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Source: Insect Systematics and Diversity, 5(2) : 1-26

Published By: Entomological Society of America

URL: https://doi.org/10.1093/isd/ixab003

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Insect Systematics and Diversity, (2021) 5(2): 1; 1–26
doi: 10.1093/isd/ixab003
Research

Molecular phylogenetics, phylogenomics, and phylogeography

Phylogenetic Systematics of the Millipede Family Xystodesmidae

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Subject Editor: István Mikó

Received 3 August, 2020; Editorial decision 3 January, 2021

Abstract

The millipede family Xystodesmidae includes 486 species distributed primarily in temperate deciduous forests in North America and East Asia. Species diversity of the family is greatest in the Appalachian Mountains of the eastern United States, with 188 species. Although the group includes notable taxa such as those that are bioluminescent and others that display Müllerian mimicry, producing up to 600 mg of cyanide, basic alpha-taxonomy of the group is woefully incomplete and more than 50 species remain undescribed in the Appalachian Mountains alone. In order to establish a robust phylogenetic foundation for addressing compelling evolutionary questions and describing species diversity, we assembled the largest species phylogeny (in terms of species sampling) to date in the Diplopoda. We sampled 49 genera (out of 57) and 247 of the species in the family Xystodesmidae, recollecting fresh material from historical type localities and discovering new species in unexplored regions. Here, we present a phylogeny of the family using six genes (four mitochondrial and two nuclear) and include pivotal taxa omitted from previous studies including *Nannaria*, *Erdelyia*, taxa from East Asia, and 10 new species. We show that 6 of the 11 tribes are monophyletic, and that the family is paraphyletic with respect to the Euryuridae and Eurymerodesmidae. Prior supraspecific classification is in part inconsistent with the phylogeny and convergent evolution has caused artificial genera to be proposed. Subspecific classification is likewise incongruent with phylogeny and subspecies are consistently not sister to conspecifics. The phylogeny is used as a basis to update the classification of the family, diagnose monophyletic groups, and to inform species hypotheses.

Key words: Polydesmida, biogeography, aposematic, taxonomy

Millipedes are an ancient terrestrial lineage with members from the Early Devonian (ca. 414 Ma) that breathed atmospheric oxygen (Wilson and Anderson 2004, Suarez et al. 2017) and later forms that grew to gargantuan body proportions (2 × 0.5 m) sustained by elevated atmospheric oxygen content in the Carboniferous (Lucas et al. 2005). Divergence between Diplopoda and its sister group Pauropoda (Dignatha) has been estimated using molecular dating to have occurred during the Ordovician (Fernandez et al. 2018, but see Szucsich et al. 2020). Although there are many Paleozoic diplopod fossils, none have been assigned to any of the 16 extant orders. Wilson (2006) suggested that diversification accelerated during the Early and mid-Silurian and superordinal stem groups were established by the beginning of the Devonian. Fossil records during the Mesozoic are generally scarce, except for many recently discovered Cretaceous (ca. 100 Mya, Burmese) amber fossils (Wesener and Moritz 2018). Thirteen of the 16 extant orders of Diplopoda are represented by amber fossils in Cretaceous (Wesener and Moritz 2018). There are 830 species of Pauropoda and 12,000 species of Diplopoda—200 species of Symphyla and 3,500 species of Chilopoda; although what major factors led to the greater diversity of millipedes is unclear, traits implicated in the radiation include diplosegmentation and metachronal gait (thereby fostering burrowing) and chemical defenses (thus deterring predation). Notably, Geophilomorpha, a centipede order that has independently gained the ability to burrow (through the evolutionary trend of trunk elongation and leg addition) and produce chemical defenses, is the most species rich non-diplopod myriapod group. As detritivores, millipedes feed on decaying plant material, thereby fragmenting detritus into smaller pieces fostering later colonization by bacteria and fungi, and some have estimated that through fragmentation that certain species [*Narceus americanus* (Palisot de Beauvois, 1817), Spirobolida, Spirobolidae], contribute about two tons of frass per acre to deciduous forests yearly (Coville 1913). This input aerates and conserves the soil, and the process releases nitrogen, carbon, simple sugars, and other nutrients back into the biosphere (Joly et al. 2020). Unfortunately, non-native earthworms—released from predation and parasites from their native

Version of Record, first published online March 1, 2021 with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

ranges—have been shown to compete with native millipedes for this seemingly limitless detrital resource (Snyder et al. 2009). Millipedes' lack of wings, absence of phoresy, and low dispersal capability fosters narrow endemism, and many individual species are known as short-range endemics (SRE), distributed in areas less than 10,000 km^2 (Harvey 2002, Harvey et al. 2011). Their narrowly restricted distributions, e.g., the Laurel Creek millipede *Apheloria whiteheadi* (Shelley, 1986) with a global range of ca. 1 km^2, exemplify that they are irreplaceable biodiversity, which is ultra-susceptible to global extinction due to habitat loss, and highlights the importance of prioritizing millipede and other SRE invertebrates in schemes seeking to maximize species diversity. Despite their antiquity and important role as detritivores, known millipede species diversity tremendously lags behind estimated global diversity (Brewer et al. 2012). For example, there are more than 50 undescribed species of the twisted-claw millipede (*Nannaria* spp., Polydesmida, Xystodesmidae) in the eastern United States alone, and globally an additional 3,000–80,000 species of Diplopoda when tropical locales and other poorly sampled regions are included (Hoffman 1980, Brewer et al. 2012). The lack of basic alpha-taxonomic information on the twisted-claw millipedes is surprising given their large body size (about 2 cm in length) and ubiquity east of the Mississippi River; one new species was even discovered within the bounds of the D.C. Metropolitan area. The group exhibits fascinating biological characteristics. The millipede family Xystodesmidae includes notable taxa such as bioluminescent species in California, *Motyxia* spp. (Marek et al. 2011); Müllerian mimics in Appalachia, apheloriine spp. (Marek and Bond 2009); the train millipede in Japan, *Parafontaria laminata* (Attems, 1909), whose aggregations of 311 individuals m^{-2} have obstructed trains (Hashimoto et al. 2004); the giant 8-cm long armadillo millipede in Mexico, *Rhysodesmus dasypus* (Hoffman 1970); and the cherry millipede, *Apheloria virginiensis corrugata* (Wood, 1864), able to generate hydrogen cyanide in an amount 18 times that necessary to be lethal to a pigeon-size bird (Eisner et al. 2005).

Taxonomic History

The family Xystodesmidae Cook, 1895 was first established for several large-bodied members of the order Polydesmida Pocock, 1887 (Fig. 1). In his pioneering yet insightful classification of Diplopoda, Cook (1895) assigned millipede genera to 49 families and remarked that it was made 'with some confidence' in all groups, that is except for those of the Polydesmida. This work did not specify characters that united polydesmidan genera into their respective families. Later, Cook (1904) provided a diagnosis of the family Xystodesmidae and differentiated its members from other polydesmidan families by the presence of spines on the prefemur, bisinuately curved tarsal claws, and the dorsal habitus (including wide contiguous paranota that impart a compact appearance). Subsequently, the family was included as part of Chelodesmidae Cook, 1895 by Pocock (1910) and Brölemann (1916). These authors' conception of the family, and later Attems's (1926), was broad and inclusive and encompassed an assemblage of heterogeneous taxa, many of which are now in other families. Later, the taxon was more narrowly diagnosed and set apart from Chelodesmidae and other large-bodied members of the suborder Leptodesmidea Brölemann, 1916 by the presence of prefemoral spines and the shape of the body and antenna (see Marek et al. 2014 for a detailed summary of taxonomic history).

The central and eastern U.S. families, Eurymerodesmidae Causey, 1951 and Euryuridae Pocock, 1909, have been regarded as close relatives of the Xystodesmidae for more than 40 yr (Hoffman 1978a, 1990, 1998; Shelley 1989). The family Eurymerodesmidae (Fig. 1E) was considered as a 'smaller, apparently derivative group' of Xystodesmidae by Hoffman (1978a, p. 24) and the two families 'as sister taxa within the Xystodesmoidea' by Shelley (1989, p. 102). Although Euryuridae (Fig. 1F) was traditionally suggested to be closely allied to the Platyrhacidae and Aphelidesmidae due to a flattened, broad epiproct (Hoffman 1954, 1980), Hoffman (1998), upon reexamination of 14 characters, considered the family as closer to Xystodesmidae, in particular close to the xystodesmid subfamily Melaphinae Hoffman, 1980. However, these two taxa were retained as distinct families due to several characters including the ventral mandibular ridge in Eurymerodesmidae and the flattened, broad epiproct and simple gonopods in the Euryuridae (Shelley 1989, Hoffman 1998). A recent study then subsumed the families Eurymerodesmidae and Euryuridae under Xystodesmidae and removed *Macellolophus rubromarginatus* (Lucas, 1846) from Melaphinae, placing it in the family Chelodesmidae Cook, 1895. These higher-level changes were justified solely on similarity of male genitalic morphology (Shelley and Smith 2018). Nonetheless, as still remains the case with most taxa of the order Polydesmida since Cook 126 yr ago, monophyly of the family is uncertain, inter- and intrafamilial relationships are poorly known, and rationale for systematic relationships is based on century-old character argumentation using overall similarity of a handful of morphological features.

Molecular Phylogenetics

Based on an ordinal-level phylogeny of the Diplopoda inferred using amino acid data sequenced from transcriptomes of a representative set of familial exemplars, Xystodesmidae is monophyletic and sister to Eurymerodesmidae, which as a clade is in turn closely related to chelodesmid, sphaeriodesmid, and paradoxosomatid taxa (Rodriguez et al. 2018). Rodriguez et al. (2018) showed that several families of Polydesmida are not monophyletic (including Chelodesmidae and Paradoxosomatidae Daday, 1889) and challenged long-held morphological-based hypotheses, including Polydesmida sister to Nematophora [i.e., (Chordeumatida, (Stemmiulida, Callipodida) as in Enghoff 1984; Blanke and Wesener 2014]. Intrafamilial phylogenetic systematic relationships of the family have been studied in separate analyses of the eastern and western U.S. xystodesmid taxa (Marek and Bond 2006, 2007; Marek et al. 2011, 2015; Means and Marek 2017). However, there has never been a phylogenetic systematic analysis of the group with species from throughout the familial geographical distribution, and with other ostensibly closely related large-bodied taxa in the Leptodesmidea as outgroups to test the monophyly of the family.

To infer a phylogeny of the Xystodesmidae, we sampled 247 species of the family (the largest dataset analyzed in the Diplopoda to date) including taxa spanning the geographical distribution of the family, and utilized six genes. The phylogeny is used as a basis to update the classification of the family, diagnose monophyletic groups, and to describe ten new species.

Materials and Methods

Fieldwork

Millipedes were collected in the field from 2014 to 2019 and brought back alive to the laboratory for DNA preservation and specimen preparation according to the methods described in Means et al.

Fig. 1. Representatives of the millipede family Xystodesmidae (Polydesmida). (A) *Apheloria whiteheadi* (Shelley, 1986), Virginia, USA. (B) *Parafontaria tonominea* (Attems, 1899), Kumamoto, Japan. (C) *Parcipromus cooki* (Causey, 1955), California, USA. (D) *Parafontaria erythrosoma* (Takakuwa, 1942), Ibaraki, Japan. (E) *Eurymerodesmus dubius* Chamberlin, 1943, Arkansas, USA. (F) *Euryurus orestes* Hoffman, 1978, Georgia, USA. (G) *Thrinaphe hargeri* Shelley, 1993, Oregon, USA. (H) *Tubaphe levii* Causey, 1954, Washington, USA. (I) *Ochthocelata adynata* Shelley, 1995, California, USA. (J) *Sigmocheir furcata* Shelley, 1995, California, USA. (K) *Levizonus takakuwai* (Verhoeff, 1941), Hokkaido, Japan. (L) *Riukiaria cornuta* (Haga, 1968), Kumamoto, Japan.

(2015). For each species, the unique color morphs at a locality were photographed with a Canon EOS 6D digital SLR camera, MT-24EX Macro Twin Lite Flash, and a 50 mm lens; a MP-E 65 mm lens was used for individuals < 20 mm (Canon Inc., Japan).

Taxon Sampling

Based on species occurrence records from revisionary monographs and other taxonomic literature, we collected material from the field, prioritizing collections from type localities and from within the known species ranges. We targeted every genus in the family, and searched type localities when feasible or nearby localities. Eurymerodesmidae and Euryuridae were recently placed in the Xystodesmidae by Shelley and Smith (2018), thus we included in our sampling four and six of their species. Outgroups were selected in the superfamily Xystodesmoidea Cook, 1895, and other presumed close relatives in the suborder Leptodesmidea. The following taxa were selected as outgroups—Xystodesmoidea: *Orodesminus* Attems, 1929 (Oxydesmidae Cook, 1895: Mozambique) and an undetermined genus and species of Gomphodesmidae Cook, 1896 (Mozambique); Chelodesmoidea Cook, 1895: *Macellolophus rubromarginatus* Lucas, 1846 (Chelodesmidae: Spain); Platyrhacoidea Pocock, 1895: *Amplinus bitumidus* (Loomis, 1969) (Aphelidesmidae Brölemann, 1916: Mexico); Rhachodesmoidea Carl, 1903: *Neoleptodesmus* Carl, 1903 (Rhachodesmidae Carl, 1903: Mexico); and Sphaeriodesmoidea Humbert & DeSaussure, 1869: an undetermined genus and species of Sphaeriodesmidae Humbert & DeSaussure, 1869 (Mexico).

DNA Extraction, Amplification, and Sequencing

Left legs from body rings 8–18 were removed with flame-sterilized forceps, immersed in RNAlater (Qiagen) or 100% ethanol, and archived at −80°C in the freezer collection of the Virginia Tech Insect Collection (VTEC, collection.ento.vt.edu) for later DNA extraction. About 50% of the taxa sampled were collected (2014–2019) specifically for this study. Their frozen tissues, archived in the VTEC freezer collection, were DNA-extracted and sequenced for additional genes. We amplified and sequenced six genes (four mitochondrial and two nuclear gene fragments): small subunit RNA (12S), tRNA-Valine, large subunit RNA (16S), cytochrome c oxidase subunit I (COI), elongation factor alpha (EF1α), and large subunit RNA (28S). Amplification of DNA was carried out as described in Means and Marek (2017). DNA amplifications were cleaned, concentrations quantified and normalized, and Sanger-sequenced using an ABI 3730 capillary sequencer (Applied Biosystems).

Previous attempts to sequence the 12S and 16S DNA from representatives of the genus *Nannaria* repeatedly failed, so transcriptomes of two species of *Nannaria* collected from Virginia Tech's campus were sequenced to develop primers: *Nannaria ericacea* Hoffman, 1949; and *Nannaria hokie* n. sp. Live specimens were frozen with liquid nitrogen, pulverized, and whole-animal RNA was extracted from the tissues using a RNeasy kit (Qiagen). A cDNA library was made using reverse transcriptase PCR and sequenced using a Kappa prep and Illumina RNA-seq with 200-bp paired-end read sequencing. Raw DNA reads were assembled into transcripts using Trinity RNA-Seq de novo transcriptome assembly (Grabherr et al. 2011). The ribosomal genes were identified in the assembled *Nannaria* transcriptome by comparison with the mitochondrial genome of *Appalachioria falcifera* (Keeton, 1959) (Swafford and Bond 2010). We used a local nucleotide BLAST search in Geneious to identify the 12S and 16S transcripts in the *Nannaria* transcriptome (Altschul et al. 1990). Primers were developed spanning the entire 12S–16S region (including the intervening tRNA-Valine), and as a primer pair within the 16S ribosomal gene region. We used phred and phrap in the Mesquite module Chromaseq for nucleotide base-calling, trimming, and quality control of Sanger sequences (Ewing et al. 1998, Maddison and Maddison 2010).

Phylogenetic Analyses

We used prank for multiple sequence alignment beginning the analysis with a neighbor-joining guide tree that was later refined after the preliminary alignment step (Löytynoja and Goldman 2005). Aligned gene sequences were partitioned by gene, codon position, and intron/exon locations in Mesquite. Partitions were assessed in PartitionFinder to determine a best-fit partitioning plan and to identify appropriate models of nucleotide evolution (Lanfear et al. 2012). Using the best-fit partitioning scheme and the aligned sequences in nexus format, we used MrBayes 3.2.5 to estimate phylogeny (Ronquist et al. 2012). Individual gene trees for the six genes were analyzed independently in MrBayes to compare alternative genealogical histories and compare varying gene tree resolution. In addition, a concatenated dataset with all of the genes and best-fit partitioning scheme was analyzed in MrBayes. Phylogenetic analyses were run on Virginia Tech's 173-node supercomputer, NewRiver, with 16 MCMC chains running in parallel on separate processors. A tree and other parameters were sampled every 100 of 30 million generations. Chains were monitored for convergence using the average standard deviation of split frequencies and a threshold of 0.01.

