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Revision of the millipede genus *Apheloria* Chamberlin, 1921 (Polydesmida, Xystodesmidae, Apheloriini)

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Abstract

We revise the millipede genus *Apheloria* Chamberlin, 1921—a colorful and often encountered group of millipedes in eastern North America. With molecular phylogenetics, we estimate the evolutionary history of the genus, and use it in combination with morphology to understand species diversity. We describe a new species, *Apheloria uwharrie* **sp. nov.** from North and South Carolina, synonymize *Apheloria tigana* Chamberlin, 1939 **syn. nov.** with *Apheloria virginiensis* (Drury, 1770), and remove *Apheloria luminosa* (Kenyon, 1893) **syn. nov.** from the genus and place it in synonymy with *Pleuroloma flavipes* Rafinesque, 1820. Currently there are six species of *Apheloria*: *Apheloria corrugata* (Wood, 1864) **stat. nov.**; *Apheloria montana* (Bollman, 1887); *Apheloria polychroma* Marek, Means & Hennen, 2018; *Apheloria uwharrie* **sp. nov.**; *Apheloria virginiensis* (Drury, 1770); and *Apheloria whiteheadi* (Shelley, 1986).

Key words: Diplopoda, Myriapoda, cyanide, gonopod, Appalachian Mountains, mimicry

Introduction

Xystodesmidae Cook, 1895 is the largest millipede family in North America in terms of number of described species. With 548 species globally, the family has the third greatest species diversity in the order Polydesmida Pocock, 1887, behind Paradoxosomatidae Daday, 1889 and Chelodesmidae Cook, 1895. In the Appalachian Mountains of eastern North America, which is its center of species diversity, 53 species of the millipede genus *Nannaria* Chamberlin, 1918 have been described in the past three years (Means *et al.* 2021a, b; Hennen *et al.* 2022). The family Xystodesmidae includes bioluminescent species, aposematic species that assemble into vast and geographically variable Müllerian mimicry rings, and those that are endemic to areas less than 20 km^2 (Means & Marek 2017, Means *et al.* 2021b).

The earliest name in the family, *Julus virginiensis*, now *Apheloria virginiensis*, was established by Drury in 1770 for millipedes sent to him by James Greenway, a physician and naturalist from Dinwiddie County, eastern Virginia. In a letter to Greenway, Drury expressed appreciation for the collection, and wrote: "I must not neglect ye present opportunity [to say] that the contents of one of ye vials you sent me was a most acceptable present. It contained some uncommon Insects. I never saw any Juli (for such they were) so large." (Cockerell, 1922). *Juli*, a plural of *Julus* (Latin *Iulus*), refers to a millipede or myriapod, and is from the Greek, *ioulos*, (*ιουλος*) meaning down, wool, or a floral catkin—the latter with its repeating linear flowers appeared like the curled, and multi-segmented body of a millipede (Brown, 1954).

Thus began the taxonomic history of the genus *Apheloria*, covered previously by Shelley (1978), Shelley & Whitehead (1986), Shelley *et al.* (2017), and Marek *et al.* (2014, 2018). The most recent history of the genus took place with R.L. Hoffman, who had been working on a revision of *Apheloria* until his death in 2012, and with later authors (Shelley *et al.* 2017, Means & Marek 2017, Marek *et al.* 2018, Means *et al.* 2021b). From conversations

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with him by the first author, Hoffman commented that completion of a revision was pending solutions to obstacles that remained concerning the disposition of the taxa *Apheloria virginiensis* (Drury, 1770), *Apheloria luminosa* (Kenyon, 1893), and *Apheloria polychroma* Marek, Means & Hennen, 2018. The latter, which at that moment, was not described and referred to him as the temporary name *Apheloria* sp. "*flavissima*". A detailed taxonomic history of the genus can be seen in our Appendix 1, and in Hoffman (1952, 1957), Shelley (1978, 1980), Shelley & Whitehead (1986), Shelley *et al.* (2017), and Marek *et al.* (2014, 2018). These works exhaustively detail historical narratives surrounding the taxon, which includes the disposition of the name *Fontaria virginiensis* Gray, 1832. This history will not be reiterated here. From 2015–2020, we cataloged and digitized 780 folders of millipede-related notes of R. L. Hoffman. In these notes were the hand-drawn sketches of millipedes, species descriptions, maps, annotated reprints, and other material that he had assembled over more than 60 years of work. Several folders contained material relating to the genera *Apheloria* and *Nannaria*. In 2021 and 2022, in two articles, we revised the genus *Nannaria*, which included the description of 53 new species. The revision of *Nannaria* leveraged these notes in combination with DNA sequencing, phylogenetics, and extensive field work by the authors. The present study concerns the genus *Apheloria*, and is an integrative taxonomic revision that likewise combines molecular phylogenetics and years of fieldwork with an analysis of morphological characters.

Apheloria is a colorful and often encountered millipede genus in eastern North America. Broadly distributed in the region, it is ubiquitous in broadleaf deciduous forests. With an aposematic color palette of reds and yellows and black, *Apheloria* participates in geographically variable Müllerian mimicry in the Appalachian Mountains with other members of the family such as *Appalachioria* Marek & Bond, 2006; *Brachoria* Chamberlin, 1939; and *Rudiloria* Causey, 1955. This system is composed of multiple overlapping mimicry rings and is analogous to those in South America that are made up of poison dart frogs or butterflies (Marek & Bond, 2009). Southwestern Virginia holds the greatest diversity of millipede related mimicry both in terms of number of species and color variation. The multicolored *Apheloria polychroma* has six unique color morphs, each of which are mimicked by separate species of *Brachoria*. The greatest species and color diversity is present at High Knob in Wise County, Virginia, with four species that are co-mimics with *A. polychroma*: *Brachoria cedra* Keeton, 1959; *Brachoria dentata* Keeton, 1959; *Brachoria hoffmani* Keeton, 1959; and *Brachoria insolita* Keeton, 1959. At this locality, in a 30-minute collecting event, the first author observed 43 individuals of these five species exhibiting four different color morphs; some species like *A. polychroma* and *B. insolita* possessed two morphs of their own—each morph mimicking the other taxon's—but all five species converged upon a single color morph as a result of mimicry (Marek & Bond, 2009). Other instances of mimicry, such as between *Rudiloria* and *Appalachioria* species with *Apheloria*, have not yet been well documented. *Apheloria* species have been studied for their detritivory (Romell 1935, Eaton 1943) and as a model for the production of hydrogen cyanide; the species *A. corrugata*, studied by T. Eisner, was determined to be capable of producing 600 micrograms of cyanide in total content per individual millipede. This quantity is 18 times the lethal threshold to a pigeon-sized bird (Eisner *et al.* 1967). Aside from these fascinating biological qualities, the genus remains poorly studied, with a new species existing in a well populated region of the southeastern U.S., which we described in this study.

In this study, we revise the genus *Apheloria*. We estimate the evolutionary history of the genus with molecular phylogenetics, describe a new species, *Apheloria uwharrie* **sp. nov.**, from North and South Carolina, and synonymize *Apheloria tigana* with *Apheloria virginiensis* and *Apheloria luminosa* with *Pleuroloma flavipes* Rafinesque, 1820.

Material and methods

Specimens collected in the field were prepared according to Means *et al.* (2015) to ensure preservation of DNA and morphology as natural history specimens. A specimen of *Apheloria* for every locality where the genus was collected over the past two decades was used. We targeted the sampling of specimens from type localities and historical records in the periphery of the genus's range.

To estimate phylogeny, we sequenced the DNA of four gene regions: three mitochondrial gene fragments (cytochrome *c* oxidase subunit I gene, abbreviated COI; large subunit ribosomal RNA gene including the tRNA-Val gene, 16S; and small subunit ribosomal RNA gene, 12S) and one nuclear gene fragment (elongation factor-1 alpha gene, EF1-a). Five specimens from the boundary region of two species in eastern North Carolina, *Apheloria virginiensis* and *Apheloria uwharrie* **sp. nov.**, which were included later in the study, were only sequenced for COI (catalog numbers: MPE05400–MPE05404). Amplification and sequencing of DNA was carried out according to

the methods described in Means & Marek (2017). Chromatograms were base called in Mesquite using the module Chromaseq with phred and phrap (Maddison and Maddison 2019, 2020; Ewing *et al.* 1998). Sequences were aligned in MAFFT (Katoh and Standley 2013), and reading frame confirmed in protein coding genes by visual inspection in Mesquite. A maximum likelihood tree search with 1000 bootstrap pseudoreplicates was accomplished with IQTREE2 for the individual genes (ribosomal genes were combined) and the four gene regions together (Minh *et al.* 2020). IQTREE2 tested for best-fit models with a Bayesian information criterion, and homogeneity of DNA nucleotide composition with a X-squared test (Kalyaanamoorthy *et al.* 2017). The outgroups were selected based on the phylogeny inferred by Means *et al.* (2021b) and included a single individual of: *Rudiloria kleinpeteri* (Hoffman, 1949) and *Rudiloria mohicana* Causey, 1955. Mesquite was used to store and curate the chromatograms, matrices, and trees.

We used a species delimitation criterion that species are groups of populations sharing gonopodal morphology and are monophyletic in the four gene phylogeny (Milne & Hedin 2023).

Gonopods were dissected and photographed according to Means *et al.* (2015). Due to the circular shape of the gonopods of *Apheloria* species, excepting the morphologically divergent telopodites of *Apheloria whiteheadi*, and that they are invariant in posterior view and no additional species diagnostic features can be seen in posterior view, only the anterior and lateral views are presented here.

All morphological measurements were made in millimeters (mm). Depository abbreviations are as follows according to Sierwald & Reft (2004): Field Museum of Natural History, Chicago (FMNH); The Natural History Museum, London (BMNH); Smithsonian Institution, Washington, D.C. (USNM); Florida State Collection of Arthropods, Gainesville (FSCA); Virginia Tech Insect Collection, Blacksburg (VTEC); and Virginia Museum of Natural History, Martinsville (VMNH).

A distribution map was generated with Simplemappr (Shorthouse 2010) from the specimens that were sequenced in this study plus historical occurrence records from the periphery of the genus's geographical range from Shelley & McAllister (2007), R.L Hoffman's notes, and vetted research-grade observations from iNaturalist.

Results

DNA from 178 specimens collected from 2003–2022 was extracted and sequenced. Eight of the COI sequences failed the composition test. The following nucleotide site substitution models were selected: COI with CODON5 codon model (MG+F3X4+G4), EF1a (JC+I for 1st and 2nd codon positions, TN+F+R3 for 3rd codon position and intron), and 16S–12S (TPM2+F+I+G4). The phylogeny is shown in Figure 1.

Taxonomy

Order Polydesmida Pocock, 1887
Suborder Leptodesmidea Brölemann, 1916
Superfamily Xystodesmoidea Cook, 1895
Family Xystodesmidae Cook, 1895
Tribe Apheloriini Hoffman, 1980

Genus *Apheloria* Chamberlin, 1921

Vernacular name: The cherry millipedes

Apheloria Chamberlin, 1921: 232. Type species: *Fontaria montana* Bollman, 1887, by original designation. Detailed taxonomic history in Appendix 1.

Six species:
Apheloria corrugata (Wood, 1864);
Apheloria montana (Bollman, 1887);
Apheloria polychroma Marek, Means & Hennen, 2018;
Apheloria uwharrie **sp. nov.**;
Apheloria virginiensis (Drury, 1770),
Apheloria whiteheadi (Shelley, 1986).

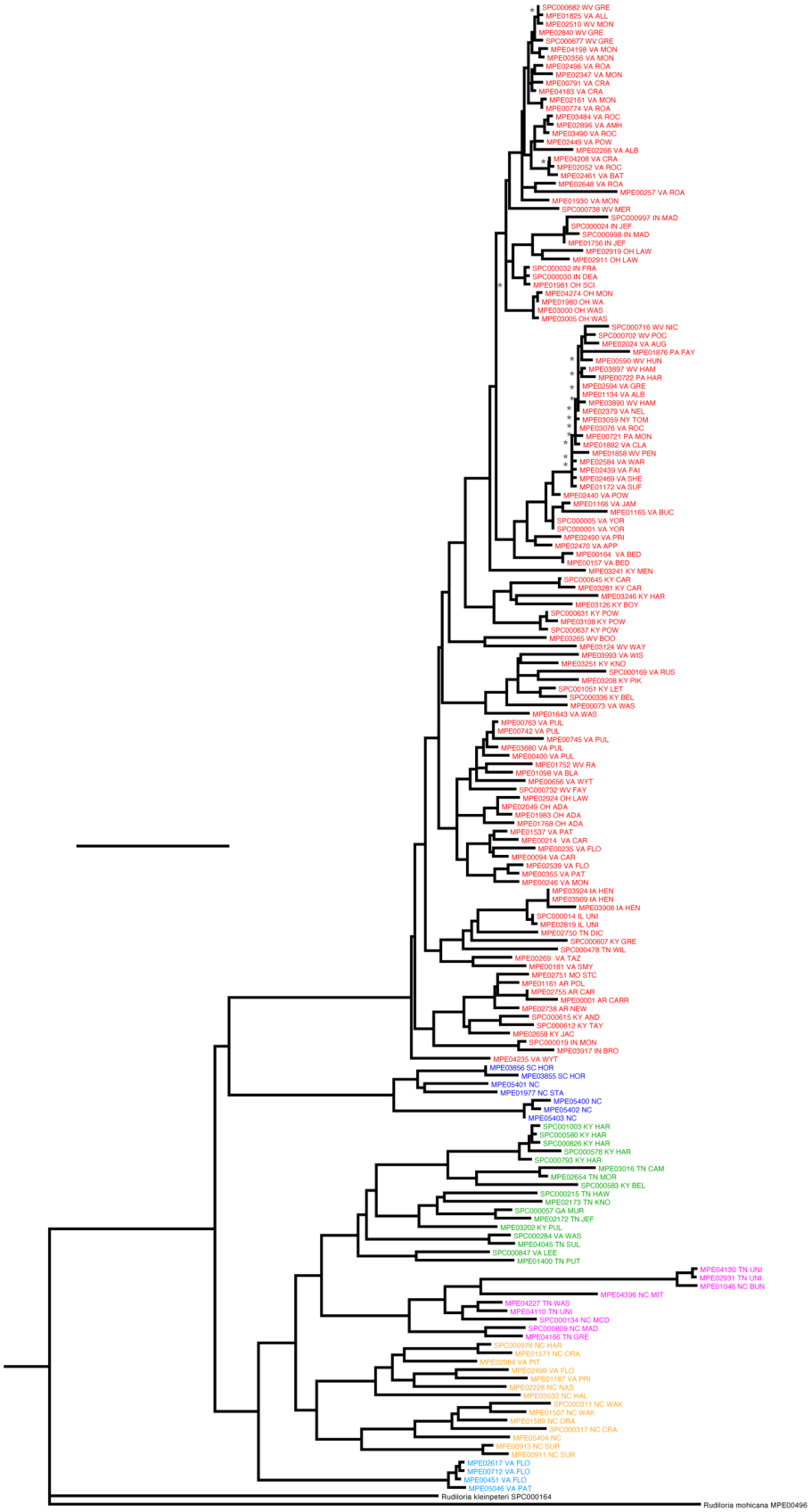

FIGURE 1. Phylogeny of *Apheloria* Chamberlin, 1921. *Apheloria corrugata* (Wood, 1864) in red; *Apheloria montana* (Bollman, 1887) in magenta; *Apheloria polychroma* Marek, Means & Hennen, 2018 in green; *Apheloria uwharrie* **sp. nov.** in blue; *Apheloria virginiensis* (Drury, 1770) in orange; and *Apheloria whiteheadi* (Shelley, 1986) in cyan. Scale bar = 0.02 substitutions. Branches with bootstrap values less than 70% are marked with an asterisk.

