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A total evidence assessment of the phylogeny of North American euctenizine trapdoor spiders (Araneae, Mygalomorphae, Cyrtaucheniidae) using Bayesian inference

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Abstract

North American trapdoor spiders of the subfamily Euctenizinae (Cyrtaucheniidae) are among the most diverse mygalomorph spiders (trapdoor spiders, tarantulas, and their relatives) on the continent in terms of species numbers and ecological habits. We present a generic level phylogenetic study of the subfamily based on a total evidence approach. Our dataset comprises ~3.7 kb of molecular characters (18S and 28S rRNA gene sequences) and 71 morphological characters scored for 32 taxa. When analyzed independently, these data sets, particularly the morphology, depict very different views of mygalomorph and euctenizine relationships, albeit with weak support. However, when these data are combined we recover a tree topology that is supported by high posterior probability for most nodes. The combined data recover a phylogenetic pattern for euctenizines different than previously published and indicate the presence of a narrowly endemic new genus from central California. While euctenizine monophyly is unequivocal, the monophyly of a number of other mygalomorph groups is questionable (e.g., Cyrtaucheniidae, Mecicobothriodina, Rastelloidina). This non-monophyly is noteworthy, as our analysis represents the first employing a total evidence approach for mygalomorphs, a group known to be morphologically conservative.

Keywords: Araneae; Bayes factors; Molecular systematics; Mygalomorphae; Spider phylogeny; Total evidence

1. Introduction

The spider infraorder Mygalomorphae (tarantulas, trapdoor spiders and their relatives) comprises 2,502 species and 311 genera, currently placed into 15 families (Platnick, 2006). Despite their relative obscurity spiders belonging to this group represent an ancient lineage (Penney, 2004) with a rich evolutionary diversity. Mygalomorphs are essentially worldwide in distribution, although the tropics (worldwide) and temperate austral regions of South America, southern Africa, and Australasia are centers of generic-level diversity (Raven, 1985; Platnick, 2006). North America also has a rich diversity of mygalomorph spider species, the majority of which (>50%) remain currently undescribed [this estimate does not include the 46 described species of *Aphonopelma* Pocock, 1901 (family Theraphosidae) because the diversity in this genus is considered to be overestimated by most workers familiar with the group]. Given the relatively large body size and life history characteristics of many of these spiders (e.g., extremely long-lived, highly sedentary, etc.), the presence of such a large number of undescribed species is anomalous. This undocumented biodiversity can be largely attributed to a few species-rich genera: the ctenizid trapdoor spider genus *Ummidia* Thorell, 1875 (40–50 undescribed species, Roth, 1993; Bond and Hendrixson, 2005), the cyrtaucheniid trapdoor spider genus *Aptostichus* Simon, 1891 (~35 undescribed species, Bond and Opell, 2002; Bond, 2005), and other closely related euctenizine genera (sensu Bond and Opell, 2002). Whereas *Ummidia* is widespread throughout North

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America and the New World Tropics, euctenizines are restricted primarily to the American Southwest with the greatest diversity in southern California.

The North American Euctenizinae was first revised by Bond and Opell (2002), and at present comprises eight genera with 29 nominal species. Euctenizines were transferred from Ctenizidae to the family Cyrtaucheniidae by Raven (1985) and positioned as a sister group to the remaining cyrtaucheniid subfamilies, Cyrtaucheniinae and Aporoptychinae. The cosmopolitan family, at present comprises 18 genera and 126 species (Platnick, 2006). Based on a cladistic analysis of 71 morphological characters scored for 29 mygalomorph taxa, Bond and Opell (2002) found the Euctenizinae (sensu Raven, 1985) to be monophyletic with the inclusion of the South African genus *Homostola* Simon, 1892 (Fig. 1). However, these authors strongly suspected, as did Goloboff (1993a), that the family Cyrtaucheniidae is paraphyletic with respect to the Domiothelina clade. For a number of reasons, namely incomplete taxon sampling, Bond and Opell were hesitant to splinter Cyrtaucheniidae into multiple families and chose to simply relimit the Euctenizinae; however, these authors speculated that increased sampling across Raven's (1985) Rastelloidina clade would resolve a number of problematic issues related to mygalomorph classification (e.g., cyrtaucheniid monophyly).