Species Discovery and Delimitation

Male specimens collected in the field were compared to type specimens (and other material in natural history collections [NHCs]) and literature for identification to species. We refrained from describing new species and making changes to the classification of the genera *Apheloria*, *Cherokia*, *Rhysodesmus*, and *Riukiaria* because revisions of these taxon are currently underway. We used morphological and molecular phylogenetic distinctness (diagnosability) to delimit species as follows. 1) We first used male gonopod morphology, and if a specimen's gonopod morphology matched the description of a known species then the specimen was ascribed to that species. However, if the specimen's gonopod morphology did not match the known species and was distinct then we established a preliminary new species, $H_{morph=yes}$ (e.g., *Appalachioria* n. sp. 'Clinch Mountain' Marek and Bond 2006, 2007; Means and Marek 2017). At this moment, we hypothesized what the closest relative of the conditional new species would be. New species represented by a single male (or female) specimen remained preliminary new species ($H_{morph=yes}$) and were not described until additional material can be collected to rule out the possibility of an aberrant form of a known species. 2) A single male exemplar of a preliminary new species ($H_{morph=yes}$) from above was sampled for the molecular phylogeny to assess phylogenetic distinctness, $H_{phy=yes/no?}$. If the preliminary new species was not sister to its closest relative (hypothesized previously) in the concatenated molecular phylogeny ($H_{morph=yes}$, $H_{phy=yes}$), or if it was sister to its closest relative but had overt morphological genitalic differences then we established a new species and described it here ($H_{morph=yes}$, $H_{phy=no}$). However, if the preliminary new species was sister to its closest relative but had slight morphological genitalic differences, when re-assessed within the phylogenetic context, then we did not describe it ($H_{morph=no}$, $H_{phy=no}$). We were optimistic that genitalic (gonopodal) differences track species boundaries. The lock-and-key theory for genitalic variation has been demonstrated in the group previously (Tanabe and Sota 2008, Wojcieszek and Simmons 2012). Therefore, we are confident in using this species delimitation method implementing primarily male gonopod morphology because shape difference between male and female genitalia prevent nonspecific matings and imparts strong reproductive isolation. In addition, a diversity of species remains undescribed (ca. 56 in *Nannaria*) and we are highly motivated to document new taxa because many of their habitats are directly threatened by habitat loss, climate change, and other processes that cause land conversion and habitat unsuitability.

Biogeographical Analysis

To infer ancestral ranges of the taxa, we plotted their observed biogeographical ranges on the phylogeny using the Dispersal–Extinction–Cladogenesis (DEC) model in BioGeoBEARS (Matzke 2013, 2014). Biogeographical ranges of the taxa were recorded based on the terrestrial ecoregion in which they are found. Terrestrial ecoregions were according to Olson et al. (2001). A chronogram was estimated with BEAST using a normal prior on the date of the root with a mean of 1 to generate relative dates (Bouckaert et al. 2014, 2019). Outgroup taxa historically not in the family Xystodesmidae were pruned from the tree prior to analysis in BioGeoBEARS. We used relative dates because there are no fossils of the family Xystodesmidae for calibration points, spare a single equivocal member of the family preserved in Miocene Chiapas amber (Riquelme and Hernández-Patricio 2018). Due to the limited dispersal capabilities of xystodesmid millipedes, species exclusively inhabit single ecoregions except for a few widespread taxa (Means and Marek 2017). As a result, the DEC+J model, which adds the parameter *j* for founder-event speciation, was hypothesized to be more likely over the DEC model (Matzke 2014). To test this hypothesis, we compared the likelihoods of the alternative models using a likelihood ratio test in Microsoft Excel. We visualized the phylogeny of Xystodesmidae on a world map and plotted the geographical coordinates of the terminal taxa in a tanglegram using the R (version 3.2.2) program phytools (version 0.7–20) (Revell 2012, R Core Team 2016).

Taxonomy

Material in NHCs was used to describe species. Specimens were examined for somatic and genitalic characters using a Leica M125 stereomicroscope. Male gonopods were dissected and photographed as above, but with two 350 nm ultraviolet flashes operated from a Visionary Digital Passport II focal-stacking photography system with Helicon Focus according to fluorescent photography techniques outlined in Marek (2017). The higher-level classification of Xystodesmidae was modified to reflect the phylogeny. Taxon groups were selected to be equally divergent, mutually exclusive, and statistically well supported. The classification system is informative, in that it provides a hierarchical guide to family diversity, and extensible in that it provides a framework to name new species. Changes to the higher-level classification of Xystodesmidae were made according to the principle that monophyletic and some paraphyletic groups receive formal names. A paraphyletic taxon retained its preexisting name when the group was morphologically distinct, and to preserve stability and familiarity of the classification scheme; in some cases, paraphyletic taxon names were retained because a revision of the taxon was currently underway. In contrast, the names of polyphyletic taxa were not retained. If existing, monophyletic taxa were named according to an available name; in contrast if there were no available names, then a new name was provided. Diagnoses of new higher-level taxa were made in part with nucleotide site substitutions based on unique and uniform states identified in Mesquite using the 'With State Distinguishing Selected Taxa' tool (Maddison and Maddison 2010). Unique and uniform states were identified from the 'full-taxa' alignment (see below 'Results, DNA extraction, amplification, and sequencing') and their site numbers are supplied in parentheses (the first number is specific to the gene locus and the second is for the whole matrix). Holotypes and other type material were deposited in the Virginia Tech Insect Collection and Virginia Museum of Natural History. Museum abbreviations are as follows: VTEC (Virginia Tech Insect Collection, Blacksburg, Virginia), VMNH (Virginia Museum of Natural History, Martinsville, Virginia), and NCSM (North Carolina Museum of Natural History, Raleigh, North Carolina).

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:A55797AF-B8E6-4E46-8FD2-53B5C79FCEF8.

Results

Fieldwork and Taxon Sampling

We collected all three nominal subfamilies, 49 of 57 genera, and 247 of 486 species (Supp Table 1 [online only]). Ten of these 247 species are new and described below. Outgroups were collected from Mozambique: *Orodesminus* sp. (Oxydesmidae) and Gomphodesmidae sp.; Spain: *Macellolophus rubromarginatus* (Chelodesmidae); and Mexico: Sphaeriodesmidae sp., *Neoleptodesmus* sp. (Rhachodesmidae), and *Amplinus bitumidus* (Aphelidesmidae). The type localities of *Parariukiaria cucphuongensis* Nguyen, 2016 from Cuc Phuong National Park, Vietnam; *Parvulodesmus prolixogonus* Shelley, 1983 from Abbeville County, South Carolina; *Lyrranea persica* Hoffman, 1963a from Peach County, Georgia; and *Lourdesia minuscula* Shelley, 1991 from Coffee County, Alabama were visited but no specimens were found. The monotypic taxa *Cheiropus plancus* Loomis, 1944 (U.S.); *Ochridaphe albanica* (Verhoeff, 1932) (Mediterranean rim); and *Pamelaphe lacustris* (Pocock, 1895) (China) were not sampled for this analysis. Species of the genera *Devillea* Brölemann, 1902 (five species, Mediterranean rim); *Kiulinga* Hoffman, 1956 (two species, China); *Koreoaria* Verhoeff, 1937 (two species, South Korea); and *Stelgipus* Loomis, 1944 (two species, United States) were not included in the study.

DNA Extraction, Amplification, and Sequencing

Amplification and direct sequencing of DNA from the six targeted genes generally worked consistently across taxa sampled. However, DNA fragments from certain taxa repeatedly failed to amplify and/or sequence. In general, rounds of amplification and sequencing were repeated two to three times for a specimen before a second specimen was substituted or attempts abandoned. The 'full-taxa' dataset included 253 species with reduced occupancy of genes (omitted due to amplification or sequencing failure), and the 'full-gene' dataset with 227 species possessing at least three of the six genes. If sequences of the following genes were attained then the specimen was included in the 'full-taxa' molecular phylogenetic analysis: 16S and either 12S, COI, EF1α, or 28S. Taxa sampled by gene are listed in Supp Table 1 (online only). RNA-seq of total RNA from *Nannaria ericacea* resulted in 56,428,924 paired-end reads and *Nannaria hokie* n. sp. in 56,662,265 paired-end reads. Amplification of DNA from *Nannaria* with primers that we developed using transcriptome sequences designed to extend through the entire 12S–16S region (including tRNA-Val) consistently failed. However, those primers developed to anneal and extend through regions within the separate 16S rRNA component successfully amplified 797 bp of DNA with high sequence identity via BLAST to other 16S fragments of Xystodesmidae in NCBI GenBank (Altschul et al. 1990). The 12S and tRNA-Val genes are hence missing from these fragments, and sequences of *Nannaria* are therefore consistently shorter than others.

Phylogenetic Analyses

Multiple sequence alignment in prank and inference of DNA evolution models in PartitionFinder resulted in a 5497 bp concatenated 'full-taxa' matrix composed of 221 bp (12S, GTR+G), 103 bp (tRNA-Val, GTR+G), 2052 bp (16S, GTR+I+G), 600 bp (COI, pos 1 & 3 GTR+I+G and pos 2 GTR+G), 1640 bp (28S, GTR+I+G), and 886 bp (EF1α, pos 1& 2 K80+I+G, pos 3 SYM+G, intron HKY+G). The 'full-gene' matrix composed 203 bp (12S, GTR+G), 77 bp (tRNA-Val, GTR+G), 1766 bp (16S, GTR+I+G), 600 bp (COI, pos 1 & 3 GTR+I+G and pos 2 GTR+G), 1367 bp (28S, GTR+I+G), and 844 bp (EF1α, pos 1 & 2 K2P+I+G, pos 3 SYM+G, intron HKY+G). The 16 separate MCMC chains for the 'full-taxa' analysis converged at 15 million generations ('full-gene' at 2 million generations), and when summarized in a consensus tree resulted in a topology with 140 of 190 nodes supported with a posterior probability > 0.95 (Figs. 2 and 3). The phylogeny indicated that the family Xystodesmidae is not monophyletic because the Mediterranean species *Melaphe vestita* (Koch, 1847) is separated from remaining species by two branches: *Macellolophus rubromarginatus* (Chelodesmidae) and the gomphodesmid (Fig. 2). Historical infrafamilial taxa such as the Apheloriini and others are monophyletic; however, some other taxa

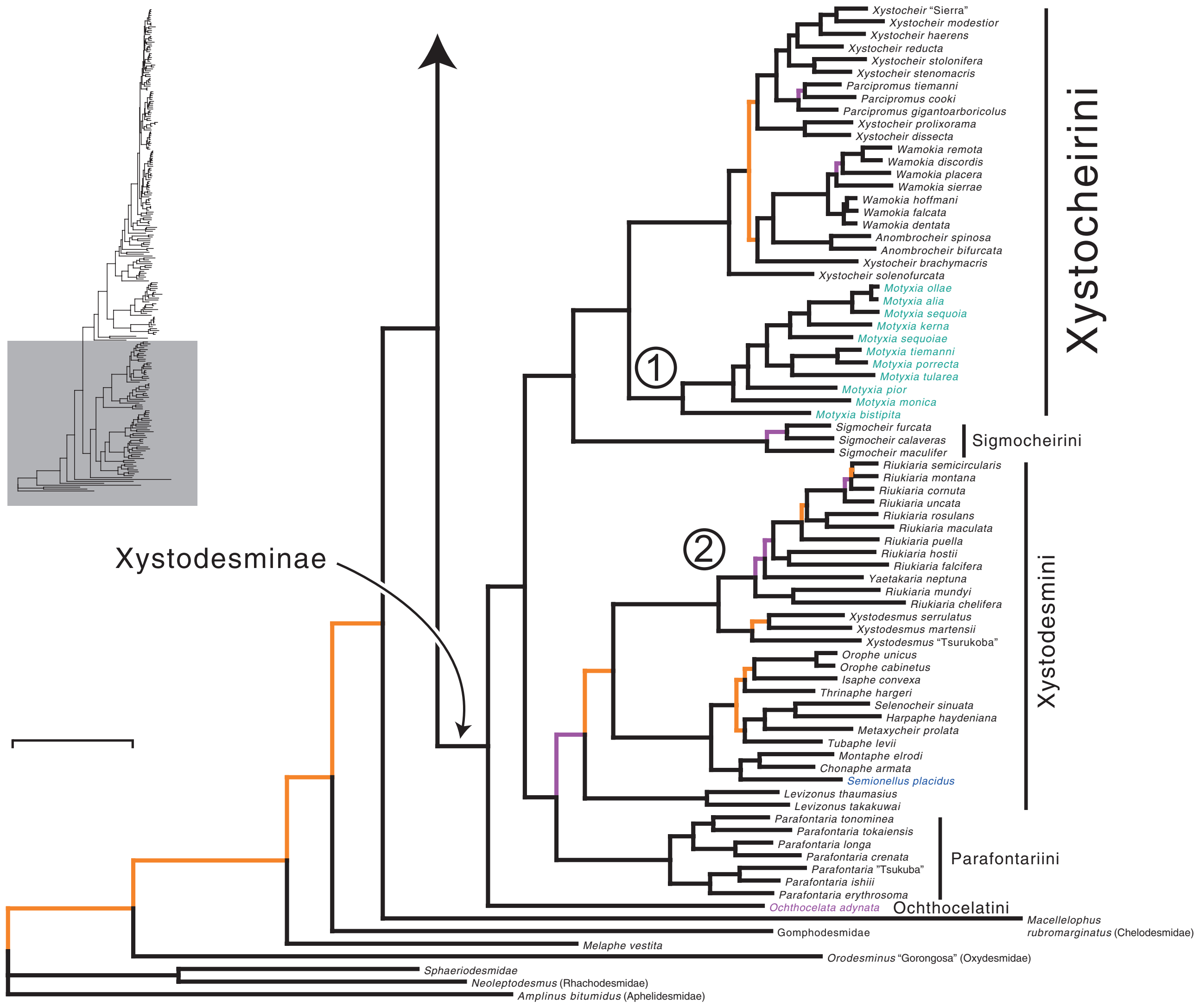

Fig. 2. Phylogeny estimated using Bayesian inference from the 'full-taxa' dataset (using all available data), part 1: subfamily Xystodesminae and outgroups. Branch colors indicate posterior probability (orange, posterior probability < 0.7; magenta, posterior probability < 0.95; black, posterior probability < 1.0). Tree notes: 1. Origin of bioluminescence in the genus *Motyxia* from California. 2. Genus *Riukiaria* from Japan with 11 taxa represented out of 33 species. Blue text. *Semionellus placidus* (Wood, 1864), a markedly disjunct species from eastern North America, is in the western North American (WNA) clade. Magenta text. *Ochthocelata adynata* Shelley, 1995, from California, is the sole adelphotaxon to the Xystodesminae. Scale bar: 0.1 expected substitutions per site. (Note: the whole tree was cut in two parts with part 1 here and part 2 in Fig. 3.)

including the Rhysodesmini and Xystodesmini are not. The status of these taxa with respect to the phylogeny vary. Separate gene trees show varying levels of support from deeper relationships in the 28S topology to shallow relationships in COI (Supp Fig. 1 [online only]). Data matrices and trees are available for download from the Supp Material (online only) (Supp Dataset 1 [online only]).

Biogeographical Analysis

Taxa were distributed in 26 ecoregions (Olson et al. 2001), including the Hokkaido deciduous forests and Taiheiyo evergreen forests in Japan, Tamaulipan mezquital and Sierra de los Tuxtlas in Mexico, and Sierra Nevada forests and Appalachian Blue Ridge forests in the United States (Fig. 4, Table 1, Supp Figs 2 and 3 [online only]). Species primarily occurred in broadleaf deciduous forests, but some taxa were found in evergreen forests and chaparral shrublands. The likelihoods of the DEC and DEC+J models were -666.54 and -505.65, respectively, and likelihood ratio test indicated that the DEC+J model was the best fit given the data (df = 1, $P < 0.0001$). The species *Melaphe vestita*, which occurred outside of Xystodesmidae on the phylogeny, is known from the Aegean and Western Turkey sclerophyllous and mixed forests (AWTS). The root node estimated from the BioGeoBEARS was equivocal between this AWTS ecoregion and the Sierra Nevada forests ecoregion (California, USA). The root node of the remaining Xystodesmidae, including Japanese species, was the Sierra Nevada forests (California). The major clades of Xystodesmidae occur in the following ecoregions: Sierra Nevada forests (California), Taiheiyo evergreen forests (Japan), and the Appalachian Blue Ridge forests (Fig. 4).