Genus diagnosis: *Apheloria* is distinct from other apheloriine genera based on the following combination of characters: **Color**. Tergites with 2–4 spots or stripes. Spot, stripe hues variable; usually yellow stripes, often with red spots on paranota (Fig. 2)—never with purple as in some species of *Sigmoria*. Those with yellow stripes often show a brick-red tinge on the inside margin of the paranotal spots. **Gonopods**. Gonopodal acropodite circular (Figs 3, 4A)—not smoothly oval-shaped (0-shaped), as in *Rudiloria*, nor D-shaped as in *Sigmoria*. Acropodite narrow, about one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite gradually tapered to curved J- or L-shaped acuminate apex (Fig. 4B). Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a scythe-like prefemoral process located medially (Fig. 4B, pfp)—not absent, rounded, nor located marginally as in *Appalachioria*, *Brachoria.* Acropodite bent 90° posteroventrally at prefemur (Fig. 4B); prostatic groove bent 90° from cannula to acropodite base. With acute angle or distinct protuberance on corner of bend, "bend tubercle" (Fig. 4B, bt).

Genus diagnosis notes: The genus diagnosis applies solely to the species of *Apheloria* besides *A. whiteheadi*, a geographically isolated species with very different looking acropodites. See diagnosis of *A. whiteheadi* below.

Genus etymology: Chamberlin did not provide an etymology of the genus name *Apheloria* when he named it in 1921. It is presumed that the name is from the Greek *apo* (*ἀπό*) meaning away or off, and the Greek *helios*, meaning sun (*ἥλιος*) (Brown 1954). Chamberlin may have selected the name because millipedes in the genus *Apheloria*, and most members of the family Xystodesmidae, flee from the sun to avoid desiccation. Similarly, the genus name appears similar to the word aphelion, which means a point on a circular orbit that is farthest from the sun. A circular orbit appears similar to the circular gonopods of the genus *Apheloria*. The circular acropodite is the basis of the single sentence description of the genus by Chamberlin (1921:232), "Erected for a group of species…in which the telopodite of the gonopod of male is a simple, coiled blade with a small spur at base." This latter explanation would be consistent with other genus names in the tribe Apheloriini Hoffman, 1980 by Chamberlin based on shape of the telopodite, such as *Brachoria* Chamberlin, 1939 and *Sigmoria* Chamberlin, 1939; and *Rudiloria* Causey, 1955.

FIGURE 2. *Apheloria corrugata* (Wood, 1864), pink-spotted yellow stripe morph (specimen # MPE00770 from Price Mountain, Montgomery Co., Virginia).

Apheloria corrugata (Wood, 1864), new status

Vernacular name: "The pink and yellow cherry millipede"
Figs 2–6, 10

Polydesmus (Fontaria) corrugatus Wood, 1864: 6.
Fontaria butleriana Bollman, 1888: 407, **new synonymy**.
Leptocircus inexpectatus Attems, 1931: 67. Synonymized by Hoffman, 1999: 307.
Apheloria adela Chamberlin, 1939: 10. Synonymized by Hoffman, 1957: 186.
Apheloria iowa Chamberlin, 1939: 10, **new synonymy**.
Apheloria reducta Chamberlin, 1939: 11, **new synonymy**.
Apheloria pinicola Chamberlin, 1947: 26. Synonymized by Hoffman, 1999: 305.
Apheloria asburna Chamberlin, 1949a: 101. Synonymized by Hoffman, 1999: 307.
Detailed taxonomic history in Appendix 1.

Material examined: Type specimens—♂ syntype (USNM) from New York, Oneida County, Trenton Falls (Coll: D. Mack), no other collection information provided (*non vidi*). Non type material examined in Appendix 2. Materials examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

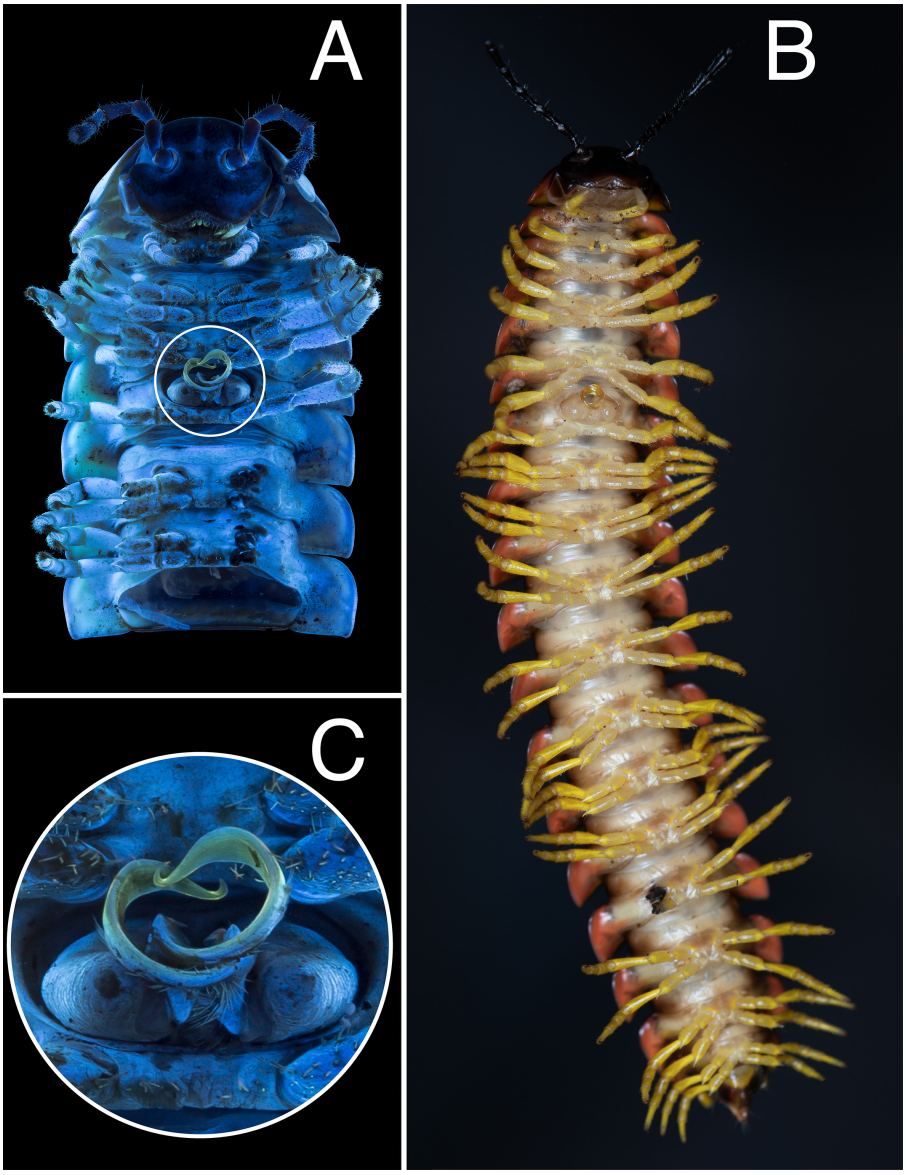

FIGURE 3. *Apheloria corrugata* (Wood, 1864), ventral views showing in situ arrangement of gonopods. **A**: Ventral view of anterior rings illuminated with ultraviolet light (specimen # MPE01930); **B**: Ventral view illuminated with white light; **C**: Magnification of the gonopods from A showing their situ arrangement.

Diagnosis: *Apheloria corrugata* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites with two pink spots and yellow metatergal stripe, anterior collum stripe, and legs (Figs 2, 3, 5A, 6). ♂ **Gonopods**. Gonopodal acropodite smoothly circular, O-shaped (Fig. 3, 4B)—without elbow as in *A. virginiensis* (Fig. 7A, elb). Not smoothly oval-shaped (0-shaped), as in *Rudiloria*, nor D-shaped as in *Sigmoria*. Acropodite narrow, about one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite tapered to L-shaped acuminate apex and abruptly twisted (Fig. 4B)—not gradually tapered to curved J-shaped apex as in *A. polychroma* (Fig. 8B). Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a long, scythe-like prefemoral process (Fig. 4B, pfp)—not short, scythe-like as in *A. polychroma* (Fig. 8A, pfp). With distinct bend tubercle at prefemur-acropodite junction (Fig. 4B, bt), not with acute angle at junction as in *A. polychroma*, *A. uwharrie* (Figs 8B, 9B).

Note about coloration: The pink-spotted yellow stripe morph unequivocally diagnoses *A. corrugata* from all other species of Xystodesmidae, except for in the Valley and Ridge Mountains of Virginia where *Appalachioria calcaria* (Keeton, 1959) is a mimic (Fig. 5). However, there are about 10 distinct color morphs of the species with some of these morphs appearing as if a product of the superimposition of distinct morphs atop one another, such as

morphs 5 and 7 below (Figs 2, 10). Because color varies considerably intraspecifically, it should be cautiously used as a diagnostic character for this species.

Variation. There are at least 10 color morphs of *A. corrugata* with a continuum of coloration between them (in order of decreasing frequency): (1) striped, with yellow metatergal stripes and pink paranotal spots, and yellow legs (Figs 2, 5A, 6); (2) striped, with yellow metatergal—paranotal stripes, anterior collum stripe, and legs (Fig. 10A); (3) two-spotted, with yellow paranotal spots, and yellow legs (Fig. 10B); (4) three-spotted, with yellow paranotal, metatergal and collum spots, and yellow legs (Fig. 10C); (5) striped/three-spotted superimposition of striped (morph 1) and three-spotted yellow morphs (morph 4) (Fig. 10D); (6) striped, with pink metatergal—paranotal stripes, anterior collum stripe, and legs (Fig. 10E); and (7) striped/three-spotted superimposition of striped (morph 6) and three-spotted yellow morphs (morph 4) (Fig. 10F). Some that appear like morphs 2 or 4 have small brick red crescents next (anterior) to their yellow paranotal spots (Figs 10A, C).

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 13) BL = 34.07–46.48 (39.53/ 3.14). CW = 6.00–8.19 (7.01/ 0.67). IW = 3.71–4.99 (4.40 / 0.35). ISW = 1.02–1.32 (1.16/0.09). B10W = 7.28–10.85 (8.94/1.12). ♀ (n = 14) BL = 37.85–57.23 (46.92/ 5.30). CW = 6.70–7.82 (7.14/0.29). IW = 4.52–5.64 (4.95/0.31). ISW = 1.20–1.57 (1.41/0.11). B10W = 9.06–10.64 (9.79/0.46).

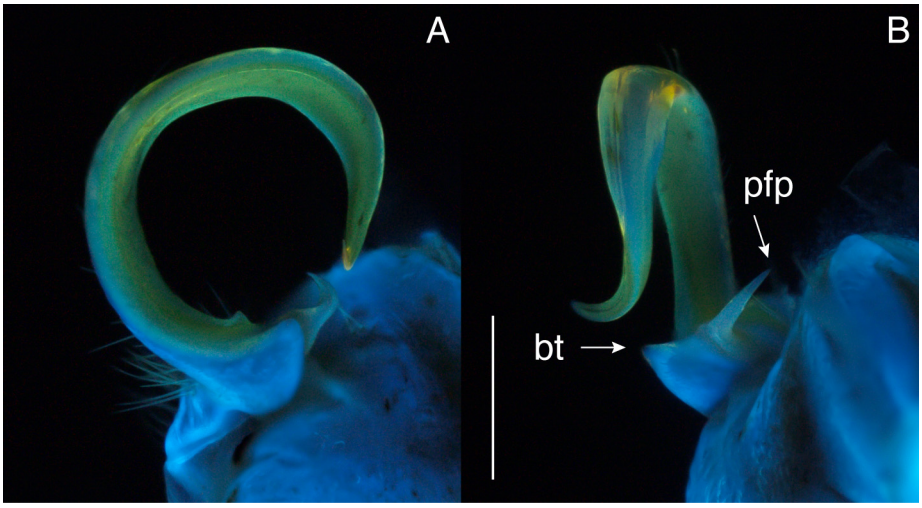

FIGURE 4. *Apheloria corrugata* (Wood, 1864), male gonopods (specimen # MPE00770). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process. bt: bend tubercle.

Ecology. *Apheloria corrugata* individuals were typically encountered in mesic habitats such as broadleaf deciduous forests (Fig. 6). More seldom were they found in mixed forests, rhododendron groves, cedar glades, and hemlock forests. Syntopic tree species recorded with *A. corrugata* included sugar maple, tulip poplar, white oak, pine, sycamore, beech, hickory, and black walnut. Individuals were normally found beneath decomposing leaves and occasionally walking atop detritus on the forest floor. Individuals of *A. corrugata* are commonly encountered walking on the lawn of the first author's home in Blacksburg, Virginia in spring, and they may also enter houses, particularly damp basements (W. Shear, pers. communication).

Due to mimicry in color and overlap in distribution, *A. corrugata* may be confused in the field with *A. polychroma*, *A. virginiensis*, *A. whiteheadi* and the following species of *Appalachioria*, *Brachoria*, *Cherokia* Chamberlin, 1949b, *Pleuroloma* Rafinesque, 1820, and *Rudiloria* Causey, 1955: *Appalachioria bondi* Marek, Means, Hennen, 2021; *Appalachioria calcaria* (Keeton, 1959) (Fig. 5B); *Appalachioria ethotela* (Chamberlin, 1942); *Appalachioria falcifera* Keeton, 1959; *Appalachioria hamata* (Keeton, 1959); *Appalachioria separanda* Chamberlin, 1947; *Appalachioria versicolor* (Hoffman, 1963); *Brachoria badbranchensis* Marek, 2010; *Brachoria blackmountainensis* Marek, 2010; *Brachoria campcreekensis* Marek, 2010; *Brachoria electa* Causey, 1955; *Brachoria flammipes* Marek, 2010; *Brachoria gracilipes* (Chamberlin, 1947); *Brachoria grapevinensis* Marek, 2010; *Brachoria hoffmani* Keeton, 1959; *Brachoria indianae* (Bollman, 1888); *Brachoria laminata* Keeton, 1959; *Brachoria ligula* Keeton, 1959; *Brachoria viridicolens* (Hoffman, 1948); *Cherokia georgiana* (Bollman, 1889); *Pleuroloma flavipes* Rafinesque, 1820; *Rudiloria guyandotta* (Shear, 1972); *Rudiloria mohicana* Causey, 1955;

Rudiloria rigida Shelley, 1986; and *Rudiloria trimaculata* (Wood, 1864). *Apheloria corrugata* can be distinguished from other species of *Apheloria* by its diagnosis, and from *Appalachioria*, *Brachoria*, *Cherokia*, *Pleuroloma* and *Rudiloria* species by gonopod morphology, specifically by the absence of a cingulum, or a mid-length transverse groove on the acropodite, and the presence of a circular acropodite (Figs 3, 4A).

