia	Lee	MMC0318	1F	AlmVLE20I	36.60780	-83.63220	FJ667056
Virginia	Lee	MMC0320	1F	AlmVLE20III	36.60780	-83.63220	FJ667058
Virginia	Lee	MMC0322	1F	AlmVLE20II	36.60780	-83.63220	FJ667057
Virginia	Lee	MMC0326	1F	AlmVLE20II	36.60780	-83.63220	FJ667057
Virginia	Lee	MMC0332	1F	AlmVLE20VII	36.60780	-83.63220	FJ667062
Virginia	Lee	MMC0333	1F	AlmVLE20VIII	36.60780	-83.63220	FJ667063
Virginia	Lee	MMC0336	1F	AlmVLE20IV	36.60780	-83.63220	FJ667059
Virginia	Lee	MMC0357	1F	AlmVLE22I	36.65277	-83.43590	FJ667064
Virginia	Lee	MMC0360	1F	AlmVLE20III	36.65277	-83.43590	FJ667058
Virginia	Lee	MMC0361	1F	AlfVLE19IV	36.65277	-83.43590	FJ667014
Virginia	Lee	MMC0363	1F	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0368	1F	AlfVLE19IV	36.65277	-83.43590	FJ667014
Virginia	Lee	MMC0369	1F	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0370	1F	AlmVLE20II	36.65277	-83.43590	FJ667057
Virginia	Lee	MMC0403	1F	AlfVLE25III	36.63716	-83.13682	FJ667018
Virginia	Lee	MMC0404	1F	AlfVLE25IV	36.63716	-83.13682	FJ667019
Virginia	Lee	MMC0405	1F	AlfVLE25V	36.63716	-83.13682	FJ667020
Virginia	Lee	SPC000335	1F	-	36.79944	-82.92391	-
Virginia	Lee	SPC000864	1F	-	36.78492	-82.98290	-
Virginia	Lee	SPC000865	1F	-	36.78492	-82.98290	-
Virginia	Lee	SPC000873	1F	-	36.78492	-82.98290	-
Virginia	Lee	SPC000878	1F	-	36.78492	-82.98290	-
Virginia	Norton	MMC0100	1M	AlfVNC01V	36.91692	-82.63795	FJ667026
Virginia	Norton	MMC0102	1M	AlfVNC01VI	36.91692	-82.63795	FJ667027
Virginia	Norton	MMC0103	1M	AlfVNC01I	36.91692	-82.63795	FJ667021
Virginia	Norton	MMC0112	1M	AlfVNC01II	36.91692	-82.63795	FJ667022
Virginia	Norton	MMC0114	1M	AlfVNC01VII	36.91692	-82.63795	FJ667028
Virginia	Norton	MMC0125	1M	AlfVNC01I	36.91692	-82.63795	FJ667021
Virginia	Norton	MMC0126	1M	AlfVNC01VIII	36.91692	-82.63795	FJ667029
Virginia	Norton	SPC000268	1M	-	36.92081	-82.63784	-
Virginia	Norton	SPC000269	1M	-	36.92081	-82.63784	-
Virginia	Norton	MMC0093	1F	AlfVNC01II	36.91692	-82.63795	FJ667022
Virginia	Norton	MMC0094	1F	AlfVNC01III	36.91692	-82.63795	FJ667023
Virginia	Norton	MMC0096	1F	AlfVNC01IV	36.91692	-82.63795	FJ667024
Virginia	Norton	MMC0127	1F	AlfVNC01IX	36.91692	-82.63795	FJ667025
Virginia	Scott	MMC0002	1M	AlfVSC04III	36.76713	-82.65067	FJ667032
Virginia	Scott	MMC0006	1M	AlfVSC04I	36.76713	-82.65067	FJ667030
Virginia	Scott	MMC0059	1M	AlmVSC05II	36.70500	-82.74510	FJ667068
Virginia	Scott	MMC0062	1M	AlmVSC05I	36.70500	-82.74510	FJ667067
Virginia	Scott	MMC0063	1M	AlmVSC05IV	36.70500	-82.74510	FJ667070
Virginia	Scott	MMC0065	1M	AlmVSC05VI	36.70500	-82.74510	FJ667072
Virginia	Scott	MMC0069	1M	AlmVSC05VIII	36.70500	-82.74510	FJ667074
Virginia	Scott	MMC0070	1M	AlmVSC05I	36.70500	-82.74510	FJ667067
Virginia	Scott	MMC0073	1M	AlmVSC05I	36.70500	-82.74510	FJ667067
Virginia	Scott	MMC0128	1M	AlfVWI02II	36.87201	-82.48473	FJ667036
Virginia	Scott	MMC0141	1M	AlvVSC03V	36.87201	-82.48473	FJ667076
Virginia	Scott	MMC0147	1M	AlvVSC03V	36.87201	-82.48473	FJ667076
Virginia	Scott	MMC0153	1M	AlfVWI02II	36.87201	-82.48473	FJ667036
Virginia	Scott	MMC0169	1M	AlmVSC07I	36.70754	-82.50076	FJ667075
Virginia	Scott	MMC0001	1F	AlfVSC04II	36.76713	-82.65067	FJ667031
Virginia	Scott	MMC0003	1F	AlfVSC04IV	36.76713	-82.65067	FJ667033
Virginia	Scott	MMC0008	1F	AlfVSC04I	36.76713	-82.65067	FJ667030
Virginia	Scott	MMC0009	1F	AlfVSC04V	36.76713	-82.65067	FJ667034
Virginia	Scott	MMC0060	1F	AlmVSC05III	36.70500	-82.74510	FJ667069
Virginia	Scott	MMC0064	1F	AlmVSC05V	36.70500	-82.74510	FJ667071