Species Discovery and Delimitation

In most cases, conditional new species ($H_{morph=yes}$) were not sister to their presumed closest relatives (hypothesized a priori based solely on morphological similarity) in the concatenated 'full-taxa' molecular phylogeny ($H_{phy=yes}$). Because these conditional

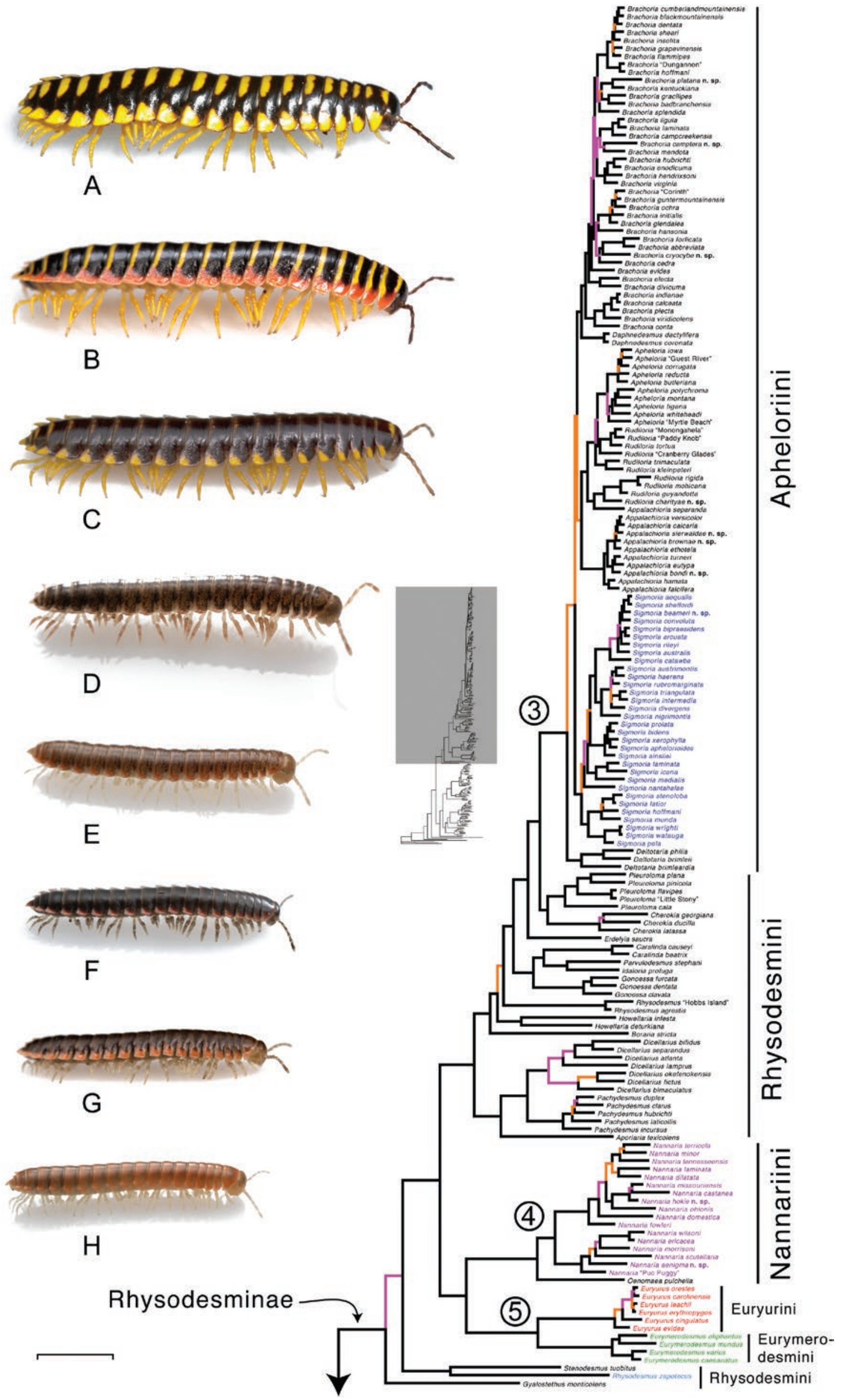

Fig. 3. Phylogeny estimated using Bayesian inference from the 'full-taxa' dataset (using all available data), part 2: subfamily Rhysodesminae. Branch colors indicate posterior probability (orange, posterior probability < 0.7; magenta, posterior probability < 0.95; black, posterior probability < 1.0). (A–H) Representative millipedes in the Rhysodesminae: (A) *Brachoria cedra* Keeton, 1959. (B) *Apheloria virginiensis corrugata* (Wood, 1864). (C) *Appalachioria calcaria* (Keeton, 1959). (D) *Parvulodesmus stephani* Shelley, 2001. (E) *Rhysodesmus* 'Hobbs Island'. (F) *Nannaria hokie* n. sp. (G) *Nannaria ericacea* Hoffman, 1949. (H) *Oenomaea pulchella* (Bollman, 1889). Tree notes: 3. The tribe Apheloriini, primarily distributed in the Appalachian Mountains and with about one-third of the family's species diversity is a possible crown group taxon. 4. The genus *Nannaria* includes a substantial number of undescribed species (ca. 56 species) predominantly in the Appalachian Mountains of the eastern United States, highlighting the region as the global center of undescribed species diversity in Xystodesmidae. 5. The Xystodesmidae is paraphyletic with respect to the families Euryuridae (red taxa) and Eurymerodesmidae (green taxa), which are now tribes of the subfamily Rhysodesminae. Light and dark blue text. Genera with species diversity > 40 including *Rhysodesmus* and *Sigmoria* (also *Nannaria* in magenta text) that have not been extensively sampled. Scale bar: 0.1 expected substitutions per site. (Note: the whole tree was cut in two parts with part 2 here and part 1 in Fig. 2.).

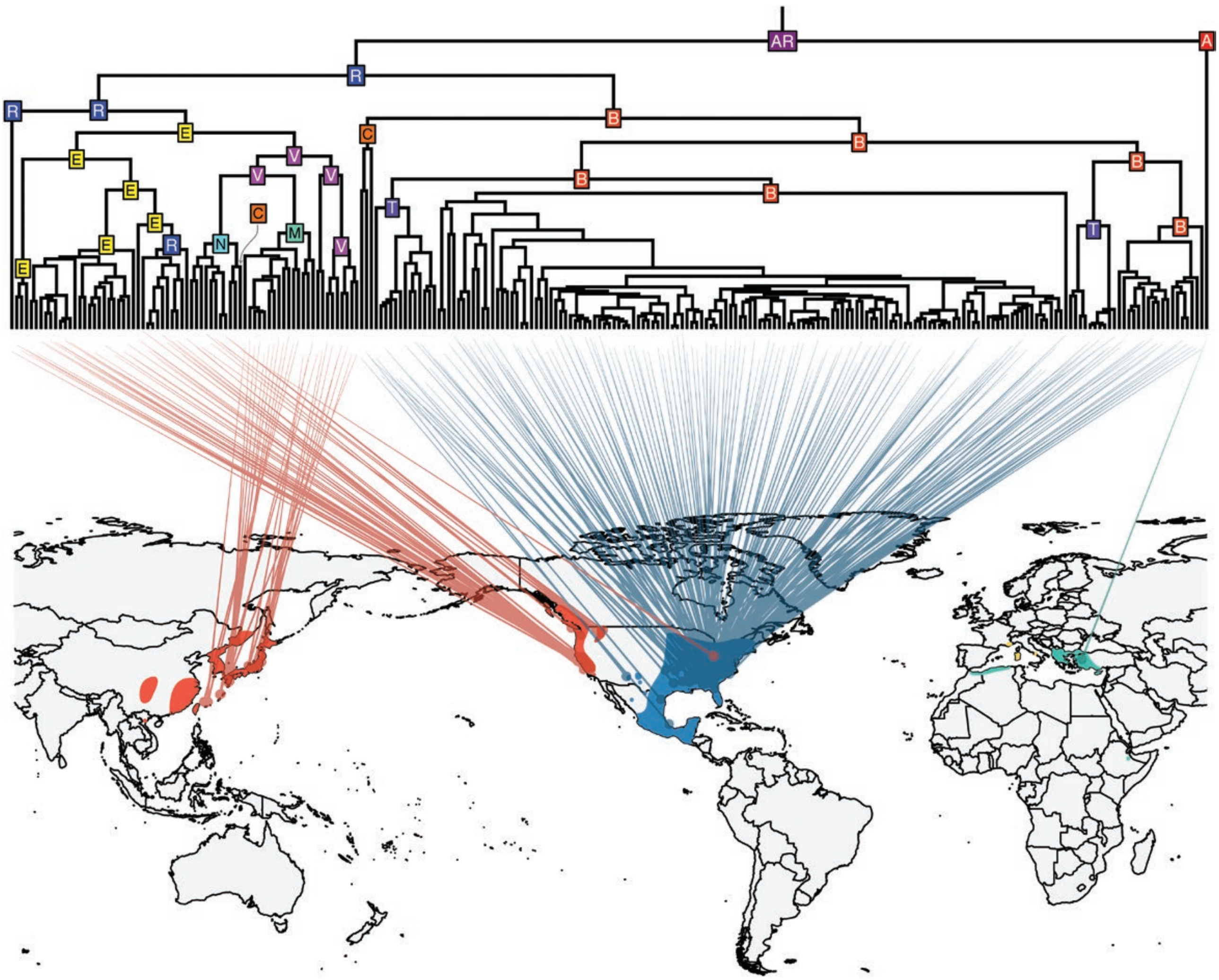

Fig. 4. Distribution map of Xystodesmidae with its phylogeny and selected ancestral areas of its taxa. Continental locations of the distribution of the subfamily Xystodesminae (red-filled outline) in East Asia and western North America, the subfamily Rhysodesminae (blue-filled outline) in eastern North America and southwestern North America, the subfamily Melaphinae (green-filled outline) in the Mediterranean Region and Ethiopia; and Devilleini (yellow-filled outline) in the Mediterranean Region. Ancestral areas: A = Aegean and Western Turkey sclerophyllous and mixed forests, B = Appalachian Blue Ridge forests, C = Appalachian mixed mesophytic forests, E = California interior chaparral and woodlands, N = North Central Rockies forests (United States), R = Sierra Nevada forests, T = Southeastern mixed forests (United States), V = Taiheiyo evergreen forests (Table 1). Terrestrial ecoregions according Olson et al. (2001).

new species were distinct morphologically and phylogenetically ($H_{morph=yes}$, $H_{phy=yes}$), they were described as new species. However, four conditional new species were separated from their closest hypothesized relatives by a single branch ($H_{phy=no}$), possessed slight morphological genitalic differences ($H_{morph=no}$) and therefore were not described as distinct species: *Brachoria* 'Corinth', *Rudiloria* 'Monongahela', *Pleuroloma* 'Little Stony', and *Rhysodesmus* 'Hobbs Island'. The following taxa were represented by a single male specimen: *Rudiloria* 'Paddy Knob', *Brachoria platana* (plus female specimen), and *Brachoria* 'Dungannon'. Therefore, we determined that the evidence supporting these three taxa as new species was lacking compared to that for others; however, we described *Brachoria platana* based on the presence of two specimens, a male and female.

Taxonomy

The species descriptions of new millipedes in the family Xystodesmidae are provided in Figs. 5–15. Diagnoses of tribes and an identification key are provided with syntheses of identification resources for each tribe. A species list and higher-level classification of Xystodesmidae, updated on the basis of the phylogenetic analysis, is provided in the Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]). The majority of previously described subspecies were not found to be conspecifics, e.g., *Rudiloria tortua*, *Appalachioria ethotela*, *Appalachioria eutypa*, *Appalachioria hamata*, *Sigmoria intermedia*, *Sigmoria nigrimontis*, *Sigmoria latior*, *Dicellarius fictus*, *Pachydesmus duplex*, and *Motyxia tularea*. Due to these results, we have therefore raised subspecies to full species status.

Xystodesmidae Taxonomy

Class **Diplopoda** de Blainville in Gervais, 1844
Infraclass **Helminthomorpha** Pocock, 1887
Order **Polydesmida** Leach, 1815
Family **Xystodesmidae** Cook, 1895
Subfamily **Rhysodesminae** Brolemann, 1916
Tribe **Apheloriini** Hoffman, 1980

A comprehensive species list and higher-level classification of the family Xystodesmidae is provided in the Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

Genus ***Appalachioria*** Marek and Bond, 2006.

Table 1. List of the terrestrial ecoregions of the world in which the taxa of the family Xystodesmidae sampled in this analysis occurs. Ecoregions according Olson et al. 2001.

Biogeographic realm	Ecoregion	Label
Palearctic		
	Aegean and Western Turkey sclerophyllous and mixed forests	A
	Hokkaido deciduous forests	J
	Nansei Islands subtropical evergreen forests	M
	Taiheiyo evergreen forests	V
	Ussuri broadleaf and mixed forests	X
Nearctic		
	Appalachian Blue Ridge forests	B
	Appalachian mixed mesophytic forests	C
	Arizona mountains forests	D
	California interior chaparral and woodlands	E
	Central forest-grasslands transition	F
	Central Pacific coastal forests	G
	Central U.S. hardwood forests	H
	Eastern Cascades forests	I
	Middle Atlantic coastal forests	L
	North Central Rockies forests	N
	Ozark mountain forests	O
	Piney woods forests	P
	Sierra Nevada forests	R
	Southeastern conifer forest	S
	Southeastern mixed forests	T
	Southern Great Lakes forests	U
	Tamaulipan mezquital	W
	Flint Hills tall grasslands	Z
Neotropic		
	Sierra de los Tuxtlas	Q

Vernacular name: 'The Appalachian Mimic Millipedes'

Type species: *Brachoria falcifera* Keeton, 1959.

Taxa included: 11 species, see Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

Appalachioria bondi Marek, Means, Hennen, New Species

Vernacular Name: 'Bond's Appalachian Mimic Millipede'

Figs. 5A–G and 6.

Brachoria 'Clinch' (Marek and Bond 2006)

Appalachioria 'n. sp. Clinch Mountain' (Marek and Bond 2007, Means and Marek 2017)

Material examined: Type specimens. ♂ holotype (VTEC SPC000282), ♂ paratype (VMNH SPC000280), and ♀ paratypes (VTEC SPC000281, 283) from Virginia, Washington County, Clinch Mountain, CR-612 (36.72317°N, -82.2985°W, Elev. 635 m), 28 May 2004, 15:00, tulip, birch, oak, sassafras (Coll: P. E. Marek). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Appalachioria bondi* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods.** Gonopodal acropodite curving ventromedially at apex, with a distal cingulum, separating it from *Apheloria* and *Rudiloria* (Fig. 6). Prefemoral process short and stout, basal zone lacking tubercles. Acropodite at anterior bend with three stout, triangular dorsal tubercles, separating it from most other *Appalachioria* species. Distal zone constricted basally, with a medially curved, blunt, uncinate tip. **Color.** *Appalachioria bondi* n. sp. has multiple color morphs, often co-occurring (Fig. 5A–G). Tergites always with white, light-pink, or yellow paranotal spots, sometimes also with concolorous metatergal middorsal spots. Dark-brown to black background. Collum always with concolorous white, light-pink, or yellow anterior and lateral spots, sometimes also with a posterior spot, never with marginal lines connecting the spots.

Description: Supp Table 3 (online only). Based on Holotype (♂) SPC000282.

Measurements (mm): BL = 42.0, CW = 8.5, IW = 5.2, ISW = 1.4, B11W = 9.9, B11H = 5.8.

Variation: The dorsal tubercles on the anterior bend of the acropodite vary in size and number, ranging from 1 to 3 (exceptionally up to 10) small to stout triangular tubercles, sometimes serrated or divided apically. The tubercles can vary from dorsal to medial in position. The tip of the acropodite may be curved medially to ventrally. The prefemoral process ranges from short and thin to long and stout and varies from small to medium in size. *Appalachioria bondi* n. sp. exhibits six unique color patterns: yellow four-spotted collum (Fig. 5A), red two-spotted, collum with one anterior and two lateral red spots (Fig. 5B), yellow two-spotted, collum with one anterior and two lateral yellow spots (Fig. 5E), white four-spotted collum (Fig. 5C), white two-spotted, collum with one anterior and two lateral white spots (Fig. 5F) and red four-spotted collum (Fig. 5D).

Ecology: Individuals of *Appalachioria bondi* n. sp. have been found in mesic deciduous forests of oak, beech, maple, tuliptree, birch, buckeye, and sassafras, with small patches of eastern redcedar nearby.

Distribution: *Appalachioria bondi* n. sp. is only known from a small range of about 8 km^2 on Clinch Mountain in Russell and Washington Counties, Virginia.

Etymology: This species is named for Dr. Jason Bond of the University of California, Davis. The specific name is a genitive noun derived as a patronym.

Appalachioria sierwaldae Marek, Means, Hennen, New Species

Vernacular Name: 'Sierwald's Appalachian Mimic Millipede'

Figs. 5H–I and 7.

