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## A reassessment of apheloriine millipede phylogeny: additional taxa, Bayesian inference, and direct optimization (Polydesmida: Xystodesmidae)

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## Abstract

Millipedes in the tribe Apheloriini occur throughout the eastern United States, predominately in the deciduous forests of the Appalachian Mountains. Herein we present a reassessment of apheloriine millipede phylogeny using mitochondrial DNA sequences and an additional 29 exemplar taxa (including 15 undescribed species and all of the species in the genus *Brachoria*, except one). In this study, first we check the results of the previous phylogeny of the tribe (Marek and Bond, 2006) with different alignment and phylogenetic techniques (direct optimization and maximum likelihood), and second reconstruct a new phylogeny evaluating it in the same way with Bayesian, maximum likelihood, and direct optimization. Using this updated and expanded phylogeny, we tested historical classifications with Bayes factor and Shimodaira-Hase-gawa hypothesis testing, consistently finding very strong evidence against their implied phylogenetic hypotheses. Lastly, using the new phylogeny as a foundation, we make taxonomic modifications and provide an updated species list of Apheloriini (106 species/17 genera).

Key words: Myriapoda, Diplopoda, taxonomy, systematics

## Introduction

The arthropod class Diplopoda (millipedes) ranks among the most diverse of the terrestrial animals in terms of nominal taxa, with over 12,000 species described and many remaining yet to be discovered. The majority of phylogenetic treatments across millipedes, to date, have focused on ordinal-level evolutionary relationships (Enghoff, 1984; Sierwald et al., 2003; Regier et al., 2005; Sierwald and Bond, 2007), with far fewer focusing on lower-level reconstructions (see Bond and Sierwald, 2003; Marek and Bond, 2006) and assessments of familial and generic boundaries. Rigorous phylogenetic reconstructions below the family level are important steps in delimiting genera, species groups, and species.

Problems associated with reconstructing relationships in millipedes were recently discussed in a reclassification of the tribe Apheloriini (Marek and Bond, 2006). The classification scheme for the tribe was instable—evolutionary hypotheses underlying the classification changed three times between 1979 and 2002, generally representing the taxonomic hypotheses of two primary authors (Hoffman, 1979, 1999; Shelley, 2000a, b, 2002; Shelley and Whitehead, 1986). Different interpretations of homoplasious genitalic characters, paucity of phylogenetically informative somatic characters, and reliance on geographical proximity appeared to contribute collectively to the instability (Marek and Bond, 2006). Reliance on a single morphological character system (male genitalia) appeared to be a major factor confounding relationships within Apheloriini. Our comments regarding the instability of Apheloriini classification (here and in Marek and Bond, 2006) should not be viewed as an attack or explicit critique of previous authors, indeed, these past works have provided the initial framework on which our study is based. Without question millipedes are a difficult group on which to