State	County	Specimen Code	Specimen	Haplotype	Latitude	Longitude	NCBI
Virginia	Scott	MMC0067	1F	AlmVSC05VII	36.70500	-82.74510	FJ667073
Virginia	Scott	MMC0068	1F	AlmVSC05I	36.70500	-82.74510	FJ667067
Virginia	Scott	MMC0129	1F	AlfVWI02II	36.87201	-82.48473	FJ667036
Virginia	Scott	MMC0136	1F	AlvVSC03VI	36.87201	-82.48473	FJ667077
Virginia	Scott	MMC0149	1F	AlfVWI02II	36.87201	-82.48473	FJ667036
Virginia	Scott	MMC0154	1F	AlvVSC03V	36.87201	-82.48473	FJ667076
Virginia	Scott	MMC0157	1F	AlfVWI02II	36.87201	-82.48473	FJ667036
Virginia	Wise	MMC0018	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0020	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0025	1M	AlfVWI02I	36.89499	-82.59027	FJ667035
Virginia	Wise	MMC0030	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0034	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0038	1M	AlfVWI02II	36.89499	-82.59027	FJ667036
Virginia	Wise	MMC0039	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0040	1M	AlfVWI02II	36.89499	-82.59027	FJ667036
Virginia	Wise	MMC0041	1M	AlfVWI02IV	36.89499	-82.59027	FJ667038
Virginia	Wise	MMC0044	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0047	1M	AlfVWI02V	36.89499	-82.59027	FJ667039
Virginia	Wise	MMC0050	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0052	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0054	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0058	1M	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0022	1F	AlfVWI02I	36.89499	-82.59027	FJ667035
Virginia	Wise	MMC0031	1F	AlfVWI02III	36.89499	-82.59027	FJ667037
Virginia	Wise	MMC0033	1F	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0042	1F	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0045	1F	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0046	1F	AlfVNC01V	36.89499	-82.59027	FJ667026
Virginia	Wise	MMC0051	1F	AlfVNC01I	36.89499	-82.59027	FJ667021
Virginia	Wise	MMC0053	1F	AlfVWI02VI	36.89499	-82.59027	FJ667040
Virginia	Wise	MMC0056	1F	AlfVNC01I	36.89499	-82.59027	FJ667021
Tennessee	Campbell	MPE03016	1M	-	36.22310	-84.09310	-
Tennessee	Claiborne	MMC0434	1M	AlmTCL27I	36.55583	-83.82147	FJ667044
Tennessee	Hancock	MMC0216	1M	AlmTHA29IV	36.41358	-83.22411	FJ667052
Tennessee	Hancock	MMC0218	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0219	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0221	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0225	1M	AlmTHA29VI	36.41358	-83.22411	FJ667054
Tennessee	Hancock	MMC0228	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0231	1M	AlmTHA29III	36.41358	-83.22411	FJ667051
Tennessee	Hancock	MMC0232	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0235	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0236	1M	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0445	1M	AlmTHA28III	36.53873	-83.31737	FJ667047
Tennessee	Hancock	MMC0446	1M	AlmTHA28II	36.53873	-83.31737	FJ667046
Tennessee	Hancock	MMC0447	1M	AlmTHA28IV	36.53873	-83.31737	FJ667048
Tennessee	Hancock	MMC0217	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0220	1F	AlmTHA29V	36.41358	-83.22411	FJ667053
Tennessee	Hancock	MMC0222	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0223	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0224	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0226	1F	AlmTHA29II	36.41358	-83.22411	FJ667050
Tennessee	Hancock	MMC0227	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0229	1F	AlmTHA29II	36.41358	-83.22411	FJ667050
Tennessee	Hancock	MMC0230	1F	AlmTHA29VII	36.41358	-83.22411	FJ667055
Tennessee	Hancock	MMC0233	1F	AlmTHA29III	36.41358	-83.22411	FJ667051
Tennessee	Hancock	MMC0237	1F	AlmTHA29I	36.41358	-83.22411	FJ667049
Tennessee	Hancock	MMC0442	1F	AlmTHA28I	36.53873	-83.31737	FJ667045
Tennessee	Hancock	MMC0443	1F	AlmTHA28II	36.53873	-83.31737	FJ667046
Kentucky	Bell	MMC0375	1M	AlmKBE23I	36.66770	-83.58262	FJ667041