Appalachioria n. sp. 'Foster Falls' Means and Marek 2017

Material examined: Type specimens. ♂ holotype (VTEC SPC000296), 1 ♂ paratype (VMNH SPC000297), and 2 ♀ paratypes (VTEC SPC000294, 295) from Virginia, Wythe County, N slope Fosters Falls Mountain, cove near road (36.89021°N,

Fig. 5. Color photographs of new species of xystodesmid millipedes and their color morphs. *Appalachioria bondi* n. sp. (A–G): A Three-spotted yellow morph with yellow legs, dorsal view, B Two-spotted pink morph with pink legs, dorsal view, C Three-spotted white morph with white legs, D Three-spotted orange morph with orange legs, E Two-spotted yellow morph with pink legs, F. Two-spotted white morph with white legs, G Three-spotted yellow morph with pink legs, dorsal view. *Appalachioria sierwaldae*, n. sp. (H–I): H. Three-spotted morph with yellow paranotal spots and orange medial spots and orange legs. I. Three-spotted yellow morph with yellow legs. *Appalachioria brownae* n. sp. (J–K): J. Three-spotted yellow morph with yellow legs. K. Two-spotted yellow morph with yellow legs. *Brachoria camptera* n. sp. (L–M): L. Two-spotted orange morph with white legs. M. Two-spotted red morph with red legs. *Brachoria cryocybe* n. sp. (N): N. Two-spotted morph with red paranotal spots and white stripe and red legs. *Brachoria platana* n. sp. (O–P): O. Striped red morph with red legs. P. Three-spotted yellow morph with yellow legs. *Rudiloria charityae* n. sp. (Q): Q. Three-spotted morph with yellow paranotal spots and orange medial spots and yellow legs. *Sigmoria beameri* n. sp. (R): R. Two-spotted red morph with light red legs. *Nannaria aenigma* n. sp. (S–T): S. Two-spotted red morph with light red legs. T. Two-spotted white morph with white legs. *Nannaria hokie* n. sp. (U): Two-spotted red morph with gray legs.

-80.8376°W, Elev. 657 m), 29 May 2004, tulip, oak, maple, rhododendron, moist cove (Coll: P. E. Marek). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Appalachioria sierwaldae* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods.** Gonopodal acropodite strongly curving ventromedially and with a strong distal cingulum, separating it from *Apheloria* and *Rudiloria* (Fig. 7). Prefemoral process short and stout. Post-cingulum area expanded, wider than pre-cingulum area. Distal zone strongly curved medially into a long, uncinate, thin tip. **Color.** Tergites with yellow paranotal spots and yellow metatergal spots (Fig. 5I), but sometimes with orange metatergal spots (Fig. 5H). Black background. Collum with yellow lateral and anterior spots, sometimes with yellow or orange posterior spots, or lacking a posterior spot.

Description: Supp Table 3 (online only). Based on Holotype (♂) SPC000296.

Measurements (mm): BL = 40.0, CW = 7.0, IW = 4.7, ISW = 1.4, B11W = 9.4, B11H = 5.4.

Variation: No significant variation from the holotype was observed.

Ecology: Individuals of *Appalachioria sierwaldae* n. sp. were found in an Appalachian cove forest that included tulip, oak, maple, and rhododendron.

Distribution: Only known from the type locality on Fosters Falls Mountain in eastern Wythe County, Virginia.

Etymology: This species is named for Dr. Petra Sierwald of the Field Museum of Natural History. The specific name is a genitive noun derived as a matronym.

Appalachioria brownae Marek, Means, Hennen, New Species

Vernacular Name: 'Brown's Appalachian Mimic Millipede'

Figs. 5J,K and 8.

Material examined: Type specimens. ♂ holotype (VTEC MPE01676), 2 ♂ paratypes (VTEC MPE01663, VMNH MPE01664), and 2 ♀ paratypes (VTEC MPE01675, 1678) from Virginia, Washington County, Jefferson National Forest, south of Laurel Bed Lake, off Tumbling Creek Rd. (36.93845°N, -81.8118°W, Elev. 956 m), 13 June 2016, ex maple, oak, big leaf magnolia woods, quite dry (Coll: J. C. Means, D. A. Hennen). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Appalachioria brownae* n. sp. are distinct from other apheloriine species based on the following combination

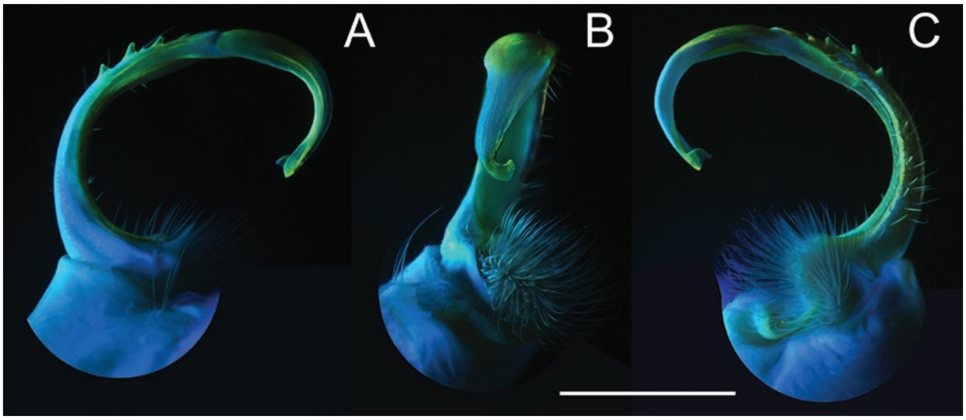

Fig. 6. *Appalachioria bondi* n. sp. holotype ♂ left gonopod (VTEC SPC000282). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

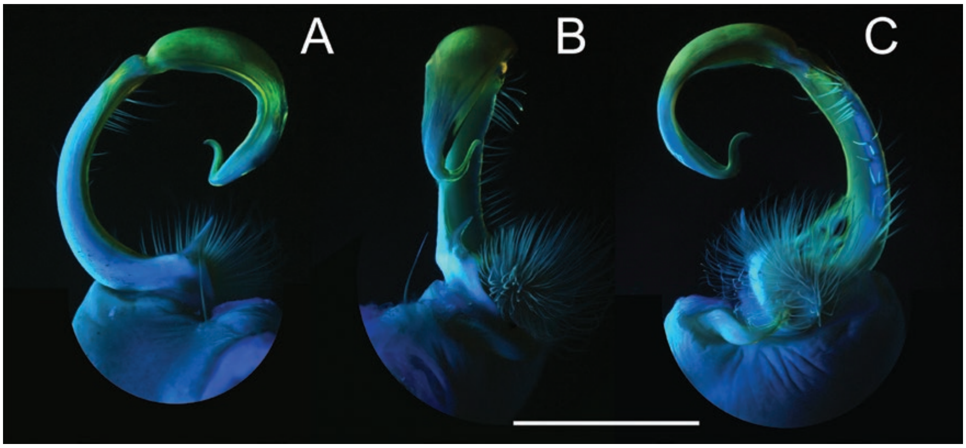

Fig. 7. *Appalachioria sierwaldae* n. sp. holotype ♂ left gonopod (VTEC SPC000296). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

of characters: **Gonopods.** Gonopodal acropodite strongly curving ventromedially and with a strong distal cingulum, separating it from *Apheloria* and *Rudiloria* (Fig. 8). Prefemoral process short and stout. Basal zone medially with small triangular tubercles, separating it from other co-occurring *Appalachioria* species. Post-cingulum area slightly expanded, with a strong twist at acropodite peak, distal zone with a lateral indentation. Acropodite tip curved medially. **Color.** Tergites with yellow paranotal spots (Fig. 5K), sometimes with small yellow metatergal spots (Fig. 5J). When metatergal spots present, midbody tergites with broken yellow caudal line connecting the paranotal and metatergal spots. Black background. Collum with yellow anterior and lateral spots connected by a yellow marginal line, sometimes also with a caudal marginal line.

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE01676.

Measurements (mm): BL = 44.0, CW = 7.0, IW = 4.8, ISW = 1.5, B11W = 9.1, B11H = 5.2.

Variation: There is slight variation in the number and position of tubercles on the acropodite basal zone, with numbers ranging from 4 to 6, spread from the base of the basal zone to halfway up the acropodite. The prefemoral process ranges from quite small and stout to long and thin, reaching to the level of the distal zone of the acropodite. *Appalachioria brownae* n. sp. has two known color morphs, 1) three-spotted yellow, with small yellow metatergal spots and a thin, broken caudal line, collum with yellow anterior and lateral spots connected by a thin yellow marginal line (Fig. 5J) and 2) two-spotted yellow, collum with yellow anterior and lateral spots with a thin anterior marginal yellow line connecting the spots (Fig. 5K).

Ecology: Individuals of *Appalachioria brownae* n. sp. were found in a deciduous forest of oak, maple, and big leaf magnolia near a stream during dry conditions.

Distribution: *Appalachioria brownae* n. sp. is known only from the type locality, situated in bottomland habitat at the base of Brush Mountain and Redrock Mountain.

Etymology: This species is named for Dr. Ellen Brown of Fredericksburg, Virginia. The specific name is a genitive noun derived as a matronym.

Genus *Brachoria* Chamberlin, 1939.

Vernacular name: 'The Mimic Millipedes'

Type species: *Brachoria initialis* Chamberlin, 1939.

Taxa included: 39 species, see Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

Brachoria camptera Means, Hennen, Marek, New Species

Vernacular Name: 'The City Lake Mimic Millipede'

Figs. 5L,M and 9.

Material examined: Type specimens. ♂ holotype (VTEC MPE01398), 6 ♂ paratypes (VTEC MPE01323, 1325, 1399; VMNH MPE01403, 1410, 1416), and 2 ♀ paratypes (VTEC MPE01405, 1413) from Tennessee, Putnam County, Cookeville, City Lake Natural Area, along trail out of parking lot (36.13143°N, -85.4439°W, Elev. 303 m), 21 May 2016, ex beech, maple, deciduous woods, tuliptree, oak, umbrella magnolia, hickory, moist litter on hillsides, understory of poison ivy, honeysuckle, mayapple (Coll: J. C. Means, D. A. Hennen). Material examined listed in Suppl Table 2 (online only).

Diagnosis: Adult males of *Brachoria camptera* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods**. Gonopodal acropodite D-shaped (Fig. 9A)—not circular as in *Apheloria* or oval as in *Rudiloria* species (Fig. 12). Acropodite (when viewed posteriorly) narrow, one-third width of tibia on leg pair 9. Acropodite gradually tapered to acuminate apex, not with a blunt apex as in *B. hubrichti*. Acropodite distal to anterior bend slightly curved cephalically. Acropodite shaft with cingulum (midlength transverse groove). Prefemur with curved sickle-shaped prefemoral process (Fig. 9B). **Color**. Tergites black with 2 orange (Fig. 5L), or red (Fig. 5M), paranotal spots, not with purple/purple-gray metatergal stripes as in *B. hubrichti* and *B. initialis*.

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE01398.

Measurements (mm): BL = 39.0, CW = 7.6, IW = 5.0, ISW = 1.5, B11W = 10.0, B11H = 5.2.

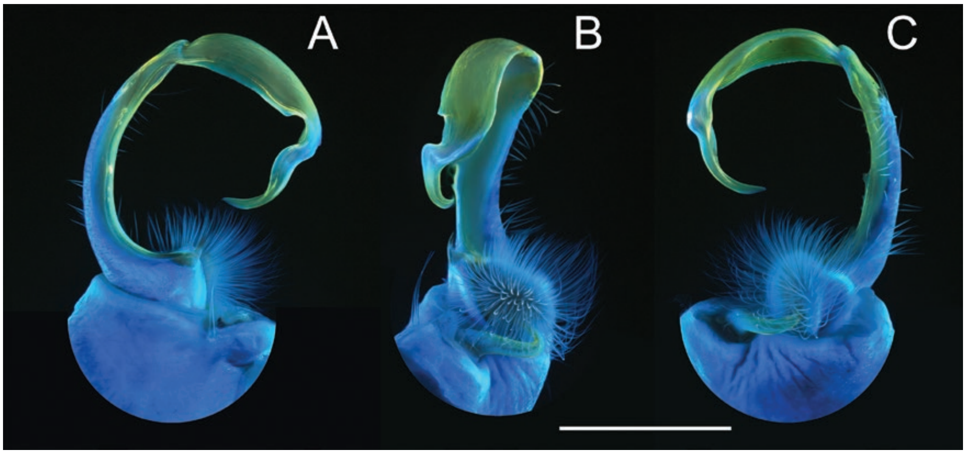

Fig. 8. *Appalachioria brownae* n. sp. holotype ♂ left gonopod (VTEC MPE01676). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

Variation: Individuals of *Brachoria camptera* n. sp. are known to exhibit two color morphs, 1) two-spotted red (Fig. 5M) and 2) two-spotted yellow-orange with a faint light blue caudal stripe (Fig. 5L).

Ecology: Individuals of *Brachoria camptera* n. sp. were collected in a mesic deciduous forest with dominant tree species of oak, maple, beech, and tuliptree.

Distribution: Known only from the type locality.

Etymology: This species is named for the shape of its acropodite, specifically the angular nature of its anterior bend. The specific name is a noun in apposition derived from the Greek *kampter*, 'bend, angle'.

Brachoria cryocybe Hennen, Means, Marek, New Species

Vernacular Name: 'The Frozen Head Mimic Millipede'

Figs. 5N and 10.

Material examined: ♂ holotype (VTEC MPE02644), 3 ♂ paratypes (VTEC MPE02582, 2583; VMNH MPE02653), and 1 ♀ paratype (VTEC MPE02652) from Tennessee, Morgan County, Wartburg, Frozen Head State Park, woods below campground (36.13206°N, -84.4978°W, Elev. 423 m), 12 May 2017, 18:45-19:38, oak, ironwood, beech, hemlock, pawpaw woods, moist litter. (Coll: D. A. Hennen, J. C. Means, V. Wong). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Brachoria cryocybe* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods**. Gonopodal acropodite smoothly oval-shaped (Fig. 10A)—not circular as in *Apheloria* or tightly oval as in *Rudiloria* species (Fig. 12). Acropodite (when viewed posteriorly) narrow, one-third width of tibia on leg pair 9. Acropodite gradually tapered to acuminate apex—curved one-dimensionally to apex, not twisted cephalically as in *Apheloria* species. Acropodal distal zone with tooth on posterior margin. Acropodite shaft with cingulum (midlength transverse groove). Prefemur with railroad spike-like prefemoral process (Fig. 10A), not bidentate as in *B. divicuma*. **Color**. Tergites black with 2 red paranotal spots, not with yellow spots as in *B. divicuma*. Caudal border of tergites with pale white stripe (Fig. 5N).

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE02644.

Measurements (mm): BL = 42.0, CW = 7.2, IW = 5.2, ISW = 1.5, B11W = 8.9, B11H = 5.3.

Variation: No significant variation from the holotype was observed.

Ecology: Individuals of *Brachoria cryocybe* n. sp. were collected in a mesic mixed forest with dominant tree species of oak, ironwood, and hemlock. They were sympatric with two other large-bodied xystodesmid species, *Apheloria montana* (Bollman, 1887) and *Brachoria forficata* (Shelley, 1986).

Distribution: Known only from the type locality.

Etymology: This species is named after Frozen Head State Park, where it was discovered. The specific name is a noun in apposition derived from the Greek *kryos*, 'icy cold', and *kybe*, 'head'.

Brachoria platana Means, Hennen, Marek, New Species

Vernacular Name: 'The Carr Creek Mimic Millipede'

Figs. 5O,P and 11.