The morphological phylogeny of Bond and Opell (2002) fully resolved the relationships among the eight described genera (including *Homostola*). As illustrated in Fig. 1, *Homostola* is hypothesized to occupy a basal position within the subfamily, a curious result given the absence of any known South American euctenizines, thus creating a noteworthy geographic break in the distribution of the group (North American–Sub Saharan Africa). The only southeastern US representative of the group, *Myrmekiaphila* Atkinson, 1886, likewise falls more basal in the phylogeny with respect to the southwestern North American taxa. Bond and Opell (2002) gave informal names to a clade comprising *Eucteniza* Ausserer, 1875 and *Neoapachella* Bond and Opell, 2002 (the Euctenizoids), and the 'California Clade' composed of largely Californian taxa (*Aptostichus*, *Promyrmekiaphila* Schenkel, 1950, and *Apomastus* Bond and Opell, 2002). *Entychides* Simon, 1888 falls to the outside of these two named clades.

The primary objective of this study is to reconstruct the phylogenetic relationships of euctenizine genera using morphological and molecular data employing an exemplar approach. For a number of reasons, both conceptual and pragmatic, euctenizine phylogeny needs revisiting. First, the paucity of morphological characters for mygalomorph phylogenetic studies echoed by Bond and Opell (2002) and elsewhere (e.g. Goloboff, 1993a) indicates that other

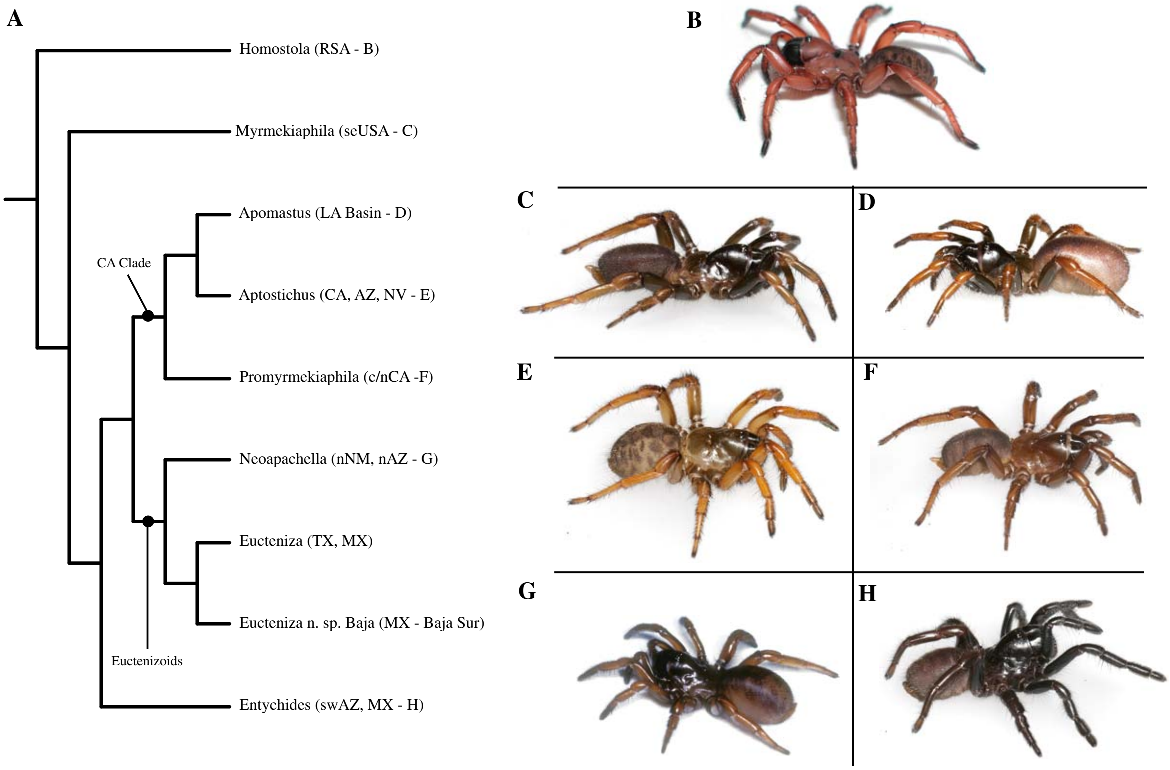

Fig. 1. (A) Phylogeny of the cyrtaucheniid subfamily Euctenizinae redrawn from Bond and Opell (2002, Fig. 6). Parenthetical notations indicate generalized distribution information and references spider images (RSA = Republic of South Africa, seUSA = southeastern United States, LA Basin = Los Angeles Basin, California, CA = California, AZ = Arizona, NV = Nevada, NM = New Mexico, c/n = central/northern, MX = Mexico, sw = southwestern; letters after hyphen refer to representative images). (B–H) Images of live euctenizine specimens. (B) *Homostola pardalina*. (C) *Myrmekiaphila fluviatilis*. (D) *Apomastus kristenae*. (E) *Aptostichus* sp. (F) *Promyrmekiaphila* sp. (G) *Neoapachella rothi*. (H) Euctenizine gen. nov., Moss Landing State Beach, California.