State	County	Specimen Code	Specimen	Haplotype	Latitude	Longitude	NCBI
Kentucky	Bell	MMC0374	1F	AlmVLE20II	36.66770	-83.58262	FJ667057
Kentucky	Harlan	MMC0413	1M	AlmKHA26I	36.73318	-83.26861	FJ667042
Kentucky	Harlan	MMC0415	1M	AlmVLE20II	36.73318	-83.26861	FJ667057
Kentucky	Harlan	MMC0416	1M	AlmVLE20II	36.73318	-83.26861	FJ667057
Kentucky	Harlan	MMC0419	1M	AlmKHA26II	36.73318	-83.26861	FJ667043
Kentucky	Harlan	MMC0420	1M	AlmKHA26I	36.73318	-83.26861	FJ667042
Kentucky	Harlan	SPC000578	1M	-	36.75603	-83.19588	EU127857
Kentucky	Harlan	SPC000793	1M	-	36.73285	-83.22161	-
Kentucky	Harlan	SPC000823	1M	-	36.73285	-83.22161	-
Kentucky	Harlan	SPC000826	1M	-	36.73897	-83.21970	-
Kentucky	Harlan	MMC0408	1F	AlmVLE20II	36.73318	-83.26861	FJ667057
Kentucky	Harlan	MMC0421	1F	AlmVLE20II	36.73318	-83.26861	FJ667057
Kentucky	Harlan	MMC0422	1F	AlmKHA26I	36.73318	-83.26861	FJ667042
Kentucky	Harlan	SPC000573	1F	-	36.75603	-83.19588	-
Kentucky	Harlan	SPC000792	1F	-	36.73285	-83.22161	-