Material examined: Type specimens. ♂ holotype (VTEC MPE03250) and ♀ paratype (VTEC MPE03253) from Kentucky, Knott County, Carr Creek State Park, woods behind campground and around marina (37.23148°N, -83.00081°W, Elev. 329 m), 27 September 2017, 15:00, dry litter of tulip poplar, sycamore, autumn olive (Coll: J. C. Means and D. A. Hennen). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Brachoria platana* n. sp. are distinct from other apheloriine species based on the following combination

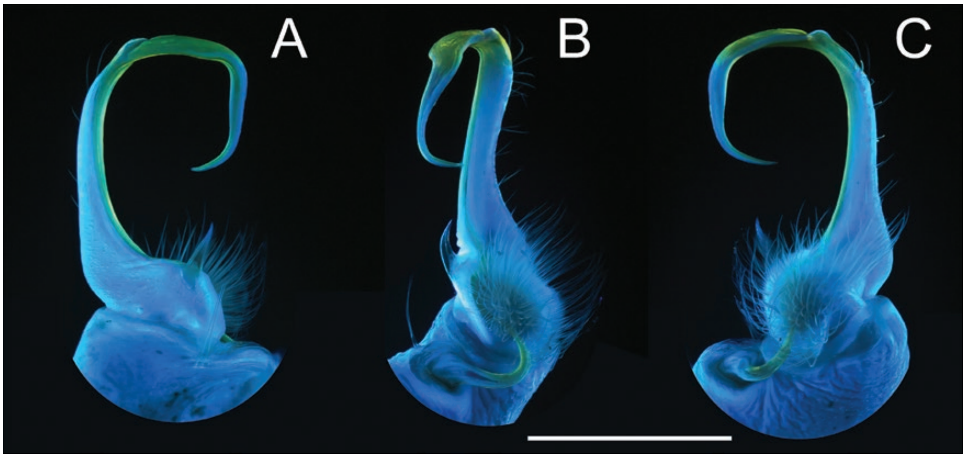

Fig. 9. *Brachoria camptera* n. sp. holotype ♂ left gonopod (VTEC MPE01398). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

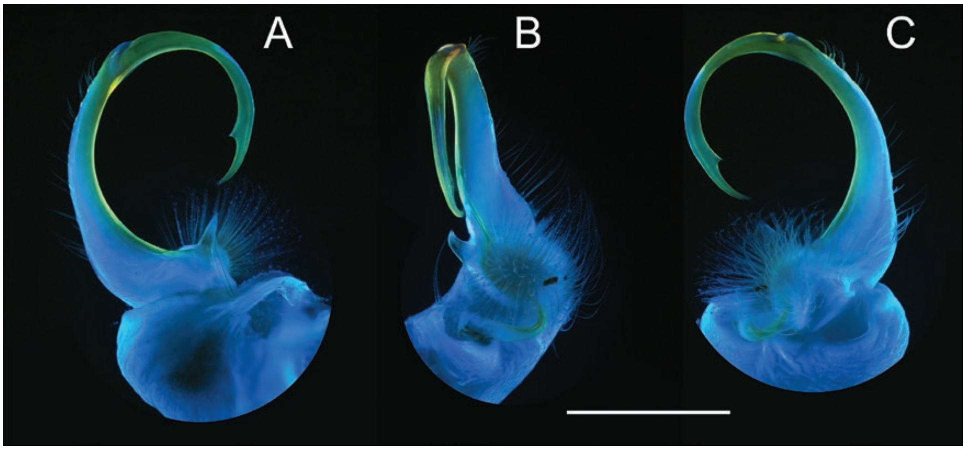

Fig. 10. *Brachoria cryocybe* n. sp. holotype ♂ left gonopod (VTEC MPE02644). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

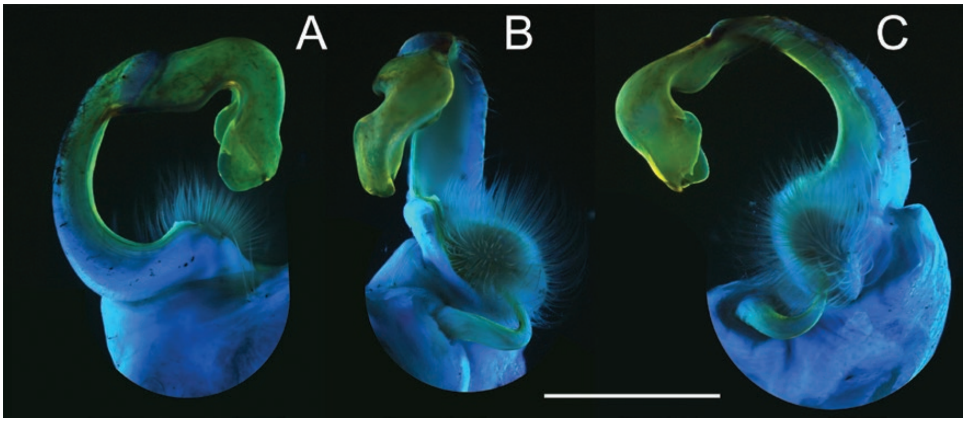

Fig. 11. *Brachoria platana* n. sp. holotype ♂ left gonopod (VTEC MPE03250). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

of characters: **Gonopods.** Gonopodal acropodite curving dorsomedially at apex, with a distal cingulum, separating it from *Apheloria* and *Rudiloria* (Fig. 11). Prefemoral process reduced to small ridge. Distal zone sinuous, curving first ventrally and then dorsally; in anterior view directed posteriorly at 90° from apex. Acropodite tip with lateral and medial flanges forming an envelope-like structure through which runs an elevated ridge carrying the solenomere (Fig. 11A). **Color.** *Brachoria platana* n. sp. has two color morphs, co-occurring. Tergites always with red or yellow paranotal spots, sometimes also with concolorous metatergal middorsal spots or stripes. Dark-brown to black background. Collum always with concolorous red or yellow anterior and lateral spots, sometimes also with a posterior spot and concolorous marginal lines connecting the spots.

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE03250. Measurements (mm): BL = 41.0, CW = 7.4, IW = 4.7, ISW = 1.6, B11W = 9.4, B11H = 5.4.

Variation: Individuals of *Brachoria platana* n. sp. are known to exhibit two color morphs, 1) striped red (Fig. 5O) and 2) three-spotted yellow (Fig. 5P).

Ecology: Individuals of *Brachoria platana* n. sp. were found in a mesic deciduous forest of tulip poplar, sycamore and autumn olive by the water's edge of Carr Creek Lake.

Distribution: *Brachoria platana* n. sp. is known only from the type locality.

Etymology: This species is named after where the holotype was discovered, in a grove of American sycamores (*Platanus occidentalis*). The specific name is a noun in apposition derived from the Latin genus name of the American sycamore, '*Platanus*'.

Genus *Daphnedesmus* Marek, Means, Hennen, New Genus

Vernacular name: 'The Gold Crowned Millipedes'

Type species: *Deltotaria coronata* Hoffman, 1949.

Taxa included:

Daphnedesmus coronata (Hoffman, 1949) (=*Deltotaria coronata*);

Daphnedesmus dactylifera (Hoffman, 1956) (=*Dixioria dactylifera*);

Daphnedesmus fowleri (Hoffman, 1956) (=*Dixioria pela fowleri*).

Diagnosis: Adult males of *Daphnedesmus* are distinct from other apheloriine genera based on the following combination of characters: **Color**. Tergites with 2 yellow paranotal spots. Collum with yellow stripe on anterior margin. (The color and pattern is constant within the genus.) **Gonopods**. Acropodite with a medial margin tooth—apex appearing forked. Prefemoral process long and stout, not longer than one-half the length of the acropodite as in the Rhysodesmini. Gonopodal acropodite D-shaped—not circular as in *Apheloria* or oval as in *Rudiloria* species (Fig. 10). Acropodite never with a cingulum, as in *Brachoria* and *Appalachioria*. **Tergites**. Caudolateral corners of paranota rounded throughout midbody segments. **Nucleotide site substitutions**. 16S: A (1192, 1497).

Distribution: *Daphnedesmus* species are known from the mountainous borderlands between North Carolina, Tennesee, and Virginia with Burkes Garden, Virginia as the northern limit and Ashe County, North Carolina as the southern limit.

Etymology: This genus is named after the yellow stripe on the collum that appears as if the millipede is wearing a gold crown, and that mountain laurels (*Kalmia latifolia* L.) are commonly encountered with members of the genus. The name is a combination of the Greek, *daphne*, 'laurel' (bay laurel, *Laurus nobilis* L.) and *desma* 'band'. The ending '*-desmus*' is commonly used for genus names in the order.

Genus *Idaloria* Marek, Means, Hennen, New Genus

Vernacular name: 'The Mount Ida Millipede'
Type species: *Cibularia profuga* Causey, 1955.
Taxa included: monotypic.

Diagnosis: Adult males of *Idaloria* are distinct from other genera of the tribe Rhysodesmini based on the following combination of characters: **Gonopods**. Acropodite linear, not curved as in the Apheloriini. Acropodite distinctly narrowed at apex, forming angular shoulder. Prefemoral process acicular, longer than one-half the length of the acropodite. Acropodite without a cingulum, as in *Brachoria* and *Appalachioria*. **Color**. Tergites with 2 red paranotal spots. **Nucleotide site substitutions**. 12S: C (94); 16S: T (146, 451); G (934, 1239); T (1017, 1322); C (1043, 1348); COI: T (265, 2541); 28S: T (1293, 5644).

Distribution: *Idaloria profuga* is known from a population in the Ouachita Mountains of Montgomery County, Arkansas and a second disjunct population in Ouachita Parish, Louisiana.

Etymology: This genus is named after where the type was discovered on Mount Ida, Arkansas. The name is a combination of 'Ida' and the Latin *-orium*, 'place for'. The ending '*-oria*' is commonly used for genera in the family.

Genus *Rudiloria* Causey, 1955

Vernacular name: 'The Brilliant Allegheny Millipedes'
Type species: *Rudiloria mohicana* Causey, 1955.
Taxa included: 7 species, see Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

Rudiloria charityae Marek, New Species

Vernacular Name: 'Charity's millipede'

Figs. 5Q and 12.

Rudiloria 'n. sp. Chagrin' Means and Marek 2017

Material examined: ♂ holotype (VTEC MTX0185) from Ohio, Cuyahoga County, Cleveland Metroparks, South Chagrin Reservation, Henry Church Rock Loop Trail, near falls and swimming hole (41.41598°N, -81.4145°W), 12 June 2010, ex on top dead leaves in maple forest (Coll: P. E. Marek). Material examined listed in Supp Table 2 [online only].

Diagnosis: Adult males of *Rudiloria charityae* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods**. Gonopodal acropodite smoothly oval-shaped (Fig. 12A)—not circular as in *Apheloria* species. Acropodite (when viewed posteriorly) narrow, one-third width of tibia on leg pair 9. Acropodite gradually tapered to acuminate apex–curved one-dimensionally to apex, not twisted cephalically as in *Apheloria* species. Acropodite shaft smooth without cingulum (midlength transverse groove) as in *Brachoria*; without teeth, swellings, joints, or projections as in other *Rudiloria* species. Prefemur with a nubbin-like prefemoral process, one-tenth length of acropodite (Fig. 12C), not long and scythe-like as in *Rudiloria kleinpeteri*, *Rudiloria trimaculata*. **Color**. Tergites with 3 spots: 1 orange metatergal spot, 2 yellow paranotal spots (Fig. 5Q). Collum with yellow spot anteriorly, gradually fading into orange metatergal spot.

Description: Supp Table 3 (online only). Based on Holotype (♂) MTX0185.

Measurements (mm): BL = 34.0, CW = 6.1, IW = 4.1, ISW = 1.2, B11W = 7.2, B11H = 4.5.

Variation: No significant variation from the holotype was observed.

Ecology: Individuals of *Rudiloria charityae* n. sp. have been collected in deciduous broadleaved forests of maple and beech.

Distribution: *Rudiloria charityae* n. sp. is known from Cuyahoga and Geauga counties in the Erie Drift Plain Region, and Monroe County in the Western Allegheny Plateau Region of eastern Ohio.

Etymology: The holotype specimen was collected on the wedding day of PEM during a family hike to his childhood swimming hole in the Chagrin River, Cuyahoga County, Ohio. The species is named for his wife Charity Hall.

Genus *Sigmoria* Chamberlin, 1939.

Vernacular name: 'The Sigmoid Millipedes'
Type species: *Sigmoria munda* Chamberlin, 1939.
Taxa included: 67 species, see Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

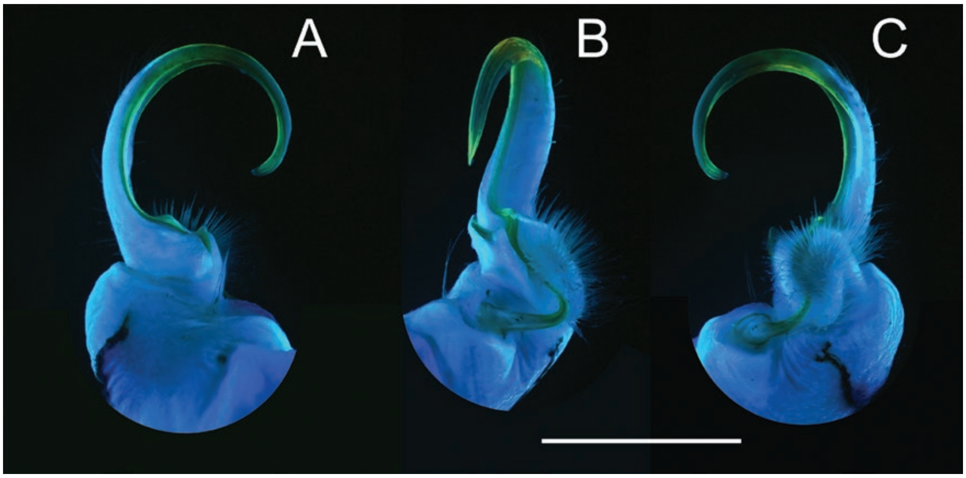

Fig. 12. *Rudiloria charityae* n. sp. holotype ♂ left gonopod (VTEC MTX0185). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

Sigmoria beameri Marek, Means, Hennen, New Species

Vernacular Name: 'Beamer's Sigmoid Millipede'

Figs. 5R and 13.

Cleptoria 'n. sp. Hagoods' Means and Marek 2017

Material examined: Type specimens. ♂ holotype (VTEC MPE00291), 1 ♂ paratype (VMNH SPC000389), and 2 ♀ paratypes (VTEC SPC000390, 394). Holotype from South Carolina, Barnwell County, Toby Creek, near Hagoods Mill, SC-64 (33.2119°N, -81.3201°W, Elev: 46 m), 23 November 2003, (Coll: D. Beamer). Paratypes from South Carolina, Barnwell County, Hagoods Mill, SC-64, 351 rd m W jct w/ Lebanon Rd., nr Toby Ck (33.21206°N, -81.3198°W, Elev: 46 m), 17 October 2004, beneath leaf litter (*Quercus, Acer*) (Coll: P. Marek, D. Beamer, M. Beamer). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Sigmoria beameri* n. sp. are distinct from other apheloriine species based on the following combination of characters: **Gonopods.** Gonopodal acropodite broad, curving dorsomedially at an almost 90° angle at anterior bend (Fig. 13A). Basal zone lacking spines or tubercles, prefemoral process absent. Medial flange thick, laminate. Acropodite peak broad, flattened, distally with a wide, laminate lateral flange which is distinctly constricted at its base, setting it off from its ventrally-directed tip, separating it from other species with a birdhead-like acropodal apex (=*Cleptoria*) *Sigmoria abbotti* (Hoffman, 1967), *Sigmoria bipraesidens* (Hoffman, 1967), *Sigmoria macra* (Chamberlin, 1939), *Sigmoria rileyi* (Bollman, 1889), *Sigmoria robusta* Shelley, 1986, *Sigmoria shelfordi* (Loomis, 1944), and *Sigmoria arcuata* (Shelley, 1981). Acropodite without a cingulum, as in *Brachoria* and *Appalachioria*. **Color.** Tergites with light-red paranotal spots (Fig. 5R). Dark brown background. Collum with light red anterior and lateral margins.

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE00291.

Measurements (mm): BL = 47.0, CW = 6.9, IW = 4.5, ISW = 1.5, B11W = 9.4, B11H = 5.8.

Variation: No significant variation from the holotype was observed.

Ecology: *Sigmoria beameri* n. sp. was collected from the riparian area around Toby Creek and was found under oak and maple leaves.

Distribution: Only known from the type locality, a small wooded area around Toby Creek, located in the Coastal Plain region of South Carolina.

Etymology: This species is named for its discoverer, Dr. David Beamer of Nash Community College. The specific name is a genitive noun derived as a patronym.

Tribe Nannariini Hoffman, 1964

Genus *Nannaria* Chamberlin, 1918

Vernacular Name: 'The Twisted-Claw Millipedes'

Type species: *Nannaria minor* Chamberlin, 1918.

Taxa included: 26 species, see Supp Material (online only) (Supp Text 1 [online only], Supp Dataset 2 [online only]).

Nannaria aenigma Means, Hennen, Marek, New Species

Vernacular Name: 'The New River Twisted-Claw Millipede'

Figs. 5S,T and 14.