Distribution. *Apheloria corrugata* has the greatest distributional area of the genus, and is known from Virginia north to Connecticut and Montreal; west to southeastern Ontario Province, southern Michigan, southeasternmost Wisconsin; south to Illinois, southeastern Iowa, southern Missouri; western Oklahoma, northern Arkansas, western Tennessee, and the far northwestern corner of Alabama (Fig. 11). *Pleuroloma flavipes* has the greatest distributional area of the family and extends further south (to northern Louisiana) and west (Shelley 1980, Shelley *et al.* 2003).

FIGURE 5. Müllerian mimicry between *Apheloria corrugata* (Wood, 1864) (A) and *Appalachioria calcaria* (Keeton, 1959) (B) in Blacksburg, Virginia.

Apheloria montana (Bollman, 1887)

Vernacular name: "The mountain cherry millipede"
Figs 12, 13

Fontaria montana Bollman, 1887: 622.
Apheloria aspila Chamberlin, 1939: 10. Synonymized by Hoffman, 1999: 306.

Apheloria unaka Chamberlin, 1939: 11. Synonymized by Hoffman, 1999: 305.
Detailed taxonomic history in Appendix 1.

Material examined: Type specimens—♂ holotype (USNM) from Tennessee, Cocke County, Wolf Creek (Coll: C. Branner), no other collection information provided (*non vidi*). Non type material examined in Appendix 2. Materials examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

Diagnosis: *Apheloria montana* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites with three yellow spots and yellow legs (Fig. 12). ♂ **Gonopods**. Gonopodal acropodite smoothly circular, O-shaped (Fig. 13A)—without elbow as in *A. virginiensis* (Fig. 7A, elb). Not smoothly oval-shaped (0-shaped), as in *Rudiloria*, nor D-shaped as in *Sigmoria*. Acropodite narrow, about one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite tapered to L-shaped acuminate apex and abruptly twisted (Fig. 13B)—not gradually tapered to curved J-shaped apex as in *A. polychroma* (Fig. 8B). Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a long, scythe-like prefemoral process (Fig. 13B, pfp)—not short, scythe-like as in *A. polychroma* (Fig. 8A, pfp). With distinct bend tubercle at prefemur-acropodite junction (Fig. 13B, bt), not with acute angle at junction as in *A. polychroma*, *A. uwharrie* (Figs 8B, 9B).

Note about coloration: The three-spotted yellow morph unequivocally diagnoses *A. montana* from all other species of *Apheloria* northeast of the Great Smoky Mountains National Park in the Blue Ridge Mountains of Tennessee and North Carolina (Fig. 12).

Variation. The three-spotted yellow morph is the single color morph of *A. montana*. Individuals from Little Switzerland, Mitchell Co., North Carolina, possess smaller orange spots and orange legs.

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 7) BL = 41.85–52.89 (46.56/3.71). CW = 6.57–7.75 (6.91/0.45). IW = 4.24–4.89 (4.50/0.27). ISW = 1.15–1.31 (1.25/0.06). B10W = 8.74–10.51 (9.49/0.72). ♀ (n = 7) BL = 46.69–54.87 (49.51/2.98). CW = 6.44–8.21 (7.11/0.71). IW = 4.08–5.26 (4.75/0.41). ISW = 1.10–1.41 (1.30/0.11). B10W = 8.42–11.20 (9.78/0.99).

Ecology. *Apheloria montana* individuals were typically encountered in mesic habitats such as broadleaf deciduous forests. They were also found in drier habitats such as mixed forests, rhododendron groves, and oak and beech forests. Syntopic tree species recorded with *A. montana* included pine, maple, oak, tulip poplar, witch hazel, alder, hemlock, sweetgum, buckeye, and maple. Individuals were typically found beneath decomposing leaves on the forest floor.

FIGURE 6. The typical habitats of *Apheloria corrugata* (Wood, 1864) individuals are mesic broadleaf deciduous forests.

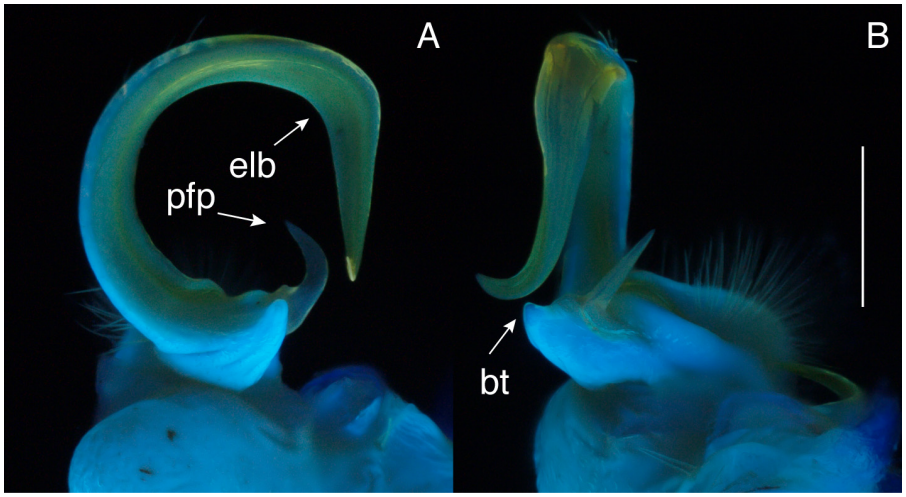

FIGURE 7. *Apheloria virginiensis* (Drury, 1770), male gonopods (specimen # SPC000312). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process. bt: bend tubercle. elb: elbow.

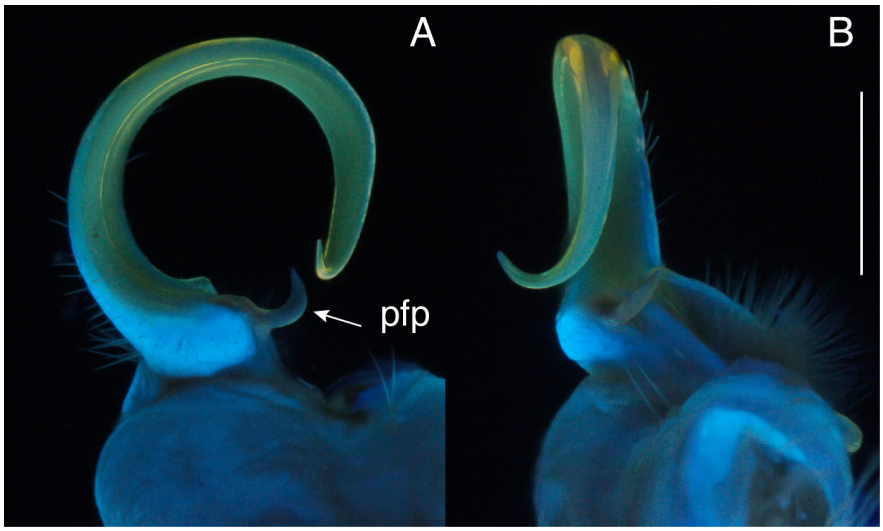

FIGURE 8. *Apheloria polychroma* Marek, Means & Hennen, 2018, male gonopods (specimen # MMC0311). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process.

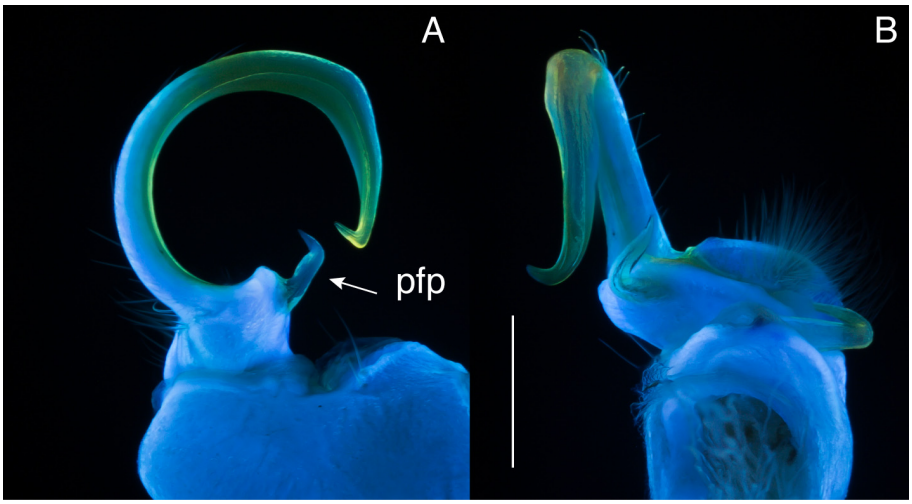

FIGURE 9. *Apheloria uwharrie* Marek, Means, Hennen & Tingley, **sp. nov.**, male gonopods (specimen # MPE03855). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process.

Due to mimicry in color and overlap in distribution, *A. montana* may be confused in the field with *A. polychroma*; *Appalachioria eutypa* (Chamberlin, 1939); *Brachoria hendrixsoni* Marek, 2010; *C. georgiana*; and *P. flavipes*. *Apheloria montana* can be distinguished from other species of *Apheloria* by its diagnosis, and from *Appalachioria*, *Brachoria*, *Cherokia* and *Pleuroloma* species by gonopod morphology, specifically by the absence of a cingulum, or a mid-length transverse groove on the acropodite, and the presence of a circular acropodite (Fig. 13A).

Distribution. Known from western North Carolina in Buncombe, Madison, McDowell, and Mitchell cos., and eastern Tennessee in Greene, Unicoi, and Washington cos. (Fig. 11). *Apheloria montana* has the second smallest distributional area of the genus; *A. whiteheadi* has the smallest distribution.

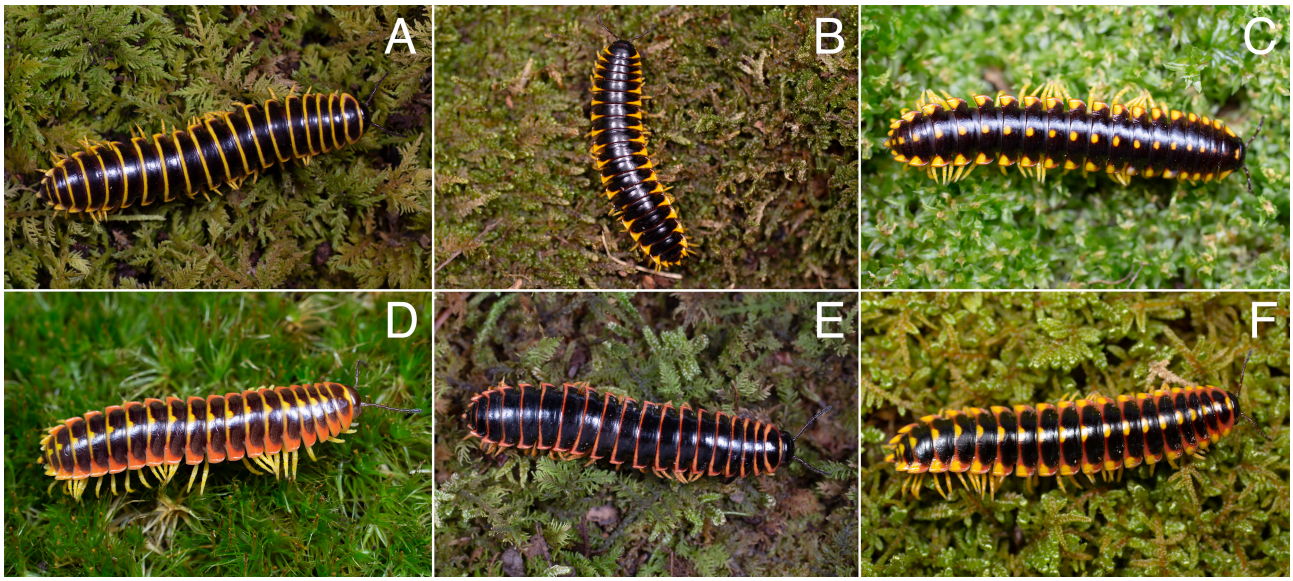

FIGURE 10. *Apheloria corrugata* (Wood, 1864), color morphs. **A**: Striped, with yellow metatergal—paranotal stripes, anterior collum stripe, and legs; **B**: Two-spotted, with yellow paranotal spots, and yellow legs; **C**: Three-spotted, with yellow paranotal, metatergal and collum spots, and yellow legs; **D**: Striped/three-spotted superimposition of striped (morph 1) and three-spotted yellow morphs (morph 4); **E**: Striped, with pink metatergal—paranotal stripes, anterior collum stripe, and legs; **F**: Striped/three-spotted superimposition of striped (morph 6) and three-spotted yellow morphs (morph 4).

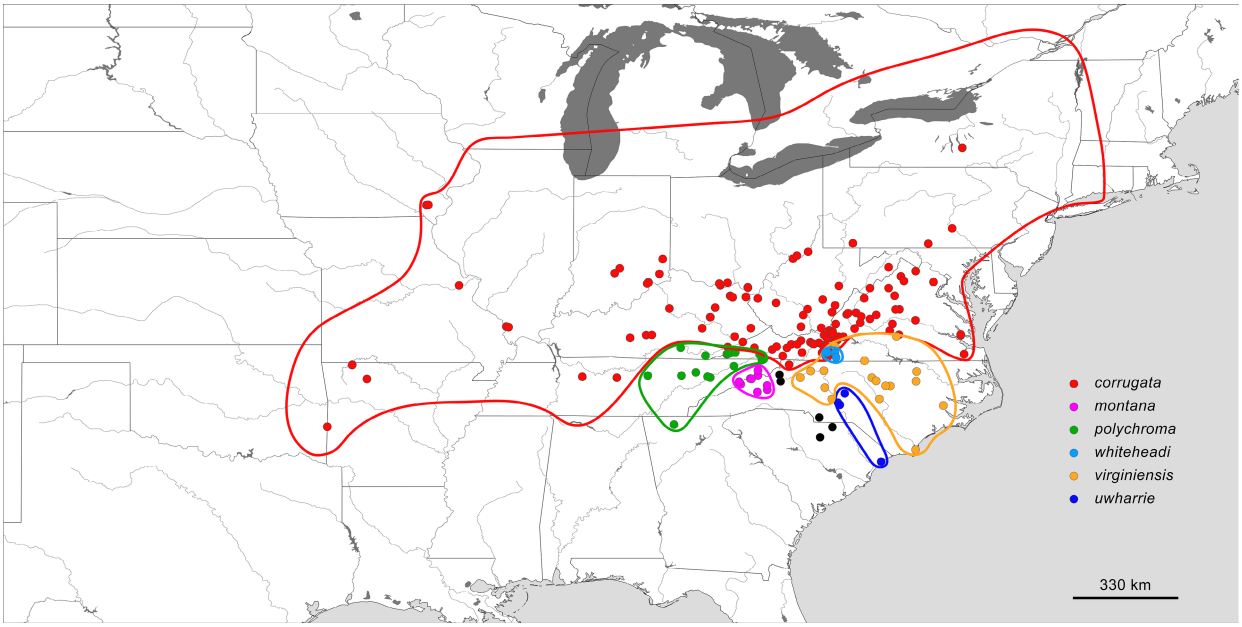

FIGURE 11. Distribution of species of the genus *Apheloria* Chamberlin, 1921. Colored dots indicate specimens used in the phylogenetic analysis. Outlines bound colored dots plus historical occurrence records from the periphery of the genus' geographical range from Shelley & McAllister (2007), R.L Hoffman's notes, and vetted research-grade observations from iNaturalist. Black dots denote unexamined material referable to *Apheloria* sp. and are undetermined.