Figure 1



AlfVWI02V
AlfVWI02IV
AlfVWI02III
AlfVWI02I
AlfVNC01VIII
AlfVNC01VII
AlfVNC01VI
AlfVNC01V
AlfVNC01IX
AlfVNC01IV
AlfVNC01III
AlfVNC01II
AlfVNC01I
AlvVSC03VI
AlvVSC03V
AlfVWI02VI
AlfVWI02II
AlfVLE16III
AlmTHA29VII
AlmTHA29V
AlmTHA29III
AlmTHA29I
AlmVSC05VII
AlmVSC05V
AlmVSC05VI
AlmVSC05IV
AlmVSC05I
AlmVSC05VIII
AlmVSC05III
AlmVSC05II
AlfVSC04V
AlfVLE25III
AlfVLE16II
AlfVLE16I
AlfVLE15I
AlfVLE25IV
AlfVLE14II
AlfVLE14I
AlmTHA28I
AlfVLE25I
AlfVLE25V
AlfVLE25II
AlfVSC04IV
AlfVSC04III
AlfVSC04II
AlfVSC04I
AlmVLE22III
AlmKBE23I
AlmVLE20II
AlmKHA26II
AlmKHA26I
AlmTHA28IV
AlmTHA28III
AlmTHA28II
AlmVLE20VII
AlmVLE20VIII
AlmVLE20I
AlmVLE22II
AlmVLE22I
AlmVLE20VI
AlmVLE20V
AlmVLE20IV
AlmVLE20III
AlmTCL27I
AlfVLE19IV
AlmTHA29VI
AlmTHA29IV
AlmTHA29II
stone
AlfVLE19II
AlfVLE19I
AlfVLE18I
AlfVLE19V
AlfVLE19III
AlfVLE17I
AlmVSC07I
Apheloria montana
Apheloria polychroma n. sp.
Apheloria tigana new combination
Apheloria whiteheadi
Apheloria virginiensis corrugata
Apheloria virginiensis butleriana
Apheloria virginiensis reducta
Rudiloria trimaculata trimaculata
Rudiloria sp. "Monongahela"
Rudiloria kleinpeteri