Material examined: Type specimens. ♂ holotype (VTEC MPE02632) and ♀ paratype (VTEC MPE02633) from Virginia, Smyth County, Raccoon Branch Wilderness, Raccoon Branch Campground, Raccoon Branch Trail (36.7454°N, -81.4259°W, Elev. 858 m), 5 May 2017, 13:55, Moist deciduous leaf litter, rhododendron and eastern hemlock (Coll: D. A. Hennen). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Nannaria aenigma* n. sp. are distinct from other nannariine species based on the following combination of characters: **Gonopods.** Gonopodal acropodite long, undivided, gently curving medially at apex, not straight as in *N. ericacea*

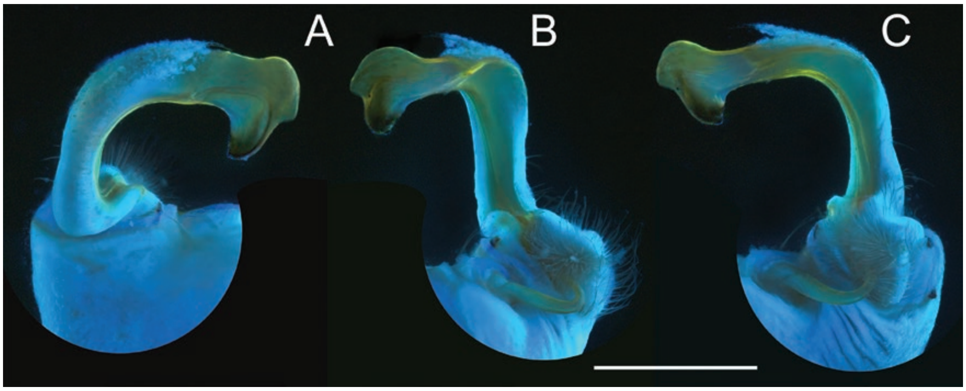

Fig. 13. *Sigmoria beameri* n. sp. paratype ♂ left gonopod (VTEC SPC000389). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

(Fig. 14A and B). Acropodite peak with a dorsal tooth and a shallow twist, separating it from *N. wilsoni*. Distal zone slightly twisted, directed ventromedially and tapering to a blunt tip. Prefemoral process long, slightly sinuous, laminate, not divided as in *N. hokie* n. sp. **Color.** Tergites with white (Fig. 5T) or sometimes light-pink (Fig. 5S) paranotal spots. Dark brown to black background. Collum with white or sometimes light-pink anterior and lateral margins.

Description: Supp Table 3 (online only). Based on Holotype (♂) MPE02632 and paratype (♀) MPE02633.

Measurements (mm): BL = 32.0, CW = 4.2, IW = 2.8, ISW = 1.0, B11W = 5.2, B11H = 3.0.

Variation: The size of the prefemoral process in *Nannaria aenigma* n. sp. ranges from about one-half to three-quarters of the length of the acropodite. The dorsal tooth of the acropodite exhibits slight size variation, but is usually the shape of a sharp or blunt 'thumb'. Gonopodal basal zone tubercle varies from very slight to pronounced. *Nannaria aenigma* n. sp. has two color forms: one with pink-peach paranotal spots (Fig. 5S) and collum margins, and one with white paranotal spots and collum margins (Fig. 5T).

Ecology: *Nannaria aenigma* n. sp. individuals were typically found under leaf litter in mesic broadleaf deciduous forests composed of oak, maple, and tuliptree. They were also found in forests with ample rhododendron and hemlock trees, and sometimes also in forests with pine and witch hazel trees. Rarely, they were found in dry habitats and walking on dirt trails during the night.

Distribution: *Nannaria aenigma* n. sp. is known only from southwest Virginia, with records from Russell, Washington, Tazewell, Smyth, Grayson, Bland, Wythe, and Pulaski counties. Its eastern extent is bounded by the New River, which may have acted as a physiographic barrier to the species. It seems likely that with more collecting, *Nannaria aenigma* n. sp. will eventually be found in neighboring counties in West Virginia, Tennessee, and North Carolina.

Etymology: This species is named for the shape of its acropodite, specifically its question-mark like appearance. The specific name is a noun in apposition derived from the Latin *aenigma*, 'riddle, mystery'.

Nannaria hokie Means, Hennen, Marek, New Species

Vernacular Name: 'The Hokie Twisted-Claw Millipede'

Figs. 5U and 15.

Material examined: Type specimens. ♂ holotype (VTEC MPE04803) from Virginia, Montgomery County, Blacksburg, Virginia Tech campus, Stadium Woods (37.22160°N, -80.41598°W, Elev. 637 m), 17 April 2019, found crawling on ground (Coll. P. Marek). 5 ♂ paratypes (VTEC MPE00880, 882, 883; VMNH MPE00884, 886), and 2 ♀ paratypes (VTEC MPE00881, 885) from Virginia, Montgomery County, Blacksburg, Virginia Tech campus, south side of Duck Pond (37.2250°N, -80.4276°W, Elev. 625 m), 13 October 2015, ex moist deciduous leaf litter and under logs, fallen bark (Coll. D. A. Hennen). Material examined listed in Supp Table 2 (online only).

Diagnosis: Adult males of *Nannaria hokie* n. sp. are distinct from other nannariine species based on the following combination of characters: **Gonopods.** Gonopodal acropodite long and curving ventromedially before apex, not medially as in *Nannaria castanea* (McNeill, 1887) or straight as in *N. ericacea* (Fig. 15A and C). Distal zone bent ventroposteriorly, with laminate flange encircling tip forming a hood-like structure around dorsoposteriorly projected, laminate solenomere, partially obscuring solenomere when viewed laterally—not with flat laminate flange, at 90° angle to solenomere as in *N. castanea* or laminate, sinuous, directed ventrocephallicaly as in *N. ericacea*. Acropodite with small medial flange near apex, not with lateral projection as in *N. ericacea*. Telopodite basal zone height > 1/4 length of acropodite, not 1/4 length as in *N. castanea*, or < 1/5 as in *N. ericacea*. Prefemoral process small, thin, curving medially, arising from top of prefemoral spine, not large, laminate as in *N. ericacea* or straight as in *N. castanea*. **Color.** Tergites with orange or red paranotal spots (Fig. 5U). Dark brown background. Collum smooth with orange or red margin.

Description: Supp Table 3 (online only). Based on Paratype (♂) MPE00880.

Measurements (mm): BL = 18.0, CW = 2.9, IW = 2.3, ISW = 0.8, B11W = 3.5, B11H = 2.2.

Variation: The prefemoral process in *Nannaria hokie* n. sp. can be bifurcate or entire. In bifurcate individuals, the two branches can

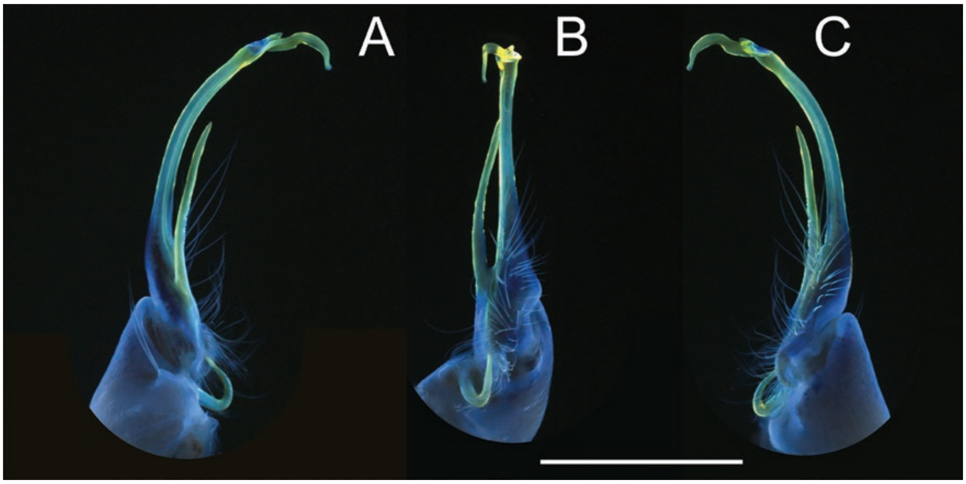

Fig. 14. *Nannaria aenigma* n. sp. holotype ♂ left gonopod (VTEC MPE02632). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

be subequal, or the anterior branch can be twice the length of the posterior branch. The distal zone of the acropodite typically curves ventrally, but may instead be angled dorsally.

Ecology: Individuals of *Nannaria hokie* n. sp. have been found in mesic deciduous forests of oak, beech, and maple, and in mixed forests that include these species as well as pine.

Distribution: *Nannaria hokie* n. sp. is known only from Montgomery, Floyd and Pulaski Counties in southwest Virginia.

Etymology: This species is named after Virginia Tech, where it was discovered on campus in Stadium Woods (an old growth oak forest) and at the Duck Pond. The specific name is a noun in apposition derived from the Old Hokie Cheer: 'Hokie, Hokie, Hokie, Hy! / Tech, Tech, VPI / Sol-a-rex, Sol-a-rah / Poly Tech Vir-gin-ia / Ray rah VPI / Team! Team! Team!'.

Key to the Tribes of Xystodesmidae

Millipedes of the family Xystodesmidae from North America between meridians 68°W (ca. Maine, USA) and 115°W (ca. New Mexico, USA)* use Key 1; all others use Key 2.

Key 1

1. Epiproct flat and broad distally (Fig. 16A)................Euryurini

   Epiproct narrow and conical distally (Fig. 16B) 2
2. Mandibular stipes with knob (Fig. 16C)....... Eurymerodesmini

   Mandibular stipes without knob 3
3. Telopodite without a prefemoral process (Fig. 16D); telopodite distinctly curved and/or twisted.................Apheloriini, in part

   Telopodite with a prefemoral process (Fig. 16E and F); telopodite variable 4
4. Prefemoral process shorter than half the length of the acropodite (Figs 16E) 5

   Prefemoral process longer than half the length of the acropodite (Fig. 16F) 6
5. Telopodite sublinear in shape, with acicular prefemoral process 7

   Telopodite distinctly curved and/or twisted, with stout prefemoral process that is usually curved, often hook-like ....Apheloriini, in part
6. Tarsal claws anterior to the gonopods twisted and spatulate (Fig. 16G) ....Nannariini

   Tarsal claws unmodified; bisinuately curved, or curved (Fig. 16H)...7
7. Paramedial spines usually present on midbody sterna (Fig. 16I). Acropodite sublinear in shape. Acicular prefemoral process, thinner than acropodite—typically long.............Rhysodesmini

   Paramedial spines absent on midbody sterna. Acropodite thin, curved in shape, hook-like with an acuminate tip (Fig. 16J). Prefemoral process long and broad, bulky and complex, much thicker than acropodite. Body rings with reduced paranota, red metatergal stripes, collum circled with red border .... Xystodesmini, in part, *Semionellus placidus* (Wood, 1864)

Key 2

1. Dorsum of exoskeleton highly sculptured (Fig. 16K–M), body with > 20 rings, body length < 10 mm (Mediterrranean Basin) ....Devilleini

   Exoskeleton smooth, body with 19+t rings, body length > 10 mm 2
2. Males with long coiled acropodite, forming 1.5 – 2 loops, without prefemoral process (Fig. 16N); females with membranous neck of the cyphopod modified into long retractable bellows (Fig. 16O) (Japan).................................Parafontariini

   Males with acropodite with ≤ 1 loop; females with membranous neck of the cyphopod short, not bellow-like, less than the length of the coxae...3
3. 3rd pair legs of males with conical coxal process (Fig. 16P), 2nd pair of legs of females with cylindrical coxal process; metatergites occasionally with small bumps (papillae), thereby reducing the glossiness of the cuticle (Figs. 1C and 16Q); not very colorful, usually bimaculate, highly fluorescent when

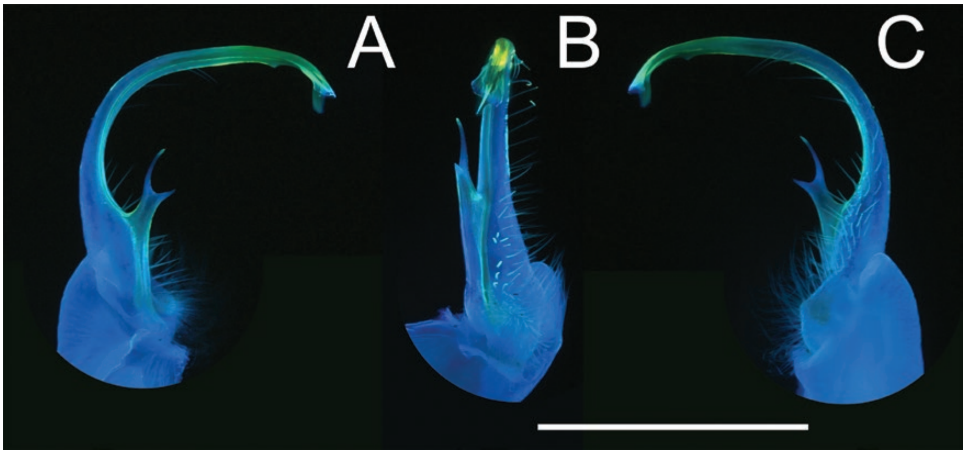

Fig. 15. *Nannaria hokie* n. sp. paratype ♂ left gonopod (VTEC MPE00880). (A) Anterior view; (B) Medial view; (C) Posterior view. Scale bar = 1.0 mm.

illuminated with ultraviolet light—some bioluminescent (California)..Xystocheirini

Coxae without processes 4

4. Males with acropodite simple, sickle shaped (Fig. 16R); colorful, yellow trimaculate—some with red paranotal spots (Mediterranean Basin and northern Africa) ....Melaphini

   Males with acropodite not sickle shaped, colors variable (WNA and EA) 5

5. Males with acropodite with postfemoral process, acropodite apex expanded and quadrate (as in Fig. 16S); not very colorful; body length < 20 mm (Kern County, California) ....Octhocelatini (*Ochthocelata adynata*)

   Males with acropodite without postfemoral process, acropodite apex variable; typically colorful; body length > 20 mm...........6

6. Colorful xystodesmid millipedes; yellow trimaculate; body appearing moniliform with flattened paranota; paranota horizontal, situated high on body rings; paranotal corners rounded (Fig. 1J). With protuberant knobs above (dorsal to) spiracles. Without spines on the prefemur. Sternal remnant between gonopodal coxae present. Large bodied, usually greater than about 35 mm. (California)..................................Sigmocheirini

   Not very colorful, usually bimaculate; body compact in general appearance and tergites arched, with paranota oriented downwards. Paranotal corners sharp (or hooked) (Fig. 1L). Without protuberant knobs above (dorsal to) spiracles. With or without spines on the prefemur. Sternal remnant between gonopodal coxae present or absent. Metatergites occasionally with small bumps (papillae), thereby reducing the glossiness of the cuticle (Fig. 16Q). Body lengths variable, usually greater than about 20 mm. Males with a long, nearly straight sternal apodeme of the gonopodal coxae......................................Xystodesmini, in part, all other members of the tribe spare *Semionellus placidus* (Wood, 1864) from WNA and EA

Diagnoses of the Tribes of Xystodesmidae

Xystodesmidae: Adults of Xystodesmidae are distinct from other members of the suborder Leptodesmidea based on the following combination of characters. Colorful, conspicuous millipedes, with few drab cryptic species. Exoskeleton weakly to strongly fluorescent when illuminated with ultraviolet light. Dorsum glossy, smooth—sometimes coriaceous. Body broad, compact, capsule-like in general appearance. Lateral margins of paranota continuous, reducing segmented appearance—usually not moniliform as in the Rhachodesmidae, Chelodesmidae, Oxydesmidae. Body length 12–80 mm, typically 20–35 mm, and rarely less than 20. Tergites arched, with paranota oriented downwards, not flat as in the Chelodesmidae, Oxydesmidae, Rhachodesmidae. Seventh antennomere unmodified (for Diplopoda), sensory cones in a simple square or circular ring, not separated by invaginations of the distal rim of the antennomere as in the Chelodesmidae. Legs usually with prefemoral spines, sharper on pregonopodal legs. Gonopod cannula present distally on coxa, separated from coxal cuticle by membrane forming a cannular socket. Gonopods composed of coxa and telopodite. Telopodite composed of a basal prefemur and distal acropodite. Acropodite apex simple, usually ≤ 2 branches. Gonopod aperture transverse relative to trunk axis, elliptical in shape; large, thereby reducing the seventh trunk ring prozonite anteriorly to a narrow cuticular bar. In life, individuals readily emit liquid chemical secretions composed of a strong cherry, almond odor (benzaldehyde byproduct of cyanogenic reaction).

Rhysodesminae: colorful (highly variable hues and patterns, Fig. 3A and B) large bodied (> 35 mm) xystodesmid millipedes from North America between meridians 68°W (ca. Maine, USA) and 115°W (ca. New Mexico, USA)*, but with some not very colorful (cryptic with background matching, Fig. 3D–H), small bodied (<35 mm) members. Metatergites usually glossy (Fig. 1A), without small bumps (papillae or tubercles)—papillae or tubercles are typically present in the Xystodesminae. Telopodite usually curved medially (Fig. 16D and E), twisted cephalically in colorful, large bodied members; telopodite usually sublinear in shape (Fig. 16S) in cryptic, small bodied members.

Apheloriini (ENA): xystodesmid millipedes with telopodites with short or no prefemoral process—not long, acicular as in the Rhysodesmini. If prefemoral process present, it is usually stout, curved—often hook-like. Sternal remnant between gonopodal coxae absent. Telopodite curved medially (Fig. 16D and E) and twisted cephalically (with torsion)—not linear as in the Rhysodesmini. Paramedial spines absent on midbody sterna. Colorful; highly variable hues and patterns. Large bodied, usually greater than about 35 mm.