FIGURE 12. *Apheloria montana* (Bollman, 1887) has a single color morph with three yellow spots and yellow legs.

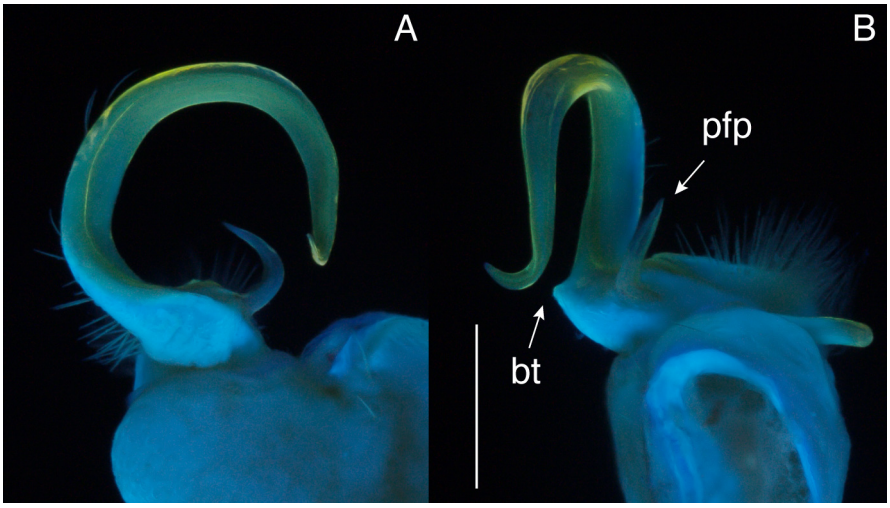

FIGURE 13. *Apheloria montana* (Bollman, 1887), male gonopods (specimen # SPC000134). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process. bt: bend tubercle.

Apheloria polychroma Marek, Means & Hennen, 2018

Vernacular name: "The colorful cherry millipede"
Figs 8, 14

Apheloria polychroma Marek, Means & Hennen, 2018: 416.
Apheloria roanea Chamberlin, 1947: 26. Synonymized by Hoffman, 1999: 306.
Detailed taxonomic history in Appendix 1.

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, The Cedars State Natural Area Preserve, CR-738 (36.65624°N, -83.20165°W, Elev. 436 m), 28 September 2006, 16:00 (Colls: P. and B. Marek) (*vidi*). Non type material examined in Appendix 2. Materials examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

FIGURE 14. Although *Apheloria polychroma* Marek, Means & Hennen, 2018 has at least six color morphs, the 4-spotted yellow morph with a collum that is uniformly covered in yellow unequivocally diagnoses it from all other species of Xystodesmidae.

Diagnosis: *Apheloria polychroma* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites usually with 4 yellow spots on a jet black background: 1 metatergal, 1 prozonal, 2 paranotal spots (Fig. 14). Collum usually uniformly covered in yellow (Fig. 10). ♂ **Gonopods**. Gonopodal acropodite smoothly circular, O-shaped (Fig. 8A)—without elbow as in *A. virginiensis* (Fig. 7A, elb). Not smoothly oval-shaped, 0-shaped, as in *Rudiloria*. Acropodite narrow, one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite gradually tapered to curved acuminate, J-shaped apex (Fig. 8B)—not L-shaped and abruptly twisted as in *A. corrugata*, *A. virginiensis*, *A. montana* (Figs 4B, 7B, 13B). Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a shorter, scythe-like prefemoral process, one-ninth length of acropodite (Fig. 8A, pfp)—not long and scythe-like as in *A. corrugata*, *A. virginiensis*, *A. montana* (Figs 4A, 7A, 13A). With acute angle at prefemur-acropodite junction (Fig. 8B), not with distinct bend tubercle at junction as in *A. corrugata*, *A. virginiensis*, *A. montana* (Figs 4B, 7B, 13B, bt).

Note about coloration: When it is present, the 4-spotted yellow color morph with a collum that is uniformly covered in yellow unequivocally diagnoses *A. polychroma* from all other species of Xystodesmidae (Fig. 14). However, this morph is geographically restricted to the Powell River Valley from Big Stone Gap, Virginia, in the north and Norris, Tennessee in the south. There are no fewer than six distinct color morphs of the species with a continuum of hues and patterns between them ("Figs 2A – T, 5" in Marek *et al.* 2018). There are often multiple color morphs of the species that are syntopic and co-occur in a small area (≥ 10 m^2). Because color varies considerably intraspecifically, it should be cautiously used as a diagnostic character for this species.

Variation. There are at least six color morphs of *Apheloria polychroma* with a continuum of coloration between them: (1) four-spotted, with yellow to orange paranotal, metatergal, prozonal and collum spots, and legs (collum often uniformly covered in yellow, Fig. 14) and sometimes with red legs; (2) striped, with yellow metatergal—paranotal stripes, anterior collum stripe, and legs ("Figs 2G, H" in Marek *et al.* 2018); (3) three-spotted, with cream-white paranotal, metatergal and collum spots, and red legs ("Figs 2I, J" in Marek *et al.* 2018); (4) three-spotted, with yellow paranotal, metatergal and collum spots, and yellow or red legs ("Figs 2K, L; 5A, B" in Marek *et al.* 2018); (5) striped/four-spotted superimposition of striped and four-spotted yellow morphs ("Figs 2M, N" in Marek *et al.* 2018); and (6) two-spotted, with yellow paranotal spots, and yellow or red legs ("Figs 2Q – T" in Marek *et al.* 2018). Some three-spotted yellow individuals have faint metatergal spots and appear nearly two-spotted ("Fig. 2S" in Marek *et al.* 2018). The dorsal color of *A. polychroma* is always yellow to red and jet black; however, the pattern varies from two, three, or four spots, to metatergal stripes, and superimposition of the latter two patterns.

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 13) BL = 39.59–58.52 (50.24/6.18). CW = 6.76–9.22 (7.69/ 0.69). IW = 4.19–5.21 (4.78/0.28). ISW = 1.10–1.72 (1.27/0.18). B10W = 9.29–12.47 (10.43/0.81). ♀ (n = 10) BL = 37.78–53.47 (44.36/5.78). CW = 6.75–8.62 (7.66/0.53). IW = 4.61–5.69 (5.09/0.32). ISW = 1.20–1.52 (1.34/0.10). B10W = 8.90–12.70 (10.61/1.09).

Ecology. *Apheloria polychroma* individuals were typically encountered in mesic habitats such as broadleaf deciduous forests, and seldom in more xeric habitats such as glades—for example in 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 normally found beneath decomposing leaves and occasionally walking atop detritus on the forest floor. These individuals were more often exposed to view than others of the family, bolder in behavior, and were more likely to writhe and flail when disturbed—compared to coiling into a ball like others. When handled, individuals would emit copious amounts of defense secretions and liquid feces.

Due to mimicry in color and overlap in distribution, *A. polychroma* may be confused in the field with *A. corrugata*, *A. montana*, *Appalachioria eutypa* (Chamberlin, 1939); *C. georgiana* (Bollman, 1889); *P. flavipes*; and eight species of *Brachoria*: *Brachoria cedra* Keeton, 1959; *Brachoria dentata* Keeton, 1959; *Brachoria hansonia* Causey, 1950; *Brachoria hoffmani* Keeton, 1959; *Brachoria insolita* Keeton, 1959; *Brachoria mendota* Keeton, 1959; *Brachoria sheari* Marek, 2010; *Brachoria splendida* (Causey, 1942). Mimetic resemblance between *A. polychroma* and *B. mendota* at Natural Tunnel State Park (Scott Co., Virginia) is one of the most accurate in the millipede mimicry system (Marek & Bond 2009, Marek *et al.* 2018). The Pennington Gap mimic millipede, *Brachoria dentata* Keeton, 1959, mimics *A. polychroma* in color morph at six of the seven localities where they were found to co-occur. Five other species of *Brachoria* co-occur with *A. polychroma* at fewer localities. When syntopic with *A. polychroma*, though rare, some individuals of the species *B. cedra*, *B. dentata*, *B. mendota*, and *B. sheari* can have 4 yellow spots, including the distinctive prozonal spot, and appear almost indistinguishable from *A. polychroma*. However, these *Brachoria* species never possess a collum that is uniformly covered in yellow. *Apheloria polychroma* can be distinguished from other species of *Apheloria* by its diagnosis, and from *Appalachioria*, *Brachoria*, *Cherokia*, and *Pleuroloma* species by gonopod morphology, specifically by the absence of a cingulum, or a mid-length transverse groove on the acropodite, and the presence of a circular acropodite (Fig. 8A).

Distribution. Known from the mountains between southwestern Virginia, southeastern Kentucky, eastern Tennessee, and northwestern Georgia (Fig. 11). Not known to occur in North Carolina. The greatest diversity in coloration of *A. polychroma* is seen in southwestern Virginia where the taxon is syntopic with six species of the genus *Brachoria*.

Apheloria uwharrie Marek, Means, Hennen & Tingley, new species

Vernacular name: "The Uwharrie cherry millipede"
Figs 9, 15

Apheloria "species"—Shelley 2000: 193.
Apheloria "Myrtle Beach"—Means *et al.* 2021b: 7.

Material examined: Type specimens—♂ holotype (VTEC, MPE03855), 1 ♀ paratype (VTEC, MPE03857), 2 ♂, 2 ♀ paratypes (VMNH, MPE03856, 3858; VTEC, 3859, 3875) from South Carolina, Horry Co., Myrtle Beach: Forested area near the intersection of Robert M Grissom Parkway and 29th Avenue North (33.711699°N, -78.882573°W, Elev. 8 m), 30 March 2018 (Coll: G. Schiermeyer) (*vidi*). Non type specimens—North Carolina, Stanly Co., 2 ♂ (VTEC, MPE01977, MPE01979), 1 ♀ (VMNH, MPE01978) Uwharrie Mountains, Morrow Mountain State Park, forest by old cabin & small parking lot (35.371667°N, -80.096111°W, Elev. 140 m), 7 August 2016, 16:00 (Coll: J. Means). Randolph Co., 3 ♂ (VTEC, MPE05400, 5402, 5403) Uwharrie National Forest, Birkhead Mountain Trail, near Tot Hill (35.6307°N, -79.9064°W, Elev. 240 m), 27 August 2022 (Coll: C. Tingley). Montgomery Co., 1 ♂ (VTEC, MPE05401) Uwharrie National Forest, Wood Run Trailhead Parking (35.3108°N, -80.0433°W, Elev. 167 m), 22 August 2022 (Coll: C. Tingley). Material examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

Diagnosis: *Apheloria uwharrie* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites with three yellow (Uwharrie Mountains, Fig. 15A) or red spots (Myrtle Beach) or red stripes (Myrtle Beach, Fig. 15B). ♂ **Gonopods**. Gonopodal acropodite smoothly circular, O-shaped (Fig. 9A)—without elbow as in *A. virginiensis* (Fig. 7A, elb). Not smoothly oval-shaped as in *Rudiloria*, nor D-shaped as in *Sigmoria*. Acropodite narrow, about one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite tapered to L-shaped acuminate apex and abruptly twisted (Fig. 9B)—not gradually tapered to curved J-shaped apex as in *A. polychroma* (Fig. 8B). Acropodite shaft without cingulum nor preapical teeth nor projections as in

Appalachioria, *Brachoria*. Prefemur with a long, scythe-like prefemoral process (Fig. 9B, pfp)—not short, scythe-like as in *A. polychroma* (Fig. 8B, pfp). With acute angle at prefemur-acropodite junction (Fig. 9B), not with distinct bend tubercle at junction as in *A. corrugata*, *A. virginiensis*, *A. montana* (Fig. 4B, 7B, 13B, bt).

Diagnosis notes: A millipede with red spots or stripes and circular acropodites occurring in Myrtle Beach, South Carolina, unequivocally diagnoses *A. uwharrie* from all other species. Similarly, a millipede with yellow spots and circular acropodites occurring in the Uwharrie Mountains unequivocally diagnoses *A. uwharrie* from all other species. However, *A. virginiensis* has similar coloration and occurs in the coastal plain and piedmont of North Carolina and Virginia, and northeast of *A. uwharrie*. Although there are no *A. virginiensis* with red stripes, there are *A. virginiensis* with yellow or red spots.

Description. Based on holotype (♂) MPE03855

Measurements: BL = 49.18, CW = 6.70, IW = 4.25, ISW = 1.27, B11W = 9.30. **Head**: Antenna length—extendable posteriorly to anterior margin of 3rd tergite; relative antennomere lengths 4>2>3>5>6>7>1. Antenna with 4 sensillum types; all sensillum shafts smooth, without barbules. Four apical cones (AS) in square pattern on 8th antennomere. Chaetiform sensilla (CS) on antennomeres 2–7. Antennomere 1 smooth without CS; antennomeres 2–4 with sparse CS vestiture; antennomeres 5–7 with dense CS vestiture. Trichoid sensilla (TS) on antennomeres 1–7; encircling apical rims. Spiniform basiconic sensilla (Bs_2) in clusters of 15 on apicodorsal surface of antennomeres 5, 6; Bs_2 1/10 length of CS. **Tergites**: Collum with straight cephalic edge, tapering laterally. Collum with carina present on anterolateral margins. Caudolateral corners of paranota rounded on body rings 1–4; body rings 5–19 with corners squared projecting caudally. Caudolateral corners of paranota 8–19 with small posterior-projecting tab. Paranota dorsal surface glossy, loosely wrinkled, appearing leathery. Ozopores opening dorsolaterally. Pore formula normal for order: 5, 7, 9, 10, 12, 13, 15–19. Paranota with anterodorsal area scooped out. Gonapophyses apically cylindrical. Pleural tubercle absent, with faint swelling between paranotal base and spiracle. Sterna without posteriorly projecting spines, with slightly anteriorly curved caudal margin. Sterna 2–9 sparsely setose (about 10 setae); sterna 10–18 lacking setae. **Gonopods**: Acropodite bent posteroventrally at base, curved medially in smooth O-shaped form (Fig. 9A). Distal-most arc of acropodite oriented laterally. O-shaped acropodite nearly closed between prefemoral process and apex (Fig. 9A). Right, left acropodites not crossed midlength, acropodites stacked. Gonocoxae with rounded protuberance apically, telopodites arising subapically. Telopodites—Prefemur with sharp prefemoral process, one-ninth length of acropodite, with apex tapered to sharp curved point, scythe-shaped, width at base 1/4 its length (Fig. 9A pfp). Acropodite bent 90° posteroventrally at prefemur (Fig. 9B); prostatic groove bent 90° from cannula to acropodite base (Fig. 9B). Not with distinct bend tubercle at prefemur-acropodite junction. Gonopodal acropodite narrow, one-half width of tibia on leg pair 9; tapered to curved acuminate apex. Acropodite with ventrobasal surface facing laterally. Acropodite without spines on dorsal surface. Acropodite basal and apical ventral surfaces not coplanar, apical surface facing ventrolaterally; anterior twist faint (Fig. 9B). Acropodite ventral surface flat, smooth, no bumps nor swellings. Acropodite without cingulum. Acropodite shaft uniform width to region with setae, tapered to acuminate apex. Acropodite elliptical in cross-section, acuminate apex thinner, transparent. Acropodite margin smooth, rounded, lacking sharp edge; marginal teeth absent. Acropodite with apical 1/9 recurved, L-shaped, projecting cephalically (Fig. 9B). Acropodite base with setae about 1/3 its total length (Fig. 9B).