Figure 2

Figure 3

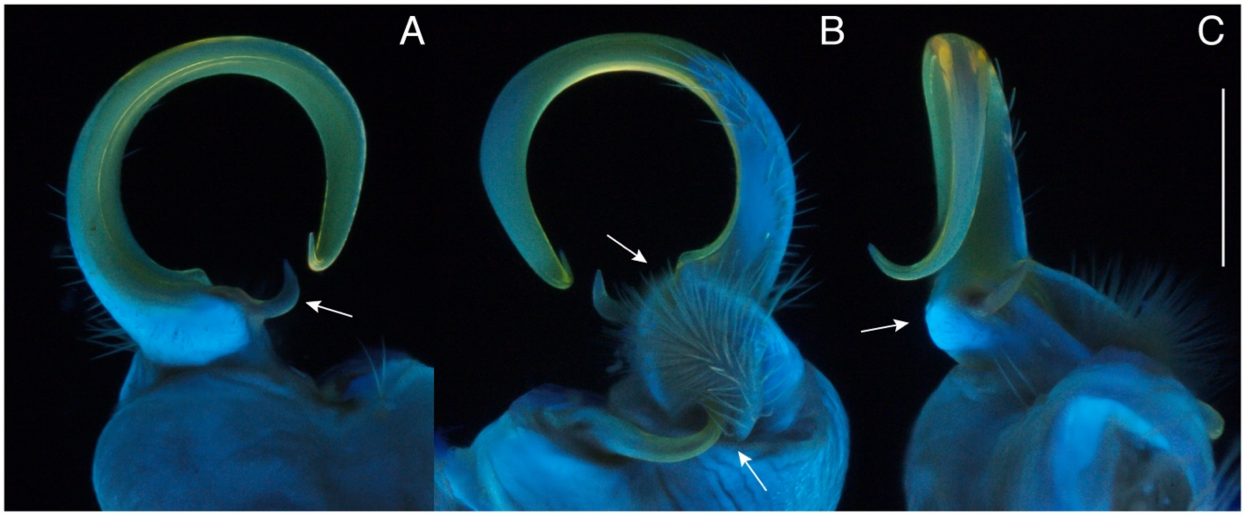


Figure 4

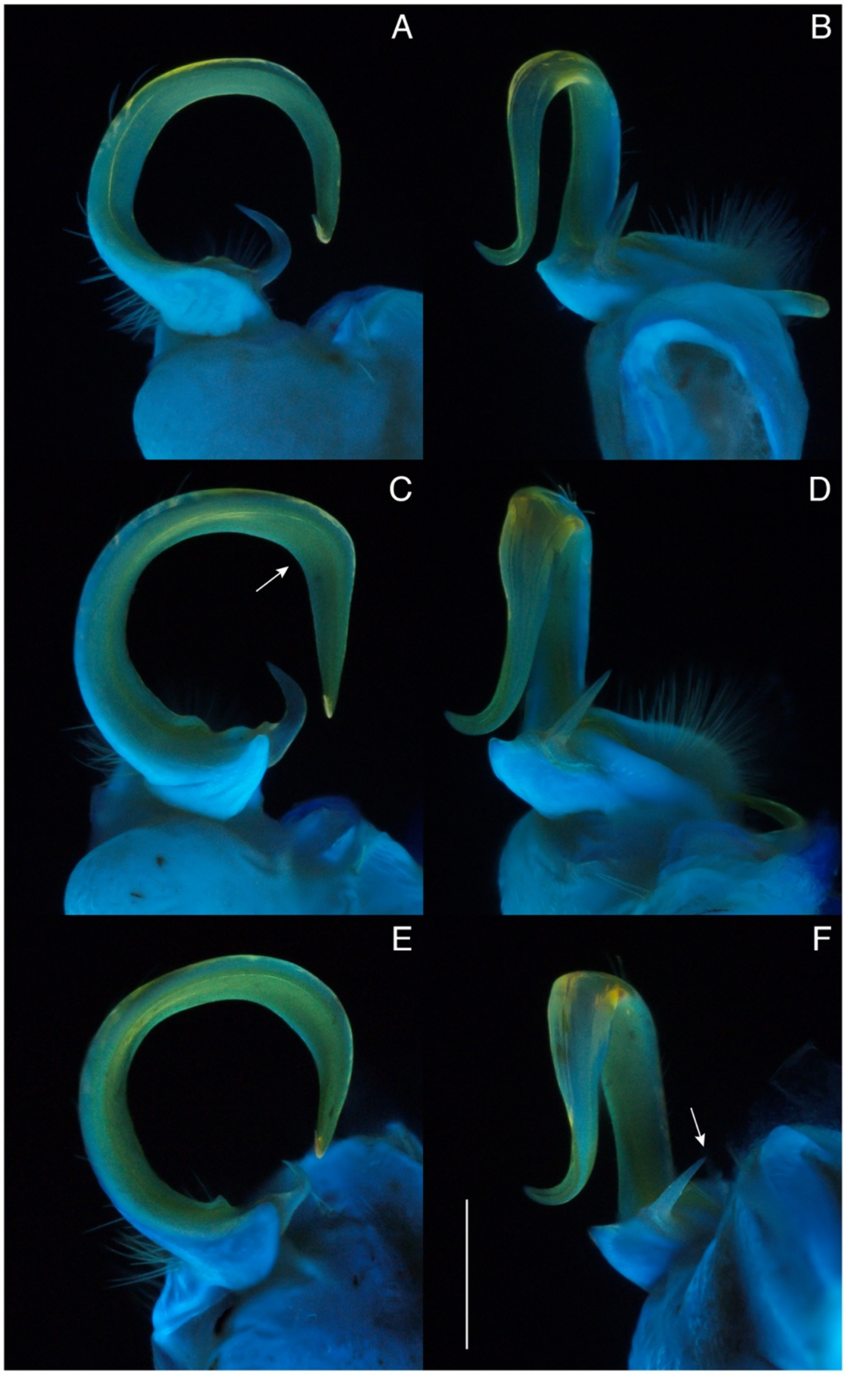


Figure 5