Taxa included, and identification resources. Seven genera: *Apheloria* (Marek et al. 2018, Zootaxa, 4735); *Appalachioria* (as

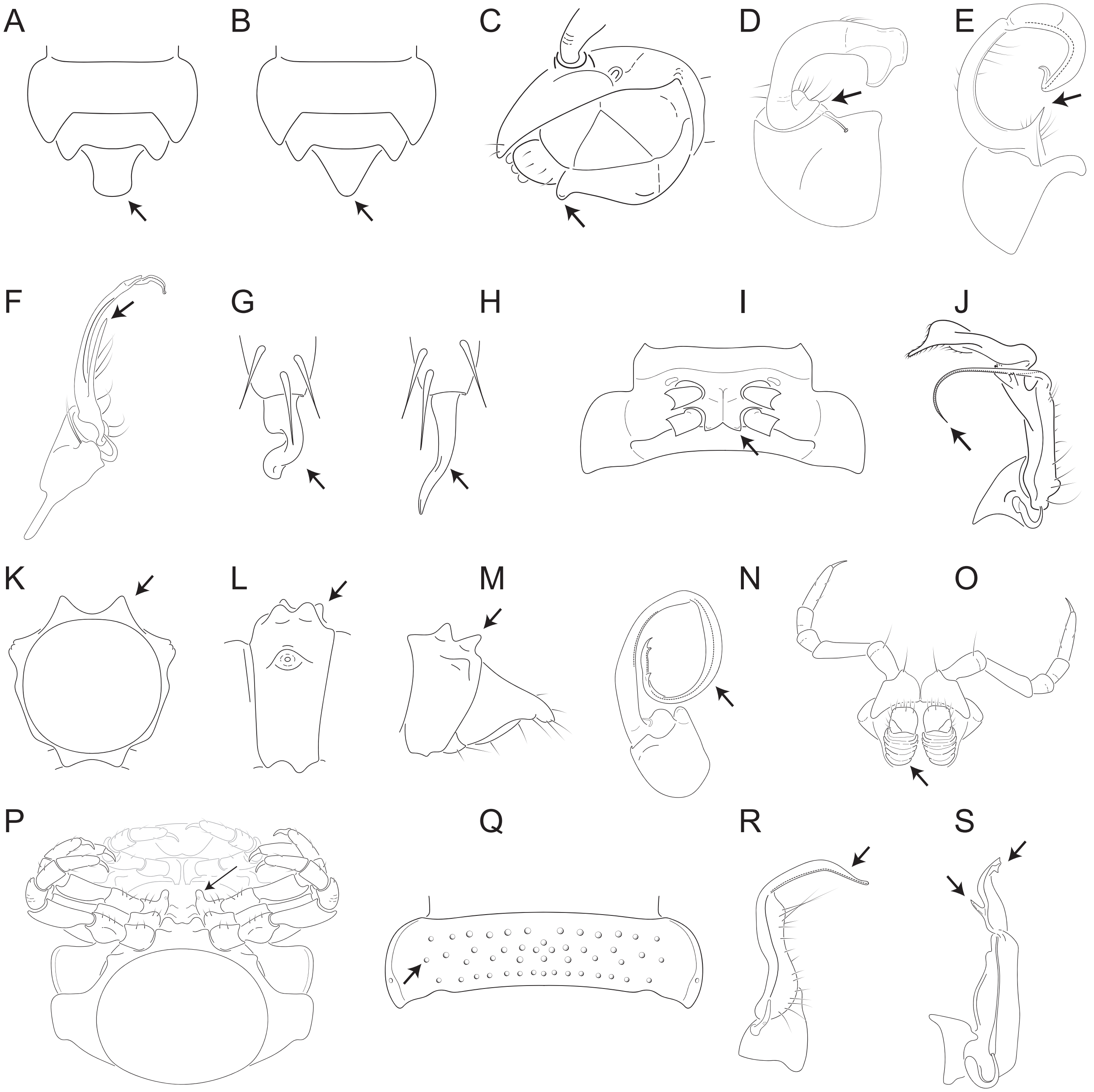

Fig. 16. Key characters for identification of tribes of Xystodesmidae. (A) Epiproct flat and broad distally (Euryurini); (B) Epiproct narrow and conical distally; (C) Mandibular stipes with knob (Eurymerodesmini); (D) Telopodite without a prefemoral process; (E) Telopodite with a prefemoral process; (F) Prefemoral process longer than half the length of the acropodite; (G) Tarsal claws anterior to the gonopods twisted and spatulate (Nannariini); (H) Tarsal claws unmodified; bisinuately curved, or curved; (I) Paramedial spines usually present on midbody sterna (Rhysodesmini); (J) Acropodite thin, curved in shape, hook-like with an acuminate tip (*Semionellus placidus*); (K–M) Dorsum of exoskeleton highly sculptured (Devilleini); (N) long coiled acropodite, forming 1.5–2 loops (Parafontariini); (O) membranous neck of the cyphopod modified into long retractable bellows (Parafontariini); (P) third pair legs of males with conical coxal process (Xystocheirini); (Q) metatergites with small papillae (Xystocheirini); (R) acropodite simple, sickle shaped (Melaphini); (S) acropodite apex expanded and quadrate (Octhocelatini).

formerly part of *Brachoria*: Keeton, 1959, Proceedings of the United States National Museum, 109; *Appalachioria versicolor*: Hoffman, 1963, Proceedings of the Biological Society of Washington, 76); *Brachoria* (Marek, 2010, Zoological Journal of the Linnean Society, 159); *Deltotaria* (Shelley, 1986, in: Shelley & Whitehead, Memoirs of the American Entomological Society, 35: 151); *Daphnedesmus* (below; as part of subgenus *Dixioria*: Shelley, 1986, in: Shelley & Whitehead, Memoirs of the American Entomological Society, 35: 151); *Rudiloria* (Shelley, 1986, in: Shelley & Whitehead, Memoirs of the American Entomological Society, 35: 151); *Sigmoria* (Shelley, 1986, in: Shelley & Whitehead, Memoirs of the American Entomological Society, 35: 151).

Rhysodesmini (NA): xystodesmid millipedes with acicular prefemoral process, typically long; not a stout, curved prefemoral process—or lacking entirely—as in the Apheloriini. Sternal remnant between gonopodal coxae usually present. Telopodite sublinear in shape, not distinctly curved or twisted as in the Apheloriini. Paramedial spines usually present on midbody sterna (Fig. 16I).

Typically not very colorful. Small bodied, usually less than about 35 mm. Non-monophyletic (Fig. 3).

Taxa included, and identification resources. 16 genera: *Aporiaria* (as formerly part of *Rhysodesmus*: Hoffman, 1970, Radford Review, 24); *Boraria* (Shelley et al. 2011, Insecta Mundi, 0194); *Caralinda* (Shelley, 1983, Florida Entomologist, 66; Shelley, 2001, Myriapodologica, 7); *Cherokia* (Hoffman, 1960, Proceedings of the United States National Museum, 112; and a revision is in preparation by Fernanda Vasquez Valverde); *Dicellarius* (Shelley, 1984, Proceedings of the Biological Society of Washington, 97); *Erdelyia* (Hoffman, 1962a, Proceedings of the Biological Society of Washington, 75); *Gonoessa* (Shelley, 1984, Florida Entomologist, 67); *Gyalostethus* (Hoffman, 1965, Proceedings of the United States National Museum, 117); *Howellaria* (as formerly part of *Boraria*: Shelley et al. 2011, Insecta Mundi, 0194); *Idaloria* (as formerly part of *Boraria*: Shelley et al. 2011, Insecta Mundi, 0194); *Lourdesia* (Shelley, 1991, Proceedings of the Entomological Society of Washington, 93); *Pachydesmus* (Hoffman, 1958, Proceedings of the United States National Museum, 108); *Parvulodesmus* (*Parvulodesmus prolixogonus*: Shelley, 1983, Proceedings of the Biological Society of Washington, 96; *Parvulodesmus stephani*: Shelley, 2001, Myriapodologica, 7); *Pleuroloma* (Shelley, 1980b, Canadian Journal of Zoology, 58); *Rhysodesmus* (except for a listing of species, there have been no taxonomic syntheses of *Rhysodesmus*, and a revision is in preparation by Ismael Huerta); and *Stenodesmus* (as formerly part of *Cibularia*: Hoffman 1966, Transactions of the American Entomological Society, 92).

Nannariini (ENA): xystodesmid millipedes with males with twisted spatulate claws (Fig. 16G)—not sinuate or bisinuate as in other xystodesmids. With long, acicular prefemoral process (Fig. 16F)—not short or no prefemoral process as in the Apheloriini. Sternal remnant between gonopodal coxae absent. Paramedial spines present on midbody sterna. Not very colorful. Small bodied, usually less than about 35 mm.

Taxa included, and identification resources. 2 genera: *Oenomaea* (Hoffman, 1964, Proceedings of the Biological Society of Washington, 77) and *Nannaria* (except for a listing of species, there have been no taxonomic synthesis of *Nannaria*, and a revision is in preparation by J.C.M. and D.A.H.).

Euryurini (ENA): xystodesmid millipedes with flattened broad epiproct (Fig. 16A)—not conical as in other xystodesmids. Consistently orange-pink trimaculate coloration. Gonopod without a prefemoral process. Sternal remnant between gonopodal coxae present. Small bodied, usually less than about 35 mm. Fluorescent when illuminated with ultraviolet light.

Taxa included, and identification resources. 2 genera: *Euryurus* (Hoffman, 1978, Transactions of the American Entomological Society, 104; as formerly part of *Auturus*: Shelley, 1982, Canadian Journal of Zoology, 60: 3262; *Euryurus lecythanoictes* Jorgensen, 2009, The Great Lakes Entomologist, 42) and *Illiniurus* (Shear, 1968, Proceedings of the Biological Society of Washington, 81).

Eurymerodesmini (ENA): xystodesmid millipedes with a ventral ridge on the mandibular stipes (Fig. 16C). Acropodite simple, sickle-shaped, caudally projecting—not projecting anteriorly as other xystodesmids. Gonopodal aperture modified, with rim elevated and variably shaped. Fluorescent when illuminated with ultraviolet light.

Taxa included, and identification resources. 1 genus: *Eurymerodesmus* (Shelley, 1989, Memoirs of the American Entomological Society, 37).

Xystodesminae: not very colorful, usually bimaculate color pattern (though usually highly fluorescent when illuminated with ultraviolet light) xystodesmid millipedes from North America between meridians 113°W (ca. Missoula, Montana, USA) and 133°W (ca. Alexander Archipelago, Alaska, USA); the Mediterranean Basin between meridians 33°E (ca. Mersin Province, Turkey) and 5°W (ca. eastern Morocco); and Asia between meridians 142°E (ca. Hokkaido, Japan) and 102°E (Muli County, Sichuan Province, China)* Metatergites occasionally with small bumps (papillae or tubercles), thereby reducing the glossiness of the cuticle (Figs. 1C, 16K–M,Q). Telopodite usually sublinear in shape with acropodite apex usually with ≥ 2 branches (Fig. 16J), but some with telopodite curved medially with a single process (Fig. 16N and R). Caudolateral corners of paranota usually sharp (or hooked), extending posteriorly beyond medial metatergal margin (Fig. 1C and L).

Xystodesmini (EA, WNA, 1 species in ENA): xystodesmid millipedes with a long, nearly straight sternal apodeme of the gonopodal coxae. Acropodite apex simple, usually ≤ 2 branches. Sternal remnant between gonopodal coxae absent or present. Caudolateral corners of paranota usually sharp (or hooked), extending posteriorly beyond medial metatergal margin (Fig. 1L). Metatergites occasionally with small bumps (papillae), thereby reducing the glossiness of the cuticle. Not very colorful, usually bimaculate. Highly fluorescent when illuminated with ultraviolet light.

Taxa included, and identification resources. 19 genera: EA—*Kiulinga* (*Kiulinga jeekeli*: Hoffman, 1956, Proceedings of the Entomological Society of Washington, 58; *Kiulinga lobosa*: Zhang & Mao, 1984, Acta Zootaxonomica Sinica, 9). *Koreoaria* (*Koreoaria amoea*: Takakuwa, 1942, Transactions of Natural History Society of Formosa, 32; *Koreoaria pallida*: Verhoeff, 1937, Zoologischer Anzeiger, 117); *Levizonus* (Japanese species: Tanabe, 1994, Japanese Journal of Entomology, 62; Russian species: Mikhaljova, 2017, The millipede fauna (Diplopoda) of the Asian part of Russia); *Pamelaphe* (Hoffman, 1964, Transactions of the American Entomological Society, 90); *Parariukiaria* (Nguyen, 2016, Zootaxa, 4121); *Riukiaria* (except for listings of species, there have been no taxonomic synthesis of *Riukiaria*—see also Korsós et al., 2011, Zootaxa, 2877); *Xystodesmus* (Tanabe & Shinohara, 1996, Journal of Natural History, 30; *Xystodesmus yamamiensis* Masuda, 2001, KUMO, 34); *Yaetakaria* (Hoffman, 1949, Chicago Academy of Sciences Natural History Miscellanea, 45). WNA—*Chonaphe* (Shelley, 1994, Brimleyana, 20); *Harpaphe* (Buckett & Gardner, 1968b, Occasional Papers of the Bureau of Entomology, California Department of Agriculture, 11); *Isaphe* (Shelley, 1993d, Canadian Journal of Zoology, 71); *Metaxycheir* (Shelley, 1994, Brimleyana, 20); *Montaphe* (Shelley, 1994, Brimleyana, 20); *Orophe* (Shelley, 1993e, Insecta Mundi, 7); *Selenocheir* (Shelley, 1994, Brimleyana, 20); *Semionellus* (Shelley, 1994, Brimleyana, 20); *Thrinaphe* (Shelley, 1993, Myriapodologica, 2); *Tubaphe* (Shelley, 1994, Brimleyana, 20);

Xystocheirini (USA, California): xystodesmid millipedes with sternal remnant present. Third pair of legs of males with conical coxal process (Fig. 16P), second pair of legs of females with cylindrical coxal process. Acropodite apex usually with ≥ 2 branches. Caudolateral corners of paranota usually sharp (or hooked), extending posteriorly beyond medial metatergal margin. Metatergites usually with small bumps (papillae), thereby reducing the glossiness of the cuticle (Fig. 16Q). Not very colorful, usually bimaculate. Highly fluorescent when illuminated with ultraviolet light; individuals in the genus *Motyxia* are bioluminescent.

Taxa included, and identification resources. 5 genera: *Anombrocheir* (*Anombrocheir bifurcata*: Gardner & Buckett, 1969, Entomological News, 80; *Anombrocheir spinosa*: Buckett & Gardner, 1969a, Entomological News, 80); *Motyxia* (Shelley, 1997, Insecta Mundi, 11; including *Motyxia bistipita*, as formerly part of *Xystocheir*: Shelley, 1996, Canadian Journal of Zoology, 74); *Parcipromus* (Shelley, 1995, Myriapodologica, 3); *Wamokia* (Buckett & Gardner, 1968c, Proceedings of the Biological Society of Washington, 81); *Xystocheir* (Shelley, 1996, Canadian Journal of Zoology, 74).

Sigmocheirini: colorful xystodesmid millipedes; yellow trimaculate (Fig. 1J). Lateral carinae of paranota discontinuous, body appearing moniliform with flattened paranota—not compact in general appearance as in other xystodesmids; paranota flat, horizontal, situated high on body rings—tergites not arched with paranota oriented downwards as in other xystodesmids. Paranotal corners rounded—corners of paranota not sharp (or hooked) as in the Xystodesmini and Xystocheirini. With protuberant knobs above (dorsal to) spiracles. Without spines on the prefemur. Sternal remnant between gonopodal coxae present. Large bodied, usually greater than about 35 mm. Highly fluorescent when illuminated with ultraviolet light.

Taxa included, and identification resources. 1 genus: *Sigmocheir* (Shelley, 1995, Entomologica Scandinavica, 26).

Octhocelatini (Kern County, California, USA): xystodesmid millipedes with acropodite with postfemoral process (Fig. 16S). Acropodite apex expanded, quadrate. Without spines on the prefemur. Not very colorful. Sternal remnant between gonopodal coxae present. Very small bodied, usually less than about 20 mm.

Taxa included, and identification resources. 1 genus: *Ochthocelata* (as formerly part of the Sigmocheirini: Shelley, 1995, Entomologica Scandinavica, 26).

Parafontariini (EA): xystodesmid millipedes with membranous neck of the cyphopod modified into long retractable bellows in females (Fig. 16O). Long telopodite with circular apex, forming one and a half to two loops (Fig. 16N). Gonopod without a prefemoral process. Gray, orange, intermediate between gray and orange, occasionally with contrasting stripe on protergite or posterior margin of metatergite. Highly fluorescent when illuminated with ultraviolet light.

Taxa included, and identification resources. 1 genus: *Parafontaria* (Tanabe, 2002, Journal of Natural History, 36).