Paratype (♀) MPE03857—Somatic measurements: BL = 56.54, CW = 6.64, IW = 4.83, ISW = 1.49, B10W = 10.07. **Cyphopods**: Cyphopod receptacle at its greatest width equal to prefemur length. Receptacle heart-shaped, pointed base facing medially. Cyphopodal valves symmetrical, anterior valve more convex. Cyphopods with valve suture facing laterally, suture without mid-length ramp-like swelling.

Variation. There are four color morphs of *Apheloria uwharrie*: (1) three-spotted, with yellow paranotal, metatergal and collum spots, and legs (Fig. 15A); (2) striped, with red metatergal—paranotal stripes, anterior collum spot, and legs (Fig. 15B); (3) striped/three-spotted superimposition of striped and three-spotted red morphs (Fig. 15C); and (4) three-spotted, with yellow paranotal spots and legs, and faint orange or missing metatergal and collum spots, appearing nearly two-spotted (Fig. 15D). There is a geographical assortment of color morphs, and *A. uwharrie* from the Uwharrie Mountains display the yellow spotted morph and those from Myrtle Beach have the red striped or spotted morphs.

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 5) BL = 46.19–55.63 (51.06/4.01). CW = 6.30–7.47 (6.95/0.50). IW = 4.02–4.86 (4.44/0.37). ISW = 1.26–1.33 (1.30/0.03). B10W = 8.72–10.24 (9.53/0.60). ♀ (n = 4) BL = 50.34–56.54 (53.38/3.15). CW = 6.64–7.82 (7.21/0.48). IW = 4.71–5.60 (4.97/0.42). ISW = 1.42–1.72 (1.56/0.13). B10W = 10.06–10.59 (10.20/0.26).

FIGURE 15. *Apheloria uwharrie* Marek, Means, Hennen & Tingley, **sp. nov.**, color morphs. **A**: Three-spotted, with yellow paranotal, metatergal and collum spots, and legs; **B**: Striped, with red metatergal—paranotal stripes, anterior collum spot, and legs; **C**: Striped/three-spotted superimposition of striped and three-spotted red morphs. **D**. Three-spotted yellow individual with a faint, orange or missing metatergal spots that appears nearly two-spotted.

Ecology. *Apheloria uwharrie* individuals were often encountered in more xeric habitats than is typical for members of the tribe. Individuals from Uwharrie National Forest were encountered in dry hardwood slopes and ridges, and those from Myrtle Beach were found in an oak, pine, magnolia forest in dry leaf litter. An individual from Morrow Mountain State Park in the Uwharrie Mountains was discovered in a damp, deciduous forest composed of live oak, huckleberry, and maple.

Apheloria polychroma and *A. corrugata* are well-known mimics with sympatric xystodesmid species, such as *Brachoria*, *Rudiloria*, and *Appalachioria*, but *A. uwharrie* is not known to mimic others. There is a resemblance between *A. uwharrie* and syntopic family members such as with *Sigmoria* species and a *Pleuroloma* species. *Sigmoria* and *Pleuroloma* species have a shared yellow spotted coloration in the Uwharrie Mountains, and appear striped red in Myrtle Beach. These resemblances are geographically clustered with yellow spotted species occurring north of the Carolinas' border and red striped species to the south (Shelley and Whitehead 1986). This resemblance is likely a result of Müllerian mimicry, or for camouflage in red light-dominated forest ecosystems (Endler 1993). Due to resemblance in color and overlap in distribution, *A. uwharrie* may be confused in the field with two species of *Sigmoria* [*Sigmoria latior* (Brölemann, 1900) and *Sigmoria simplex* (Shelley, 1977)] and a species of *Pleuroloma*, *Pleuroloma pinicola* Shelley, 1980. *Apheloria uwharrie* can be distinguished from these taxa by gonopod morphology, specifically by the presence of a circular acropodite (Fig. 9A).

Distribution. Known from two areas: the Uwharrie Mountains, NC, and Myrtle Beach, SC (Montgomery, Randolph, and Stanly cos., NC; and Horry Co., SC; Fig. 11). Several localities intervening these were cited by Shelley (2000, 2007), and may be *A. uwharrie*. These counties are as follows: Richmond and Union cos., NC; and Chesterfield, Kershaw, and Georgetown cos., SC. The location from Georgetown Co., SC, is close to the type locality of *A. uwharrie*. The outline of the distribution of *A. uwharrie* in Figure 11 reflects these probable locations.

Etymology. The specific name is a noun in apposition, and derived from the northernmost localities of *A. uwharrie* in the Uwharrie Mountains, North Carolina. The Uwharrie Mountains are inselbergs formed by erosion of ancient terrains and are a rich repository of unusual and rare biological, geological and archaeological heritage (Lewis 2023).

Apheloria virginiensis (Drury, 1770)

Vernacular name: "The Virginia cherry millipede"
Figs 7, 16

Julus virginiensis Drury, 1770: 1.
Apheloria tigana Chamberlin, 1939: 11. **New synonymy**.
Apheloria virginia Chamberlin, 1939: 12. Synonymized by Hoffman, 1999: 306.
Apheloria waccamana Chamberlin, 1940: 284. Synonymized by Shelley, 1978: 63.
Detailed taxonomic history in Appendix 1.

Material examined: Type specimens—type material lost (BMNH?) from Virginia, Dinwiddie County (Coll: J. Greenway), no other collection information provided. ♂ Neotype (FSCA), 1 ♀, 2 ♂ paratypes (FSCA), 1 ♂ paratype (USNM), 1 ♀ paratype (VMNH) from Virginia, Dinwiddie County, McKenney, VA-40, 1.3 km west VA-644 (36.993611°N, -77.739444°W), 8 July 2016 (Colls: R. Shelley, G. Phillips) (*non vidi*). Non type material examined in Appendix 2. Material examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

Diagnosis: *Apheloria virginiensis* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites with three yellow spots and yellow legs (Fig. 16A). ♂ **Gonopods**. Gonopodal acropodite circular but with elbow (Fig. 7A, elb)—not uniformly circular as in *A. polychroma* (Fig. 8A). Not smoothly oval-shaped, 0-shaped, as in *Rudiloria*, nor D-shaped as in *Sigmoria*. Acropodite narrow, about one-half width of tibia on leg pair 9; of uniform width throughout. Acropodite tapered to L-shaped acuminate apex and abruptly twisted (Fig. 7B)—not gradually tapered to curved J-shaped apex as in *A. polychroma* (Fig. 8B). Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a long, scythe-like prefemoral process (Fig. 7, pfp)—not short, scythe-like as in *A. polychroma* (Fig. 8B, pfp). With distinct bend tubercle at prefemur-acropodite junction (Fig. 7B, bt), not with acute angle at junction as in *A. polychroma*, *A. uwharrie* (Figs 8B, 9B).

Note about coloration. A millipede with two or three yellow spots and circular acropodites occurring in the coastal plain and piedmont of North Carolina, excepting the Uwharrie Mountains, unequivocally diagnoses *A. virginiensis* from all other species. However, there are at least five distinct color morphs of the species. Because color varies intraspecifically, caution should be exercised with using it as a diagnostic character for identification of this species.

Variation. There are five color morphs of *A. virginiensis* with a continuum of coloration between them (in order of decreasing frequency): (1) two-spotted, with yellow paranotal spots, and yellow legs (Fig. 16B); (2) three-spotted, with yellow paranotal, metatergal and collum spots, and yellow legs (Fig. 16A); (3) three-spotted, with pink paranotal spots, yellow metatergal and collum spots, and yellow legs (Fig. 16D); (4) two-spotted, with orange paranotal spots, and orange legs; (5) three-spotted, with pink paranotal, metatergal and collum spots, and pink legs (Fig. 16C). The two-spotted morphs often have faint metatergal spots on posterior rings 15 or 17–19. Morph 3 often have pink paranotal spots connected by a faint and thin pink stripe.

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 10) BL = 26.73–58.86 (47.41/8.96). CW = 5.02–8.30 (7.11/0.87). IW = 3.73–4.96 (4.57/0.36). ISW = 1.08–1.52 (1.33/0.13). B10W = 6.77–10.93 (9.68/1.21). ♀ (n = 7) BL = 33.02–51.56 (44.54/7.24). CW = 6.41–7.38 (6.97/0.33). IW = 4.25–5.21 (4.77/0.31). ISW = 1.24–1.64 (1.43/0.15). B10W = 8.42–10.21 (9.39/0.73).

Ecology. *Apheloria virginiensis* individuals were typically encountered in mesic habitats such as broadleaf deciduous forests. They were also found in mixed forests, and in sandy soils. Syntopic tree species recorded with *A. virginiensis* included pine, birch, beech, maple, oak, sweet gum, walnut, oak, magnolia, hickory, rhododendron, tulip poplar, and cherry. Individuals were normally found beneath decomposing leaves and logs, and occasionally walking atop leaf litter or on trails at night. They were often encountered beside streams and low sandy woods.

FIGURE 16. *Apheloria virginiensis* (Drury, 1770), color morphs. **A**: Three-spotted, with yellow paranotal, metatergal and collum spots, and yellow legs; **B**: Two-spotted, with yellow paranotal spots, and yellow legs; **C**: Three-spotted, with pink paranotal, metatergal and collum spots, and pink legs; **D**: Three-spotted, with pink paranotal spots, yellow metatergal and collum spots, and yellow legs.

Apheloria polychroma and *A. corrugata* are well-known mimics with sympatric xystodesmid species, such as *Brachoria*, *Rudiloria*, and *Appalachioria*, but *A. virginiensis* is not well known to mimic others. Due to similarity in color and overlap in distribution, *A. virginiensis* may be confused in the field with *A. corrugata* and *A. whiteheadi* and the following syntopic taxa of its family: *Sigmoria latior* (Brölemann, 1900) and *Pleuroloma flavipes* Rafinesque, 1820. The latter two species share with *A. virginiensis* a two-spotted yellow coloration. This resemblance is likely a result of Müllerian mimicry, however similarity may be due to another convergent evolution. *Apheloria virginiensis* can be distinguished from other species of *Apheloria* by its diagnosis, and from *Sigmoria* and *Pleuroloma* species by gonopod morphology, specifically by the absence of a cingulum, or a mid-length transverse groove on the acropodite, and the presence of a circular acropodite (Fig. 7A).

Distribution. Known primarily from the coastal plain and piedmont of North Carolina (Fig. 11). *Apheloria virginiensis* is commonly encountered in parks and natural areas in the Research Triangle of North Carolina, such as William B. Umstead State Park. *Apheloria virginiensis* also occurs in the north of its distribution in the coastal plain, piedmont, and Blue Ridge Mountains of Virginia. The westernmost localities are Wilkes County, North Carolina, and the Blue Ridge Mountains in Floyd County, Virginia. In the piedmont of Virginia, in Prince Edward County, *A. virginiensis* occurs on the campus of Hampden-Sydney College, but 10 km northeast is replaced by *A. corrugata* in Farmville. Material provided to the first author by W. Shear collected from these two locales have confirmed this allopatry and northernmost limit of *A. virginiensis* at Hampden-Sydney College.

***Apheloria whiteheadi* (Shelley, 1986)**
Vernacular name: "The Laurel Creek millipede"
Figs 17, 18

Sigmoria (Sigiria) whiteheadi Shelley, 1986: 102.
Detailed taxonomic history in Appendix 1.

Material examined: Type specimens—♂ holotype (VMNH), 1 ♂, 2 ♀ paratypes (VMNH) from Virginia, Patrick County, along Laurel Creek on Blue Ridge Parkway at mile 174.3, 20 May 1983, 16:00 (Colls: R. Hoffman). (*vidi*). (1 paratype collected by R. Hoffman from same locality on 23 June 1984.) Non type material examined in Appendix 2. Material examined are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

Diagnosis: *Apheloria whiteheadi* is distinct from other apheloriine species based on the following combination of characters: **Color**. Tergites with yellow stripes and legs (Fig. 17). ♂ **Gonopods**. Gonopodal acropodite ρ-shaped (Fig. 18A)—not uniformly circular as in other *Apheloria* species nor smoothly oval-shaped as in *Rudiloria*. Acropodite apex flange-like and abruptly twisted (Fig. 18B)—not of uniform width throughout as in other *Apheloria* species. Acropodite shaft without cingulum nor preapical teeth nor projections as in *Appalachioria*, *Brachoria*. Prefemur with a short, blunt prefemoral process located marginally (Fig. 18B, pfp)—not long, scythe-like as in other *Apheloria* species nor located medially (Figs 4B, 7B, 8B, 9B, 13B, pfp). Acropodite not bent 90° posteroventrally at prefemur (Fig. 17B), prostatic groove generally straight from cannula to acropodite base, without bend tubercle nor acute angle on corner of bend (Figs 4B, 7B, 13B, bt).

Note about coloration: The anterior and posterior metatergal stripes of the collum meet at the paranota and appear as a continuous yellow ring around the collum's periphery.

Variation. There is a single color morph of *A. whiteheadi*: striped, with yellow metatergal—paranotal stripes, anterior collum stripe, and legs (Fig. 17).

There is typical sexual size dimorphism between males and females, where females are larger, and negligible variation of measurements within individuals of the same sex. Somatic measurements: ♂ (n = 2) BL = 40.53–40.78 (40.66/0.18). CW = 5.54–5.59 (5.57/0.04). IW = 3.65–3.77 (3.71/0.08). ISW = 1.01–1.05 (1.03/0.03). B10W = 6.89–6.91 (6.90/0.01). ♀ (n = 10) BL = 31.42–45.96 (38.71/5.32). CW = 5.59–6.59 (5.89/0.30). IW = 3.89–4.48 (4.17/0.18). ISW = 1.06–1.22 (1.13/0.06). B10W = 7.09–8.39 (7.59/0.36).