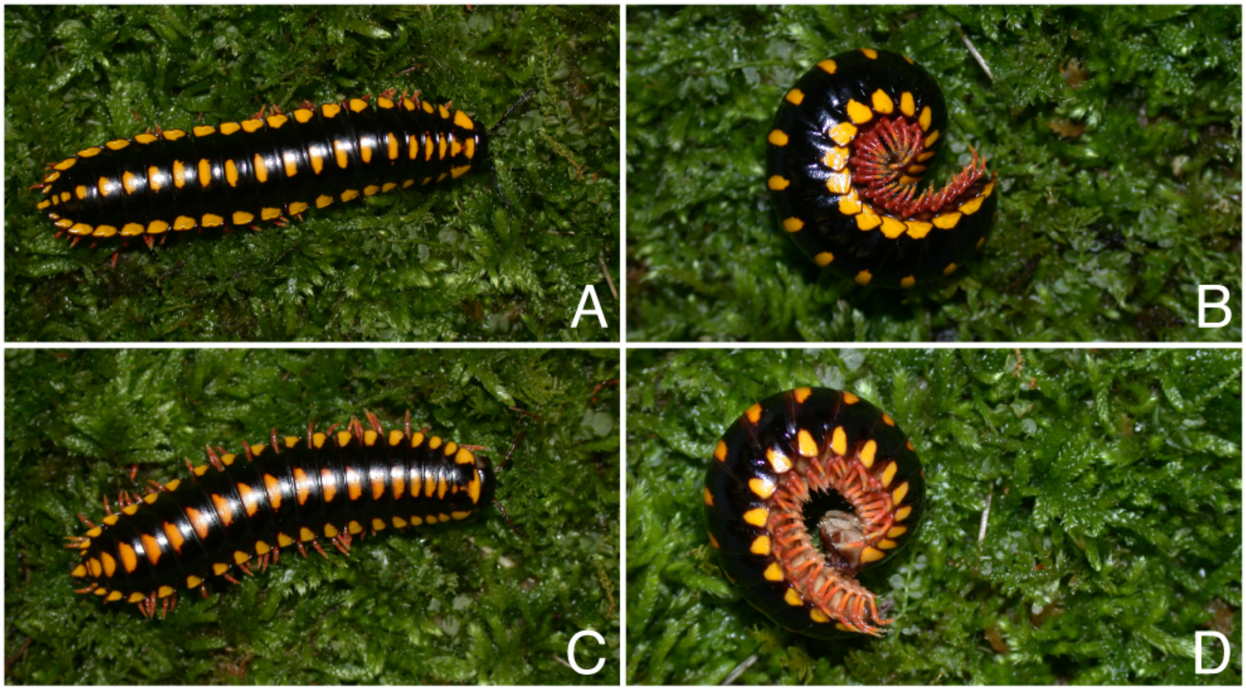
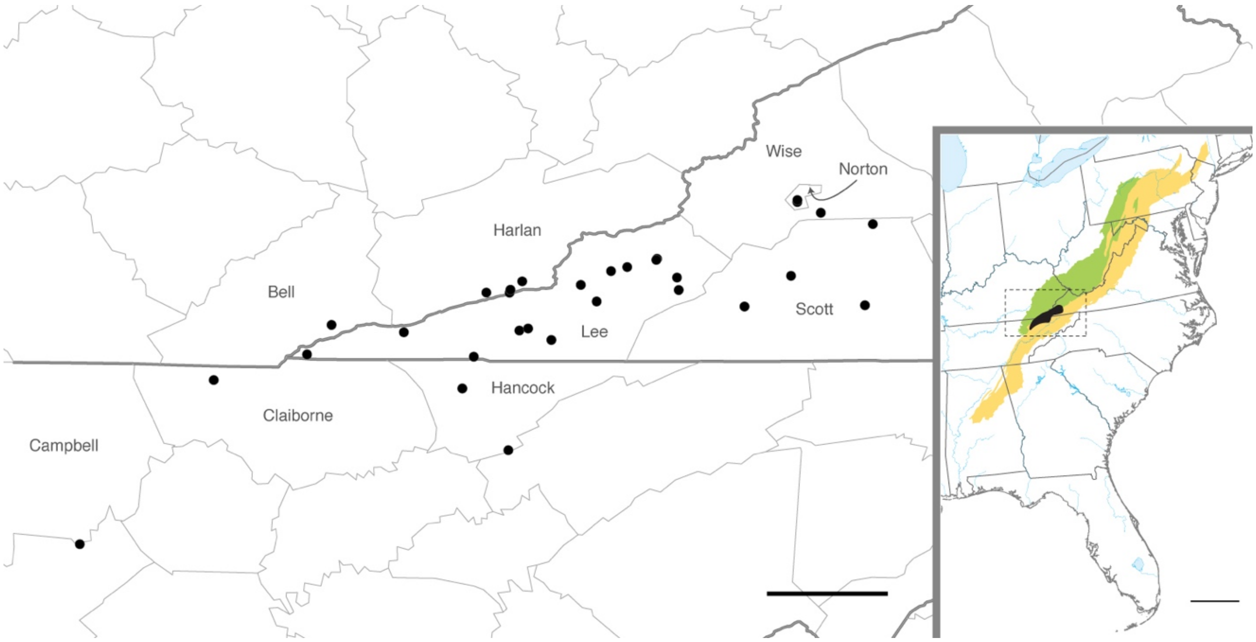


Figure 6


Wise
Norton
Harlan
Bell
Scott
Lee
Hancock
Claiborne
Campbell