Devilleini (Mediterranean Basin): xystodesmid millipedes with a highly sculptured tuberculate exoskeleton (Fig. 16K–M). Body with additional supernumerary segments (more than the typical 19+t in Polydesmida)—up to 27+t in *Devillea doderoi*. Very small bodied, usually less than about 10 mm. Primarily cave-dwelling.

Taxa included, and identification resources. 1 genus: *Devillea* (except for a listing of species, there has been no taxonomic synthesis of *Devillea*—see also Strasser, 1960, Fragmenta entomologica, 3; Kime & Enghoff, 2011, Atlas of European millipedes, 1).

Melaphini (Mediterranean Basin and northern Africa): xystodesmid millipedes with the acropodite simple, sickle-shaped (Fig. 16R). Gonopod without a prefemoral process. Colorful, yellow trimaculate—in some species, paranotal spots are red. Lateral carinae of paranota discontinuous, body appearing moniliform with flattened paranota—not compact in general appearance as in other xystodesmids; paranota flat, horizontal—tergites not arched with paranota oriented downwards as in other xystodesmids. Paranotal corners rounded—corners of paranota not sharp (or hooked) as in the Xystodesmini and Xystocheirini. Without spines on the prefemur. Sternal remnant between gonopodal coxae present.

Taxa included, and identification resources. 2 genera: *Melaphe* (Hoffman & Lohmander, 1968, Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut, 65) and *Ochridaphe* (Hoffman, 1962, Opuscula Zoologica, München, 59).

**Semionellus placidus* is the sole species of the subfamily Xystodesminae that occurs in the ENA (Shelley 1994, Brimleyana, 20).

Discussion

The phylogeny of Xystodesmidae recovered mainly western and eastern North American clades, which itself as a monophyletic group is sister to Mediterranean taxa (Fig. 4). The eastern North American (ENA) clade also contains the Madrean genera *Rhysodesmus* and *Stenodesmus*, and the western North American (WNA) clade includes species from East Asia (EA); the WNA clade also includes the markedly disjunct species *Semionellus placidus* from ENA. Noted by Shelley in 1994, and sister to species from the Pacific Northwest, *S. placidus* is biogeographically noteworthy as the sole ENA member of a uniformly WNA+EA subfamily Xystodesminae (Fig. 4, box 'C' with arrow). The biogeography of the Xystodesmidae illustrates a disjunct temperate fauna that evokes the classic patterns of co-distributed flora in the northern hemisphere (Manos and Meireiles 2015). This pattern is similar to the Old and New World floristic distribution of the hawthorn genus *Crateagus* (Lo et al. 2009). Prior biogeography of the Xystodesmidae suggested that the 'holarctic group Xystodesmidae, including several mediterranean genera of uncertain status, appears to be the modern representative of older palearctic taxa which also gave rise to the two groups Oxydesmidae and Gomphodesmidae' (Hoffman 1978a, pg. 28). Hoffman's generalization of the family is broadly consistent with our own phylogeny (he even refers to the Eurymerodesmidae as a smaller, apparently derivative group) but omits the Euryuridae, which was later integrated into the family by Shelley and Smith (2018). Another millipede group with molecular phylogenetic data, *Brachycybe*, is distributed in the northern hemisphere. Also distributed in ENA, WNA, and EA, the biogeographical pattern of the genus is different, with the center of species diversity in WNA, and an ENA species, *Brachycybe lecontii* Wood, 1864, that is a sister to the EA species *Brachycybe nodulosa* (Verhoeff, 1935). Although there seems to be congruent disjunctions between EA and NA in unrelated floral and faunal taxa, the variable patterns shown by molecular phylogenetic analyses indicate continuous splitting, expansion, and retraction during the Paleogene mediated by cooling and warming that lead to 'pseudocongruent' distributions (Manos and Meireiles 2015).

The WNA+EA clade, here named the subfamily Xystodesminae, includes five tribes; the ENA clade, named the subfamily Rhysodesminae, encompasses five tribes. Several historical tribes are monophyletic; in contrast, some past tribes in the Xystodesmidae are paraphyletic and include the Rhysodesmini, Sigmocheirini and Xystodesmini. The Chonaphini is polyphyletic and makes up an assemblage of unrelated taxa in the phylogeny. The non-monophyly of these taxa are ostensibly due to the historical (over-)reliance on gonopodal characters for higher-level systematics, which Means and Marek (2017) showed that the majority of which (95%) are homoplasious. The changes to the higher-level classification here, therefore, rely upon phylogeny instead of gonopodal morphology (see 'Materials and Methods, Taxonomy'). The WNA and EA species of the subfamily Xystodesminae were divided into five tribes: Xystodesmini, Parafontariini, Sigmocheirini, Ochthocelatini, and Xystocheirini. All of the WNA species of Chonaphini, Xystodesmini, and Orophini were placed in a restructured, and now monophyletic, Xystodesmini. The EA genera (spare the genus *Parafontaria*) are retained in the Xystodesmini. The species *Ochthocelata adynata* Shelley, 1995, from California, is the sole adelphotaxon to the Xystodesminae (Fig. 2). Previously included in the tribe Sigmocheirini with the nominative genus *Sigmocheir*, *O. adynata* is distantly related; therefore, *Sigmocheir* and *Ochthocelata* were placed in their own tribes: Sigmocherini and Ochthocelatini. The EA genus *Parafontaria*, on the basis of its distinct elongate bellows subtending the cyphopods in females, was placed in the subfamily Parafontariinae (Hoffman 1978b, Tanabe and Sota 2014). Although a monophyletic group, its phylogenetic placement sister to the Xystodesmini does not warrant subfamilial status, and is placed in the tribe Parafontariini. *Melaphe vestita*, the only taxon sampled from the xystodesmid subfamily Melaphinae (seven species), is not sister to the remaining members of the Xystodesmidae (Fig. 2). Instead the chelodesmid species *Macellolophus rubromarginatus* is sister to the family. This species was recently removed from Xystodesmidae and put in Chelodesmidae due to 'general anatomical features [that] conform to those of Chelodesmidae' (Shelley and Smith 2018). The relationships of the Mediterranean taxa deserve future investigation. Because the Mediterranean taxa were not broadly sampled for this analysis and nodal support at the base of the tree is generally low (posterior probability < 0.7), the Melaphini and Devilleini are retained as tribes of Xystodesmidae with uncertain subfamilial status, and *Macellolophus* is kept in the Chelodesmidae. Suprafamilial classification within the Polydesmida remains that of Cook and Brölemann from more than a century ago; interfamilial relationships of the order are poorly known, and rationale for systematic relationships are based on century-old character argumentation using overall similarity of gonopodal morphological features—characters which we now consider replete with homoplasy. A phylogenomic analysis of the order using genomes is now needed.

The tribe Nannariini, composed of the genera *Nannaria* and *Oenomaea*, is sister to the tribes Eurymerodesmini and Euryurini, a relationship supported by a posterior probability of 1.0 (Fig. 3). The Eurymerodesmini, previously a family-level group, was suggested to be a derived lineage, or a sister-group, of Xystodesmidae by Brölemann (1916), Hoffman (1978a), Shelley (1989), and Rodriguez et al. (2018). Later, Shelley and Smith (2018) formally made Nannariini a subtribe (their 'Nannariina') equivalent with their subtribe 'Eurymerodesmina' and placed it within the tribe Eurymerodesmini. (Their 'Euryurina', for the Euryuridae, and 'Melaphina', for the Melaphinae, were put in the tribe Euryurini.) These supraspecific changes were reasoned on the basis of gonopodal morphology. Because Nannariini, Eurymerodesmini, and Euryurini clades are each monophyletic in the molecular phylogeny (Fig. 3) and distinct morphologically and genetically (with long branches subtending each clade), their statuses are changed to the tribes Nannariini, Eurymerodesmini and Euryurini. These taxa possess 28, 25, and 12 species each. The recently re-established genus *Mimuloria* is polyphyletic and therefore synonymized with the genus *Nannaria* (Hennen and Shelley 2015). The unique bow-shaped acropodite appears to be a homoplasious character, uninformative at the supraspecific level, and therefore unreliable for higher-level classification (Means and Marek 2017). The genus *Nannaria*, characterized by strongly twisted spatulate claws in males, composes two clades: the *wilsoni*-group and the *minor*-group. These groups include a substantial number of undescribed species (ca. 56 species) that are the subject of pending revisions by the authors. The undescribed species diversity of *Nannaria*, predominantly in the Appalachian Mountains of the eastern United States, highlights the region as the global center of familial diversity in Xystodesmidae.

Also, in the Appalachian Mountains, the genus *Sigmoria* is monophyletic and the second largest genus in the family (in terms of number of species—67 species—of which about half were sampled in this analysis, Fig. 3 blue text). Located mainly in the southern Appalachian Mountains and foothills, its species are distributed in parapatry in largely contiguous mostly nonoverlapping ranges, and the pattern resembles a nonadaptive radiation where species diversified from a single common ancestor into a set of ecologically similar parapatric replacements of one another (Rundell and Price 2009, Marek and Moore 2015). *Sigmoria* species are densely packed into numerous parapatric ranges (many each < 20 km^2), but gonopodal morphology among species in the genus is greatly heterogeneous and the historical (over-)reliance on these gonopodal characters caused many artificial generic names to be proposed, for example—*Brevigonus*, *Cleptoria*, *Cheiropus*, *Dynoria*, *Furcillaria*, *Hubroria*, and seven others (Hoffman 1999; Marek and Bond 2006, 2007; Marek et al. 2014; Means and Marek 2017). Although these names were defined by distinct gonopodal morphology, none of these historical genera are monophyletic, morphological similarities are homoplasious, and the taxa are therefore included as synonyms of a monophyletic and geographically circumscribed—yet morphologically varied—genus *Sigmoria*.

The same changes to the classification of *Sigmoria* and *Nannaria*, which were driven by phylogeny, monophyly, and taxonomic priority, were applied to *Euryurus* and *Dicellarius*; specifically, nonmonophyletic genera were subsumed into higher-level taxa (e.g., *Auturus* into *Euryurus* and *Thrinaxoria* into *Dicellarius*). Based on the same principle, some taxa were split from their previous group. In the case of *Howellaria infesta* (Chamberlin, 1918), *Howellaria deturkiana* (Causey, 1942), and *Idaloria profuga*—once members of the genus *Boraria*—these species are not monophyletic with *Boraria stricta* (Brölemann, 1896), the type species of the genus, and are given their own names. Similarly, *Daphnedesmus* species and *Aporiaria texicolens* Chamberlin, 1938—once members of the genera *Dixioria* (now *Sigmoria*) and *Rhysodesmus*—are not monophyletic with these taxa and are given names that accord with the phylogeny (Fig. 3).

From our phylogenetic analysis leveraging a broad sampling of the species of the Xystodesmidae, the family has a center of diversity in the Appalachian Mountains with 188 species (Fig. 4). The Appalachian Mountains include possible crown group taxa such as the Apheloriini (Means and Marek 2017). California encompasses potential stem group taxa including *O. adynata* and others in the subfamily Xystodesminae that spans East Asia and western North America. This pattern of diversity is consistent with concepts of diversification of the family by Hoffman (1978a) and with the diversification of co-distributed groups such as the lungless salamanders in the family Plethodontidae (Means and Marek 2017). The taxon, like the Plethodontidae and the hawthorns (*Crateagus* spp.), appears to be of a cool and moisture loving fauna that has affinities to the so-called 'Tertiary relict' biogeographical type (Weakley 2005, Manos and Meireiles 2015). The Plethodontidae, co-distributed in the northern hemisphere with Xystodesmidae, ranges to Amazonia (in contrast, xystodesmid millipedes reach their southernmost extent in Guatemala) (Frost 2019). A recent study showed a vast underestimation of plethodontid species diversity in the region (Jaramillo et al. 2020). Historically poorly sampled for millipedes, South and Central America may hold uncovered species diversity of the family, perhaps of the genus *Rhysodesmus* or other relatively young derivative lineages. The xystodesmid fauna in California, a biome with generally higher temperatures and more arid conditions than in Appalachia, encompasses high-elevation clades such as *Parcipromus* and *Wamokia* and bioluminescent species like *Motyxia sequoiae* that originated from low-elevation taxa (Marek and Moore 2015). This pattern of multiple waves of specialization from seemingly generalized ancestral 'stock' lineages (e.g., *Xystocheir*) appears to be a common mode of diversification in California (Marek and Moore 2015, Emata and Hedin 2016). This mode of speciation in a group of non-mobile moisture dependent organisms may also be commonplace in Appalachian taxa, and centers of clade-level diversity and endemism occur in the Cumberland Mountain region (with the genus *Brachoria*), the mountains of South Carolina and Georgia (with the genus *Sigmoria*), and Valley and Ridge Province (with the genus *Nannaria*).

Of the 10 new species, six are known from only their type localities. In some well sampled taxa, such as *Apheloria whiteheadi*, the species are micro range endemics (MRE) and are distributed in geographical areas of less then 1,000 km^2 (Means and Marek, 2017). (In the case of *A. whiteheadi*, a taxon that is extremely limited in distribution, has a global range restricted to less than 1 km^2.) *Nannaria hokie*, which persists in forest habitats in Montgomery County, Virginia, occurs in highly fragmented and threatened areas. For example, Stadium Woods, a 4.5-hectare old-growth white oak forest on the Virginia Tech campus, is surrounded by the university football stadium on its western side and residential housing on its eastern side. The species also occurs on the south side of a pond on the university's campus (Duck Pond, 37.2250°N, -80.4276°W). Though it now persists in several small forest fragments, the species is globally endemic to only 100 km^2. Because these species are distributed in extremely restricted distributions, which themselves are highly fragmented, the potential for loss of substantial amounts of species diversity is very high. Since human industry is nearly entirely responsible for the fragmentation and loss of habitat, the irrevocable extinction of these species and co-occurring species is not without moral neutrality, and eventual detriment to environmental and human health. Stadium Woods, and other forest fragments in the region, are refuges for migratorial birds, indigenous flora and pollinating insects as well, and they sequester atmospheric carbon, so preservation of these habitats should be highly prioritized.

More than half of the species diversity (247/486 species), and 86% of the genus diversity of the family was sampled. However, a handful of xystodesmid taxa from outlying locations in China, Vietnam, Ethiopia, and the Mediterranean Basin have been omitted from this analysis such as *Devillea*, *Kiulinga*, *Koreoaria*, *Ochridaphe*, *Pamelaphe*, *Parariukiaria*, and the enigmatic *Melaphe corrupta* Attems, 1944 from the Ethiopian Highlands (Fig. 4). Some groups with species diversity > 40 including *Rhysodesmus*, *Nannaria*, and *Sigmoria*, have not been extensively sampled. Omission of these taxa, especially the Mediterranean species, may later prove to be pivotal for a more thorough understanding of the early diversification of the family. Furthermore, a larger genomic dataset and expanded outgroup selection including representatives of Chelodesmidae, Oxydesmidae, and Gomphodesmidae will help comprehend the bounds of the taxon and build a more developed understanding of the morphological and evolutionary extremes of the family. This will provide an important context for studying the fascinating biological qualities of the group, to document the undescribed species diversity, and to conserve biodiversity.

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

Acknowledgments

This research was supported by a National Science Foundation Advancing Revisionary Taxonomy and Systematics grant to PEM (Division of Environmental Biology, Systematics and Biodiversity Sciences #1655635). We thank Patrick Lorch at the Cleveland Metroparks, Robert Cherry at the US National Park Service, as well as the Virginia, North Carolina, South Carolina, Tennessee, West Virginia, Georgia, Kentucky, Ohio, Maryland, Pennsylvania, New York, Alabama, Mississippi, Louisiana, Arkansas, Missouri, Illinois and Indiana Departments of Game and Inland Fisheries, Natural Heritage, and State Parks for providing scientific collecting permits. We are grateful to Sergei Golovatch, Pavel Stoev, Teiji Sota, Toni Perez, Michael Jorgensen, Bruce Synder, Mark Janowiecki, Gary Phillips, Curt Harden, Tom Astle, N. Niamte, and Ahn Duc Nguyen for contributing valuable specimens for this study. We thank Charity Hall, Patricia Shorter, Deren Ross, Ryosuke Kawahara, and Taiga Kato for their help in the field. Advanced Research Computing at Virginia Tech provided access to the supercomputer for phylogenetic analyses. University of Arizona Genetics Core provided DNA sequencing services. We thank anonymous reviewers who provided comments on previous versions. Bronwyn Williams and Megan McCuller (NCSM), and Kal Ivanov and Liberty Hightower (VMNH) provided loans of material. We thank Bill Shear and Zoltan Korsos for discussions about the family Xystodesmidae.

Author Contributions

JCM, DAH, and PEM designed and performed the experiments, and analyzed the data. JCM, DAH, PEM, and TT conducted field work, contributed samples, prepared figures and/or tables, and wrote and reviewed drafts of the paper. PEM conceived the study and obtained funding.

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