Ecology. *Apheloria whiteheadi* individuals were typically encountered in rhododendron cove forests (Means and Marek, 2017). More seldom were they found in montane mixed oak forest (Means *et al.* 2021c). Syntopic tree species recorded with *A. whiteheadi* included oak, maple, tulip poplar, witch hazel, pine, beech, paper birch, and sweet gum.

FIGURE 17. *Apheloria whiteheadi* (Shelley, 1986) has a single color morph with yellow stripes and legs.

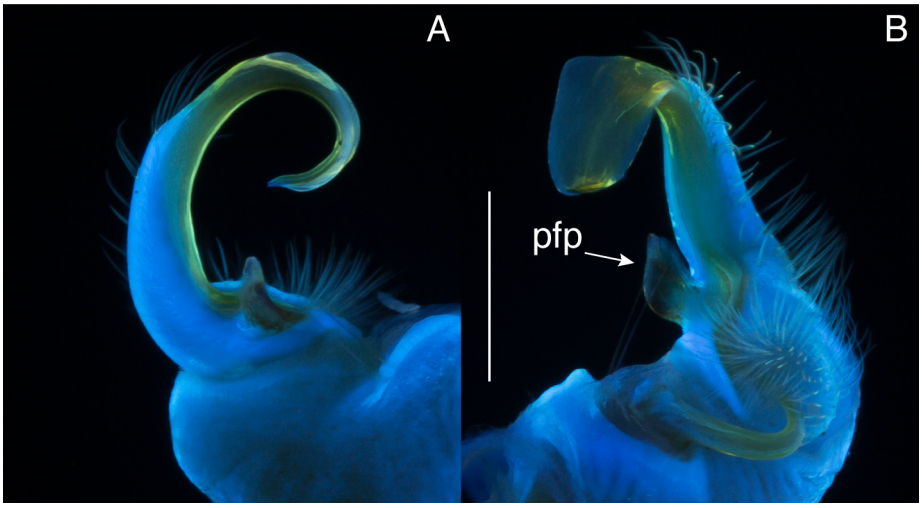

FIGURE 18. *Apheloria whiteheadi* (Shelley, 1986), male gonopods (specimen # MPE00541). **A**: Anterior view; **B**: Medial view. pfp: prefemoral process.

Due to potential mimicry in color and overlap in distribution, *A. whiteheadi* may be confused in the field with *A. corrugata*, *A. virginiensis*, and *P. flavipes*. *Apheloria whiteheadi* can be distinguished from these taxa by its distinctive gonopod morphology, specifically by its ρ-shaped acropodite (Fig. 18A), which is not uniformly circular as in other *Apheloria* species, nor sublinear in shape, with an acicular prefemoral process as in *P. flavipes*. *Pleuroloma flavipes* also possesses a distinctive claw-like bifurcated acropodite composed of a tibial process and a solenomere (Shelley, 1980).

Distribution. *Apheloria whiteheadi* has the smallest distributional area of the genus, and is known from Floyd and Patrick counties in Virginia (Fig. 11). The species is listed as a threatened species in Virginia and is afforded protection by state law.

Removal from *Apheloria*: *Fontaria luminosa* Kenyon, 1893

Pleuroloma flavipes Rafinesque, 1820

Pleuroloma flavipes Rafinesque, 1820: 8.
Fontaria luminosa Kenyon, 1893: 16. **New synonymy**.
Detailed taxonomic history in Appendix 1.

Remarks. The status of *Fontaria luminosa* Kenyon, 1893 has been uncertain for some time. See the following articles for a discussion of the matter: Hoffman (1999), Shelley & Whitehead (1986), Shelley & McAllister (2007), and Marek *et al.* (2014). It was described as a luminous or phosphorescent member of the genus *Fontaria* from Omaha, Nebraska (Bruner 1891, Kenyon 1893). There are other bioluminescent family members: the 11 species of the genus *Motyxia* in California (Marek & Moore 2015). However, Kenyon's and Bruner's description of the shape of its photic organs as round and dorsally situated do not correspond with *Motyxia* nor any bioluminescent millipede known. The entire exoskeleton is bioluminescent in these millipedes. The type specimens of Kenyon's are lost, but Shelley did find material in the USNM that is labeled "Fontaria luminosa (Type?)". Although this material is labeled from Omaha, which is the type locality mentioned by Kenyon, the single male specimen's gonopods were missing (Shelley & Whitehead 1986). Despite searching the Omaha area, Shelley and Hoffman were unable to find any millipedes of the genus *Apheloria*. *Pleuroloma flavipes* is known to occur in the Omaha area and is commonly encountered in eastern Nebraska (Shelley 1980). For more than 130 years since its discovery, the only material of the family found in the area was that of *P. flavipes*. Based on this information, and to bring order to the classification, we here synonymize *F. luminosa* with *P. flavipes*. In the unlikely event there is a bioluminescent *Apheloria* from the region, then *F. luminosa* can be revived, but for the present time and based on much collections of *P. flavipes* in the area, the synonymy seems justifiable.

The description of the bioluminescence (Bruner 1891) matches that of the glowworm beetle genus *Phengodes* (Phengodidae), whose adult females are larviform and predaceous on millipedes, and are sometimes themselves confused for millipedes (Ferreira *et al.* 2024). It may be that Bruner observed *Phengodes* females glowing and collected their millipede prey, thereby convincing himself that the millipedes were producing the bioluminescence.

Key to *Apheloria* species, based on adult males

1a. Gonopod acropodite ρ-shaped (Fig. 18A); prefemur with a short, blunt prefemoral process located marginally (Fig. 18B, pfp) . . . . . ***A. whiteheadi***

1b. Gonopod acropodite circular, O-shaped (Figs 4A, 7A, 8A, 9A, 13A); prefemur with a long, scythe-like prefemoral process (Figs 4A, 7A, 8A, 9A, 13A) pfp) **2**

2a. With distinct bend tubercle at prefemur-acropodite junction (Fig. 4B, 7B, 13B, bt) **3**

2b. With acute angle at prefemur-acropodite junction (Fig. 8B, 9B), lacking a distinct bend tubercle at junction **5**

3a. Gonopod acropodite circular but with elbow (Fig. 7A, elb) . . . . . ***A. virginiensis***

3b. Gonopod acropodite smoothly circular, O-shaped (Figs 4A, 13A), lacking elbow **4**

4a. Base of gonopod acropodite with a triangular tubercle posteriorly (Fig. 4B, bt); prefemoral process shorter and broader basally . . . . . ***A. corrugata***

4b. Base of gonopod acropodite with small, indistinct rounded tubercle posteriorly (Fig. 13B, bt); prefemoral process longer and of uniform width basally . . . . . ***A. montana***

5a. Acropodite gradually tapered to curved acuminate, J-shaped apex (Fig. 8B); prefemoral process short . . . . . ***A. polychroma***

5b. Acropodite tapered to L-shaped acuminate apex and abruptly twisted (Fig.9B); prefemoral process long ***A. uwharrie* sp. nov.**

Discussion

We use molecular phylogenetics in combination with an analysis of morphology to provide a revision of the millipede genus *Apheloria*. We find that the genus includes six species: *Apheloria corrugata* (Wood, 1864); *Apheloria montana* (Bollman, 1887); *Apheloria polychroma* Marek, Means & Hennen, 2018; *Apheloria uwharrie* **sp. nov.**; *Apheloria virginiensis* (Drury, 1770); and *Apheloria whiteheadi* (Shelley, 1986). Despite these millipedes being commonly seen in forests of eastern North America, remarkably we named a new species: *A. uwharrie* **sp. nov.**, from Myrtle Beach, a popular resort city in South Carolina. This study was successful by way of previous work on the genus by R. L. Hoffman who helped conceptualize *A. uwharrie* and *A. polychroma*, and by R. Shelley who synonymized *A. tigana* and mapped the genus in North America. Both authors retraced the meandering taxonomic history of *Apheloria*, synonymized several names of R. V. Chamberlin and others and did much to clarify taxonomic confusion that helped make the present work come to fruition.

Our molecular phylogenetic analysis in combination with an analysis of the interspecific variation in gonopod morphology and geographical distribution largely achieved the results that we present here. We found that *Apheloria* is a distinctive taxon with high statistical support as a monophyletic group and possesses a unique circular acropodite. *Apheloria whiteheadi* does not have circular acropodites like the other species, and its gonopods appear more similar to those of the genus *Sigmoria*. However, *A. whiteheadi* individuals do have a similar coloration to others in the genus and are black with yellow stripes, and importantly, the species is placed as a sister to a clade composed of *A. virginiensis*, *A. polychroma*, and *A. montana* based on genetic data. The *A. whiteheadi* clade is subtended by the longest branch in the phylogeny, thereby supporting its evolutionarily divergent nature. Based on the placement of *A. whiteheadi* nested within the phylogeny, its *Sigmoria*-like gonopod shape likely originated after the smoothly oval-shaped and circular-shaped acropodites of *Rudiloria* and *Apheloria*. Why are the circular-shaped acropodites of *A. corrugata*, *A. polychroma*, *A. uwharrie*, and *A. virginiensis* so similar to each another, but so divergent from *A. whiteheadi*? Amongst studies that have estimated molecular phylogenies, both conspicuous and inconspicuous divergence of gonopods between closely related species of millipedes has been shown. Cases of conspicuous divergence include *Brachoria* (Marek, 2009), *Oxidus* (Nguyen *et al.* 2017), and the *Nannaria wilsoni* species group (Hennen *et al.* 2022); and inconspicuous cases include *Anadenobolus excisus* species group (Bond *et al.* 2003), *Riukiaria* (Tanabe & Sota 2014), and the *Nannaria minor* species group (Means *et al.* 2021a). The evolutionary processes generating morphological differences in gonopods include Eberhard's (1985) rapid divergence as a result of sexual selection by female choice, and others discussed by Bond *et al.* (2003) and Tadler (1996). The origin of *A. whiteheadi* may have occurred more recently and its gonopods may have differentiated under rapid divergence, and

the speciation of the others may have ensued over a longer period of time with gradualistic change in male gonopods. *Apheloria corrugata*, *A. polychroma*, *A. uwharrie*, and *A. virginiensis* are mostly parapatric in their distributions, but *A. whiteheadi* broadly overlaps with *A. virginiensis* and *A. corrugata*. Here, rapid divergence in sympatry may have occurred, or another type of species evolution. Based on examination of the cyphopods of a female *A. whiteheadi* (MPE00479) versus *A. corrugata* (MPE03126), the valves of the former appear much more widely separated and appear to correspond in width to its male's wider acropodite; similarly, the valves of the latter appear narrow and correspond in width to its male's narrow acropodite. This correspondence has been shown in other members of the order Polydesmida (Tanabe & Sota 2008, Sloan *et al.* 2023) and Julida (Tadler 1996).

Apheloria corrugata, as opposed to the other species, is widely distributed to the north and west in historically glaciated and presently non-glaciated regions of eastern North America (Fig. 11). One of its clades contains individuals from northern sites in New York and Pennsylvania and exhibits relatively low genetic divergence (Fig. 1, clade with 11 asterisks). This low genetic diversity is consistent with rapid founding colonization(s) into a newly deglaciated area. Perhaps *A. corrugata* became adapted to colder conditions during glacial maxima, and with the retreat of the glaciers, was in a position to move into territory now unoccupied by any other xystodesmid. This pattern is also observed in the spirobolid millipede genus *Narceus* and other taxa such as amphibians (Walker et al 2009, Zamudio & Savage 2003, Lee-Yaw *et al.* 2007). The distributions of *A. uwharrie*, *A. montana*, and *A. whiteheadi* are small in area, and the latter has among the smallest of the family Xystodesmidae and comprises a short-range endemic defined as having a range of less than 10,000 km^2 (Harvey *et al.* 2011, Harvey 2002, Means and Marek 2017). Conserving these and other species with highly localized, disjunct, or restricted geographic ranges is vital to maintaining the diversity and resilience of ecosystems that we and other forms of life depend on.

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Addendum

Shortly after the acceptance of this manuscript, we collected and analyzed additional material of *Apheloria* from North Carolina in Ashe, Davidson, Stanly, Surry and Wilkes counties. These counties correspond to a region where several species distributions meet and had previously been unsampled for fresh DNA-grade material. We found that from DNA sequencing of the cytochrome c oxidase subunit 1 mitochondrial barcoding region (COX1) and subsequent molecular phylogenetic analysis (using the same techniques explained in the 'Material and methods'), specimens from Ashe Co. reside within the clade composed of *A. corrugata* and those from Davidson, Stanly, Surry, and Wilkes cos. with *A. virginiensis*. The map in figure 11 has been updated to reflect these new data, and an updated phylogeny with these specimens are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

New material:

Apheloria corrugata

North Carolina, Ashe Co., Johnson Hollow Rd, road bank with UV, Coll: C. Tingley, 17 May 2025, MPE05618, 36.44380°N, -81.45889°W

Apheloria virginiensis

North Carolina, Wilkes Co., near Moravian Falls, Coll: C. Tingley, 18 May 2025, MPE05616, 36.07613°N, -81.15071°W • Surry Co., Elkin, Coll: Joe Mickey, 27 April 2025, MPE05617, 36.26048°N, -80.86074°W • Stanly

Co., Richfield Park, disturbed woodland, Coll: C. Tingley, 23 May 2025, MPE05619, 35.4761°N, -80.2587°W • Davidson Co., Boones Cave Rd, on leaf litter, with UV, Coll: C. Tingley, 23 May 2025, MPE05620, 35.7955°N, -80.4641°W

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Appendix 1. Species catalog of the millipede genus *Apheloria* Chamberlin, 1921

Family Xystodesmidae Cook, 1895
Subfamily Rhysodesminae Brolemann, 1916
Tribe Apheloriini Hoffman, 1980

Genus *Apheloria* Chamberlin, 1921
6 species

Apheloria Chamberlin, 1921, 232. Type species: *Fontaria montana* Bollman, 1887, by original designation.
Leptocircus Attems, 1931, Zoologica, 30(79): 67. Type species: *Leptocircus inexpectatus* Attems, 1931, by original designation. Preoccupied by *Leptocircus* Swainson, 1833 (Lepidoptera).

Apheloria corrugata (Wood, 1864) new status

Fontaria virginiensis (nec Gray, 1832; nec Drury & Westwood 1837; nec Wood, 1865; nec Bollman, 1888) C.L. Koch, 1847, in: Kritische Revision der Insectenfaune Deutschlands, 141. MALE? HT? (ZMB?). "North America".
Polydesmus (Fontaria) corrugatus Wood, 1864, Proceedings of the Academy of Natural Sciences of Philadelphia, 16: 6. MALE ST (USNM). United States: New York, Oneida County.
Fontaria coriacea (nec C.L. Koch, 1847)—sensu Bollman, 1889a, Proceedings of the United States National Museum, 11: 406. See Hoffman (1957) for a discussion of the *nomen dubium*, *Fontaria coriacea* C.L. Koch, 1847.
Fontaria butleriana Bollman, 1889, Proceedings of the United States National Museum, 11: 407. FEMALE HT (USNM). United States: Indiana, Franklin County. **New synonymy.**
Leptocircus inexpectatus Attems, 1931, Zoologica, 30(79): 67, figs. 102-104. MALE HT (NMW). "North America". Synonymized by Hoffman, 1999, Checklist: 307 (295 pdf).
Apheloria inexpectata—Attems, 1938, Das Tierreich, 69: 169, fig. 186.
Apheloria corrugata—Attems, 1938, Das Tierreich, 69: 170.
Apheloria iowa Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 10, fig. 28. MALE HT (USNM). United States: Iowa, Henry County. **New synonymy**.
Apheloria adela Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 10, fig. 34. MALE HT (USNM). United States: New York, Tompkins County. Synonymized with *corrugata* by Hoffman, 1957, Proceedings of the Biological Society of Washington, 70: 186.
Apheloria reducta Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 11, fig. 35. MALE HT (USNM). United States: Arkansas, Lawrence County. **New synonymy**.
Apheloria pinicola Chamberlin, 1947, Proceedings of the Academy of Natural Sciences of Philadelphia, 99: 26, figs. 6, 7. MALE HT (ANSP). United States: Kentucky, Bell County. Synonymized with *montana* by Hoffman, 1999, Checklist: 305 (293 pdf), but clearly *corrugata* based on telopodite morphology and distribution.
Apheloria asburna Chamberlin, 1949, Journal of the Washington Academy of Sciences, 39: 101. MALE HT (USNM). United States: Tennessee, Davidson County. Synonymized with *butleriana* by Hoffman, 1999, Checklist: 307 (295 pdf).
Apheloria coriacea—Hoffman, 1949b, American Museum Novitates 1405: 3, figs. 1-4. Misidentification of the name *Fontaria coriacea* Koch, 1847.
Apheloria corrugata corrugata—Hoffman, 1957, Proceedings of the Biological Society of Washington, 70: 183.
Apheloria corrugata butleriana—Hoffman, 1957, Proceedings of the Biological Society of Washington, 70: 186, footnote.
Apheloria butleriana—Chamberlin & Hoffman, 1958, Bulletin of the United States National Museum, 212: 18.
Apheloria (Apheloria) corrugata corrugata—Kevan, 1983, Canadian Journal of Zoology, 61(12): 2968.
Apheloria virginiensis butleriana—Hoffman, 1999, Checklist: 307 (295 pdf).
Apheloria virginiensis corrugata—Hoffman, 1999, Checklist: 307 (294 pdf).
Apheloria virginiensis iowa—Hoffman, 1999, Checklist: 307 (295 pdf).
Apheloria virginiensis reducta—Hoffman, 1999, Checklist: 307 (295 pdf).
Apheloria "Clade B"—Marek & Bond 2009, Proceedings of the National Academy of Sciences, 106(24): 9755.

Apheloria montana (Bollman, 1887)

Fontaria montana Bollman, 1887a, Proceedings of the United States National Museum, 10: 622. MALE HT (USNM). United States: Tennessee, Cocke County.
Apheloria montana—Chamberlin, 1921, Canadian Entomologist, 53: 232, pl. 9, fig. 2.
Apheloria aspila Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 10, fig. 28. MALE HT (USNM). United States: North Carolina, Jackson County. Synonymized with *tigana* by Hoffman, 1999, Checklist: 306 (294 pdf).

Apheloria unaka Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 11, fig. 33. MALE HT (USNM). United States: Tennessee, Unicoi County. Synonymized with *montana* by Hoffman, 1999, Checklist: 305 (293 pdf).

Apheloria polychroma Marek, Means & Hennen, 2018

Apheloria polychroma Marek, Means & Hennen, 2018, Zootaxa, 4375(3): 416, figs 1-6. MALE HT (FMNH). United States: Virginia, Lee County.
Apheloria roanea Chamberlin, 1947, Proceedings of the Academy of Natural Sciences of Philadelphia, 99: 26, fig. 8. MALE HT (ANSP). United States: Tennessee, Roane County. Synonymized with *montana* by Hoffman, 1999, Checklist: 306 (294 pdf), but clearly *polychroma* based on telopodite morphology, distribution and color, see remark.
Apheloria "flavissima"—Hobson 2010, Powell Mountain Karst Preserve, 50.
Apheloria "Stone"—Marek & Bond 2007, Zootaxa, 1610: 29.
Apheloria "Casteel"—Marek & Bond 2007, Zootaxa, 1610: 29.
Apheloria "Clade A"—Marek & Bond 2009, Proceedings of the National Academy of Sciences, 106 (24): 9755.

Remarks: *Apheloria roanea* was described from Roane County, which falls within the range of *Apheloria polychroma* and is outside the range of *A. montana*. Hoffman synonymized it under *Apheloria montana*, but the original description fits better with *A. polychroma*, potentially making *A. polychroma* a junior synonym. Unfortunately, fresh material from the type locality is not available, and the type and only known specimen of *A. roanea* cannot be located. Additionally the name *Apheloria polychroma* has now been used in a multitude of publications. For taxonomic stability we do not list *A. polychroma* as a junior synonym of *A. roanea*.

Apheloria uwharrie Marek, Means, Hennen & Tingley, new species

Apheloria uwharrie Marek, Means, Hennen & Tingley, 2025. MALE HT (VTEC). United States: South Carolina, Horry County.

Apheloria virginiensis (Drury, 1770)

Julus virginiensis Drury, 1770, Illustrations of natural History, 1: pl. 43, fig. 8. Type material lost. MALE? HT? (BMNH?). United States: "Virginia".
Polydesmus (Fontaria) virginiensis (nec Gray, 1832; nec C.L. Koch, 1847; nec Wood, 1865; nec Bollman, 1888)—Drury & Westwood, 1837, Illustrations of exotic entomology: containing upwards of six hundred and fifty figures and descriptions of foreign insects, interspersed with remarks and reflections on their nature and properties, 1: 96, pl. 43, fig. 8.
Apheloria tigana Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 11, fig. 29. MALE HT (USNM). United States: North Carolina, Wake County. **New synonymy**.
Apheloria virginia Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 12, fig. 30. MALE HT (USNM). United States: Virginia, Pittsylvania County. Synonymized with *virginiensis* by Hoffman, 1999, Checklist: 306 (294 pdf).
Apheloria waccamana Chamberlin, 1940, Entomological News, 51: 284, fig. 3. MALE HT (USNM). United States: North Carolina, Columbus County. Synonymized with *tigana* by Shelley, 1978, Journal of Natural History, 12: 63.
Apheloria virginiensis—Shelley, 1980b, Canadian Journal of Zoology, 58: 131, footnote 6.
Apheloria virginiensis virginiensis—Hoffman, 1999, Checklist: 306 (294 pdf).

Apheloria whiteheadi (Shelley, 1986)

Sigmoria (Sigiria) whiteheadi Shelley, 1986, in: Shelley & Whitehead, Memoirs of the American Entomological Society, 35: 102, figs. 73-76. MALE HT (USNM). United States, Virginia, Patrick County.
Sigmoria whiteheadi—Hoffman, 1999, Checklist: 336 (322 pdf).
Apheloria whiteheadi—Means & Marek, 2017, PeerJ, 5: 21, figs. 2, 3, 6.

Tribe Rhysodesmini Brolemann, 1916

Genus *Pleuroloma* Rafinesque, 1820

4 species

Pleuroloma Rafinesque, 1820, Annals of Nature, p. 8. Type species: *Pleuroloma flavipes* Rafinesque, by monotypy.
Zinaria Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 4. Type species: *Zinaria cala* Chamberlin, 1939, by original designation. Synonymized by Hoffman & Crabill, 1953, Florida Entomologist, 36: 80.

Note: The most recent revision of *Pleuroloma* was accomplished by Shelley, 1980, Canadian Journal of Zoology, 58.

Pleuroloma flavipes Rafinesque, 1820

Pleuroloma flavipes Rafinesque, 1820, Annals of Nature, p. 8.
Polydesmus (Fontaria) virginiensis (nec Gray, 1832; nec Drury & Westwood, 1837; nec C.L. Koch, 1847; nec Bollman, 1888)—sensu Wood, 1865, Transactions of the American Philosophical Society, 13: 221, fig. 49, pl. 3, fig. 8.
Fontaria virginiensis—(nec Drury & Westwood, 1837; nec Gray, 1832; nec C.L. Koch, 1847; nec Wood, 1865)—sensu Bollman, 1888, Entomologica Americana, 4: 3.
Fontaria virginiensis brunnea Bollman, 1887b, American Naturalist, 21: 82. MALE HT (USNM). United States: Minnesota, Hennepin County, Minnesota. Synonymized by Shelley, 1980, Canadian Journal of Zoology, 58: 139.
Polydesmus butlerii McNeill, 1888, Bulletin of the Brookville Society of Natural History, 3: 6, figs. 1-3. Type material lost. United States: Indiana, Franklin County. Synonymized by Shelley, 1980, Canadian Journal of Zoology, 58: 139.
Fontaria virginiensis castanea Bollman, 1893, Bulletin of the United States National Museum, 46: 132.
Fontaria luminosa Kenyon, 1893, Publications of the Nebraska Academy of Sciences, 3: 16. Type material lost. MALE HT (USNM). United States: Nebraska, Douglas County. **New synonymy.**
Fontaria brunnea—Barber, 1915, Proceedings of the Entomological Society of Washington, 17: 122.
Zinaria virginiensis—Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 4.
Zinaria urbana Chamberlin, 1939, Bulletin of the University of Utah, 30(2): 5, pl. 1, fig. 5. MALE HT (USNM). United States: Illinois, Champaign County. Synonymized by Shelley, 1980b, Canadian Journal of Zoology, 58: 139.
Zinaria iowa Chamberlin, 1942, Canadian Entomologist, 74: 16, fig. 3. MALE HT (USNM). United States: Iowa, Story County. Synonymized by Shelley, 1980b, Canadian Journal of Zoology, 58: 139.
Zinaria brunnea—Chamberlin, 1943, Bulletin of the University of Utah, 8(2): 16.
Zinaria butleri—Chamberlin, 1943, Bulletin of the University of Utah, 8(2): 16.
Zinaria mima Chamberlin, 1949, Journal of the Washington Academy of Sciences, 39: 101, fig. 26. MALE HT (USNM). United States: Pennsylvania, Greene County. Synonymized by Shelley, 1980, Canadian Journal of Zoology, 58: 140.
Zinaria rubrilata Hoffman, 1949c, Proceedings of the Biological Society of Washington, 62: 84. MALE HT (USNM). United States: Virginia, Lancaster County. Synonymized by Shelley, 1980, Canadian Journal of Zoology, 58: 140.
Zinnaria butlerii—Causey, 1951, Proceedings of the Arkansas Academy of Science, 4: 81, pl. 1, figs. 1e, 2b; pl. 2, figs. 8g, 11.
Zinaria warreni Causey, 1951, Proceedings of the Arkansas Academy of Science, 4: 83, pl. 1, figs. 1c, 3b, 6; pl. 2, 8c, 10. MALE HT (ANSP). United States: Akansas, Carroll County. Synonymized by Shelley, 1980, Canadian Journal of Zoology, 58: 140.
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APPENDIX 2. Non-type material examined. Detailed materials examined, and other accession numbers, are archived in the Virginia Tech Data Repository at: https://doi.org/10.7294/29829209

Species	State	County	Specimen	Sex	Latitude	Longitude	NCBI
corrugata	Arkansas	Carroll	MPE00001	1M	36.44294	-93.75115	MF953680
corrugata	Arkansas	Carroll	MPE02755	1M	36.43071	-93.75764	PV743395
corrugata	Arkansas	Newton	MPE02738	1M	36.03763	-93.34127	PV743392
corrugata	Arkansas	Polk	MPE01161	1M	34.69389	-94.45556	PV743342
corrugata	Illinois	Union	SPC000014	1M	37.51373	-89.42266	PV743448
corrugata	Illinois	Union	MPE02819	1M	37.49646	-89.35723	PV743396
corrugata	Indiana	Brown	MPE03917	1F	39.15009	-86.23277	PV743427
corrugata	Indiana	Dearborn	SPC000030	1F	38.99427	-85.11749	PV743451
corrugata	Indiana	Franklin	SPC000032	1M	39.41162	-85.02467	PV743452
corrugata	Indiana	Jefferson	SPC000024	1M	38.76079	-85.42864	PV743450
corrugata	Indiana	Jefferson	MPE01756	1M	38.75357	-85.42225	PV743354
corrugata	Indiana	Madison	SPC000997	1M	38.72190	-85.46120	MF953754
corrugata	Indiana	Madison	SPC000998	1M	38.72190	-85.46120	PV743479
corrugata	Indiana	Monroe	SPC000019	1F	39.01363	-86.37594	PV743449
corrugata	Iowa	Henry	MPE03909	1F	40.92887	-91.66942	PV743426
corrugata	Iowa	Henry	MPE03908	1M	40.93238	-91.61317	MN699720
corrugata	Iowa	Henry	MPE03924	1M	40.93238	-91.61317	PV743428
corrugata	Kentucky	Anderson	SPC000615	1F	38.02163	-84.83765	PV743464
corrugata	Kentucky	Bell	SPC000336	1M	36.93663	-83.19538	PV743458
corrugata	Kentucky	Boyd	MPE03126	1F	38.34754	-82.68667	PV743411
corrugata	Kentucky	Carter	MPE03281	1M	38.37819	-83.12827	PV743418
corrugata	Kentucky	Carter	SPC000645	1M	38.33792	-83.05760	PV743467
corrugata	Kentucky	Green	SPC000607	1M	37.27314	-85.49036	PV743462
corrugata	Kentucky	Hart	MPE03246	1M	37.19498	-85.94118	PV743415
corrugata	Kentucky	Jackson	MPE02658	1M	37.46674	-83.91641	PV743391
corrugata	Kentucky	Knott	MPE03251	1M	37.23148	-83.00081	PV743416
corrugata	Kentucky	Letcher	SPC001051	1F	37.08020	-82.77232	PV743481
corrugata	Kentucky	Menifee	MPE03241	1M	38.04554	-83.54946	PV743414
corrugata	Kentucky	Pike	MPE03208	1M	37.46902	-82.54621	PV743413
corrugata	Kentucky	Powell	SPC000631	1F	37.77825	-83.69485	PV743465
corrugata	Kentucky	Powell	SPC000637	1M	37.77415	-83.68987	PV743466
corrugata	Kentucky	Powell	MPE03108	1M	37.77483	-83.68251	PV743409
corrugata	Kentucky	Taylor	SPC000612	1F	37.27890	-85.32960	PV743463
corrugata	Missouri	St. Charles	MPE02751	1F	38.67069	-90.75150	PV743394
corrugata	New York	Tompkins	MPE03059	1M	42.54334	-76.60181	PV743407
corrugata	Ohio	Adams	MPE01768	1M	38.72200	-83.43309	PV743355
corrugata	Ohio	Adams	MPE01983	1M	38.67126	-83.40370	PV743364
corrugata	Ohio	Adams	MPE02049	1M	38.72137	-83.43355	PV743366
corrugata	Ohio	Lawrence	MPE02911	1M	38.62125	-82.63093	PV743399
corrugata	Ohio	Lawrence	MPE02919	1M	38.60641	-82.62890	PV743400
corrugata	Ohio	Lawrence	MPE02924	1M	38.61546	-82.63407	PV743401
corrugata	Ohio	Monroe	MPE04274	1M	39.61510	-80.93657	PV743438
corrugata	Ohio	Scioto	MPE01981	1M	38.74173	-83.20233	PV743363

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APPENDIX 2. (Continued)

Species	State	County	Specimen	Sex	Latitude	Longitude	NCBI
corrugata	Ohio	Washington	MPE03000	1M	39.42118	-81.36102	PV743404
corrugata	Ohio	Washington	MPE03005	1M	39.50929	-81.25088	PV743405
corrugata	Ohio	Washington	MPE01980	1F	39.50880	-81.25037	PV743362
corrugata	Pennsylvania	Fayette	MPE01876	1F	39.85722	-79.67741	PV743358
corrugata	Pennsylvania	Harrisburg	MPE00722	1M	40.27319	-76.88670	PV743332
corrugata	Pennsylvania	Mont Alto	MPE00721	1M	39.84426	-77.55832	PV743331
corrugata	Tennessee	Dickson	MPE02750	1F	36.10172	-87.28539	PV743393
corrugata	Tennessee	Wilson	SPC000478	1M	36.07506	-86.31454	PV743459
corrugata	Virginia	Albemarle	MPE01134	1F	37.99830	-78.36764	PV743341
corrugata	Virginia	Albemarle	MPE02266	1M	37.99528	-78.47833	PV743372
corrugata	Virginia	Alleghany	MPE01825	1M	37.85263	-79.85123	PV743356
corrugata	Virginia	Amherst	MPE02896	1M	37.72692	-79.19819	PV743398
corrugata	Virginia	Appomattox	MPE02470	1M	37.39700	-78.64200	PV743380
corrugata	Virginia	Augusta	MPE02024	1M	38.30893	-79.36030	PV743365
corrugata	Virginia	Bath	MPE02461	1M	37.88992	-79.81125	PV743378
corrugata	Virginia	Bedford	MPE00164	1M	37.45819	-79.62956	PV743318
corrugata	Virginia	Bedford	MPE00157	1M	37.45819	-79.62956	PV743317
corrugata	Virginia	Bland	MPE01098	1M	37.11781	-81.13641	PV743340
corrugata	Virginia	Buckingham	MPE01165	1M	37.58410	-78.56460	PV743343
corrugata	Virginia	Carroll	MPE00094	1M	36.77610	-80.54463	PV743316
corrugata	Virginia	Carroll	MPE00214	1F	36.77610	-80.54463	PV743320
corrugata	Virginia	Clarke	MPE01882	1F	39.07173	-77.91200	PV743359
corrugata	Virginia	Craig	MPE04183	1M	37.37952	-80.25034	PV743433
corrugata	Virginia	Craig	MPE00791	1M	37.40352	-80.34148	PV743336
corrugata	Virginia	Craig	MPE04208	1F	37.58330	-80.16049	PV743336
corrugata	Virginia	Fairfax	MPE02439	1M	38.76664	-77.41044	PV743375
corrugata	Virginia	Floyd	MPE02539	1M	36.75056	-80.40500	PV743385
corrugata	Virginia	Floyd	MPE00235	1F	36.97893	-80.51470	PV743321
corrugata	Virginia	Greene	MPE02594	1M	38.38023	-78.50368	PV743387
corrugata	Virginia	James City	MPE01166	1F	37.26294	-76.64777	PV743344
corrugata	Virginia	Montgomery	MPE02347	1F	37.18912	-80.31958	PV743373
corrugata	Virginia	Montgomery	MPE00356	1M	37.27644	-80.48372	PV743326
corrugata	Virginia	Montgomery	MPE04198	1M	37.23254	-80.27317	PV743434
corrugata	Virginia	Montgomery	MPE01930	1M	37.17987	-80.40112	PV743360
corrugata	Virginia	Montgomery	MPE00246	1M	36.96624	-80.41797	PV743322
corrugata	Virginia	Montgomery	MPE02161	1F	37.33885	-80.32642	PV743368
corrugata	Virginia	Nelson	MPE02379	1M	37.83889	-79.02139	PV743374
corrugata	Virginia	Patrick	MPE01537	1M	36.68667	-80.44151	PV743349
corrugata	Virginia	Patrick	MPE00355	1M	36.80736	-80.33114	PV743325
corrugata	Virginia	Powhatan	MPE02449	1M	37.68940	-77.91620	PV743383
corrugata	Virginia	Powhatan	MPE02440	1F	37.69060	-77.91770	PV743376
corrugata	Virginia	Pr. Edward	MPE02490	1M	37.28470	-78.38060	PV743376
corrugata	Virginia	Pulaski	MPE03680	1M	37.05639	-80.63194	PV743422

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APPENDIX 2. (Continued)

Species	State	County	Specimen	Sex	Latitude	Longitude	NCBI
corrugata	Virginia	Pulaski	MPE00400	1M	37.07308	-80.87308	PV743327
corrugata	Virginia	Pulaski	MPE00763	1M	37.03324	-80.80874	PV743334
corrugata	Virginia	Pulaski	MPE00742	1M	37.02528	-80.77522	PV743334
corrugata	Virginia	Pulaski	MPE00745	1F	37.02528	-80.77522	MF953686
corrugata	Virginia	Roanoke	MPE02648	1M	37.23214	-80.08678	PV743389
corrugata	Virginia	Roanoke	MPE00257	1F	37.23098	-79.95028	PV743323
corrugata	Virginia	Roanoke	MPE00774	1M	37.32728	-80.24266	PV743335
corrugata	Virginia	Roanoke	MPE02496	1M	37.13694	-80.11083	PV743382
corrugata	Virginia	Rockbridge	MPE03490	1M	37.90211	-79.58829	PV743420
corrugata	Virginia	Rockbridge	MPE02052	1M	37.61859	-79.47098	PV743367
corrugata	Virginia	Rockingham	MPE03076	1F	38.59483	-78.67343	PV743408
corrugata	Virginia	Rockingham	MPE03484	1M	37.79563	-79.44273	PV743419
corrugata	Virginia	Russell	SPC000169	1M	36.86711	-81.94638	PV743454
corrugata	Virginia	Shenandoah	MPE02469	1M	38.92400	-78.32800	PV743379
corrugata	Virginia	Smyth	MPE00181	1F	36.91126	-81.53172	PV743319
corrugata	Virginia	Suffolk City	MPE01172	1F	36.73444	-76.55056	PV743345
corrugata	Virginia	Tazewell	MPE00269	1M	37.01488	-81.41010	PV743324
corrugata	Virginia	Warren	MPE02584	1M	38.79581	-78.24282	PV743386
corrugata	Virginia	Washington	MPE00073	1M	36.68427	-81.64814	PV743315
corrugata	Virginia	Washington	MPE01643	1F	36.94777	-81.82424	PV743352
corrugata	Virginia	Wise	MPE03993	1M	36.91761	-82.44585	MN699719
corrugata	Virginia	Wythe	MPE04235	1M	36.78142	-81.10834	PV743437
corrugata	Virginia	Wythe	MPE00656	1M	37.01604	-81.24366	PV743330
corrugata	Virginia	York	SPC000001	1F	37.29398	-76.64622	PV743446
corrugata	Virginia	York	SPC000005	1M	37.29398	-76.64622	PV743447
corrugata	West Virginia	Boone	MPE03265	1M	38.18020	-81.83849	PV743417
corrugata	West Virginia	Fayette	SPC000732	1F	38.00447	-80.95201	PV743472
corrugata	West Virginia	Greenbrier	MPE02840	1M	37.92010	-80.26360	PV743397
corrugata	West Virginia	Greenbrier	SPC000677	1M	37.91796	-80.25960	PV743468
corrugata	West Virginia	Greenbrier	SPC000682	1M	37.92067	-80.26808	PV743469
corrugata	West Virginia	Hampshire	MPE03890	1M	39.18102	-78.67297	PV743424
corrugata	West Virginia	Hampshire	MPE03897	1F	39.18102	-78.67297	PV743425
corrugata	West Virginia	Mercer	SPC000738	1M	37.50820	-81.13700	PV743473
corrugata	West Virginia	Monroe	MPE02510	1M	37.47497	-80.56732	PV743384
corrugata	West Virginia	Nicholas	SPC000716	1M	38.27285	-80.52504	PV743471
corrugata	West Virginia	Pendleton	MPE01858	1M	38.59485	-79.19827	PV743357
corrugata	West Virginia	Pocahontas	SPC000702	1M	38.11191	-80.17836	PV743470
corrugata	West Virginia	Raleigh	MPE01752	1F	37.83382	-81.07353	PV743353
corrugata	West Virginia	Randolph	MPE00590	1M	38.65502	-80.07136	PV743329
corrugata	West Virginia	Wayne	MPE03124	1M	38.30473	-82.35124	PV743410
montana	North Carolina	Buncombe	MPE01046	1M	35.66981	-82.36285	PV743339
montana	North Carolina	Madison	SPC000809	1M	35.88969	-82.83270	PV743475
montana	North Carolina	McDowell	SPC000134	1M	35.73446	-82.08378	KR135989

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APPENDIX 2. (Continued)

Species	State	County	Specimen	Sex	Latitude	Longitude	NCBI
montana	North Carolina	Mitchell	MPE04396	1M	35.85610	-82.08760	PV743439
montana	Tennessee	Greene	MPE04166	1M	35.96093	-82.87535	PV743432
montana	Tennessee	Unicoi	MPE04110	1M	36.13898	-82.34686	PV743430
montana	Tennessee	Unicoi	MPE04130	1F	36.04829	-82.56155	PV743431
montana	Tennessee	Unicoi	MPE02931	1M	36.04056	-82.52833	PV743402
montana	Tennessee	Washington	MPE04227	1F	36.27708	-82.34615	PV743436
polychroma	Georgia	Murray	SPC000057	1M	34.75646	-84.70615	PV743453
polychroma	Kentucky	Bell	SPC000583	1M	36.69112	-83.82113	PV743461
polychroma	Kentucky	Harlan	SPC000580	1M	36.75100	-83.20240	PV743460
polychroma	Kentucky	Harlan	SPC000793	1M	36.73285	-83.22161	PV743474
polychroma	Kentucky	Harlan	SPC000826	1M	36.73897	-83.21970	PV743476
polychroma	Kentucky	Harlan	SPC000578	1M	36.75603	-83.19588	MF953743
polychroma	Kentucky	Harlan	SPC001003	1M	36.76070	-83.14000	PV743480
polychroma	Kentucky	Pulaski	MPE03202	1M	36.91564	-84.51827	PV743412
polychroma	Tennessee	Campbell	MPE03016	1M	36.22307	-84.09306	PV743406
polychroma	Tennessee	Hawkins	SPC000215	1F	36.40205	-83.02312	PV743455
polychroma	Tennessee	Jefferson	MPE02172	1F	36.08005	-83.68674	PV743369
polychroma	Tennessee	Knox	MPE02173	1M	36.10437	-83.76337	PV743370
polychroma	Tennessee	Morgan	MPE02654	1F	36.13206	-84.49780	PV743390
polychroma	Tennessee	Putnam	MPE01400	1M	36.13143	-85.44386	PV743347
polychroma	Tennessee	Sullivan	MPE04045	1F	36.57037	-82.23569	PV743429
polychroma	Virginia	Lee	SPC000847	1M	36.78492	-82.98290	PV743477
polychroma	Virginia	Washington	SPC000284	1M	36.72317	-82.29852	PV743456
uwharrie	North Carolina	Montgomery	MPE05401	1M	35.31080	-80.04330	PV743442
uwharrie	North Carolina	Randolph	MPE05400	1M	35.63070	-79.90640	PV743441
uwharrie	North Carolina	Randolph	MPE05402	1M	35.63070	-79.90640	PV743443
uwharrie	North Carolina	Randolph	MPE05403	1M	35.63070	-79.90640	PV743444
uwharrie	North Carolina	Stanly	MPE01977	1M	35.37167	-80.09611	PV743361
uwharrie	North Carolina	Stanly	MPE01978	1F	35.37167	-80.09611	NA
uwharrie	North Carolina	Stanly	MPE01979	1F	35.37167	-80.09611	NA
uwharrie	South Carolina	Horry	MPE03855	1M	33.71170	-78.88257	MN699718
uwharrie	South Carolina	Horry	MPE03856	1M	33.71170	-78.88257	PV743423
uwharrie	South Carolina	Horry	MPE03857	1F	33.71170	-78.88257	NA
uwharrie	South Carolina	Horry	MPE03858	1F	33.71170	-78.88257	NA
uwharrie	South Carolina	Horry	MPE03859	1F	33.71170	-78.88257	NA
virginiensis	North Carolina	Craven	SPC000317	1M	35.29167	-77.13333	PV743457
virginiensis	North Carolina	Halifax	MPE03532	1M	36.24786	-77.88570	PV743421
virginiensis	North Carolina	Hanover	MPE05404	1M	34.04880	-77.91370	PV743445
virginiensis	North Carolina	Harnett	SPC000976	1M	35.47520	-78.93250	PV743478
virginiensis	North Carolina	Nash	MPE02228	1F	35.97488	-77.90127	PV743371
virginiensis	North Carolina	Orange	MPE01571	1M	36.07305	-79.14401	PV743350
virginiensis	North Carolina	Orange	MPE01589	1M	35.98564	-79.02380	PV743351
virginiensis	North Carolina	Surry	MPE00911	1F	36.26733	-80.49055	PV743337

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APPENDIX 2. (Continued)

Species	State	County	Specimen	Sex	Latitude	Longitude	NCBI
virginiensis	North Carolina	Surry	MPE00913	1F	36.26733	-80.49055	PV743338
virginiensis	North Carolina	Wake	MPE01507	1M	35.84026	-78.62356	PV743348
virginiensis	North Carolina	Wake	SPC000311	1M	35.84460	-78.75750	MF953721
virginiensis	Virginia	Floyd	MPE02499	1M	36.95111	-80.17472	PV743383
virginiensis	Virginia	Pittsylvania	MPE02984	1M	36.55000	-79.35000	PV743403
virginiensis	Virginia	Pr. Edward	MPE01187	1M	37.23694	-78.45250	PV743346
whiteheadi	Virginia	Floyd	MPE00451	1M	36.77245	-80.40544	PV743328
whiteheadi	Virginia	Floyd	MPE02617	1F	36.78638	-80.39944	PV743388
whiteheadi	Virginia	Floyd	MPE00712	1M	36.77106	-80.40723	MF953685
whiteheadi	Virginia	Patrick	MPE05046	1M	36.76620	-80.18270	PV743440
whiteheadi	Virginia	Patrick	MOL00054	2M	36.64830	-80.14970	NA