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A phylogeny of the "evil tribe" (Vernonieae: Compositae) reveals Old/New World long distance dispersal: Support from separate and combined congruent datasets (*trn*L-F, *ndh*F, ITS)

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Abstract

The Vernonieae is one of the major tribes of the largest family of flowering plants, the sunflower family (Compositae or Asteraceae), with ca. 25,000 species. While the family's basal members (the Barnadesioideae) are found in South America, the tribe Vernonieae originated in the area of southern Africa/Madagascar. Its sister tribe, the Liabeae, is New World, however. This is the only such New/Old World sister tribe pairing anywhere in the family. The Vernonieae is now found on islands and continents worldwide and includes more than 1500 taxa. The Vernonieae has been called the "evil tribe" because overlapping character states make taxonomic delimitations difficult at all levels from the species to the subtribe for the majority of taxa. Juxtaposed with these difficult-to-separate entities are monotypic genera with highly distinctive morphologies and no obvious affinities to any other members of the tribe. The taxonomic frustration generated by these contrary circumstances has resulted in a lack of any phylogeny for the tribe until now. A combined approach using DNA sequence data from two chloroplast regions, the *ndh*F gene and the noncoding spacer *trn*L-F, and from the nuclear rDNA ITS region for 90 taxa from throughout the world was used to reconstruct the evolutionary history of the tribe. The data were analyzed separately and in combination using maximum parsimony (MP), minimum evolution neighbor-joining (NJ), and Bayesian analysis, the latter producing the best resolved and most strongly supported tree. In general, the phylogeny shows Old World taxa to be basal and New World taxa to be derived, but this is not always the case. Old and New World species are found together in two separate and only distantly related clades. This is best explained by long-distance dispersal with a minimum of two trans-oceanic exchanges. Meso/Central America has had an important role in ancient dispersals between the Old and New World and more recent movements from South to North America in the New World.

Keywords: Vernonieae; Vernonia; Compositae; Old and New World; Phylogeny; ITS; *trn*L-F; *ndh*F; Congruence; Mesoamerica: Central America

1. Introduction

The Vernonieae is one of the most poorly understood of the >20 recognized tribes of the Compositae (Funk et al., 2005). A perplexing array of intergrading morphologies and overlapping character states juxtaposed with highly autapomorphic character state combinations (Keeley and Turner, 1990; Robinson, 1999a,b) make the Vernonieae among the most refractory of tribes to elucidating systematic relationships of any members of the family. The frustration felt by those who have attempted to understand relationships within the Vernonieae has given rise to its nickname as the "evil tribe" (Funk et al., 2005). No phylogeny has ever been proposed for the tribe and only a few relationships have been suggested even among the best known species groups before the present study (Jones, 1977; Jeffrey, 1988; Robinson, 1999a,b, 2007). Despite difficulties understanding relationships within the tribe, the

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monophyly of the Vernonieae has never been in doubt. The overall circumscription of the tribe has changed little since its initial description by Cassini (1819, 1828) and Bentham (1873) and only minor changes have been made as a result of recent molecular work (Keeley and Jansen, 1994; Kim et al., 1998). The tribe has been traditionally placed in the subfamily Cichorioideae, a position reconfirmed in a recent study of the family (Funk et al., 2005).

The "*Vernonia* problem" (Bremer, 1994) is one of the major reasons for the historical difficulties in establishing relationships within the tribe. Until recently (Robinson, 1999a,b), the vast majority of species (>1000) was found within a single worldwide core genus, *Vernonia.* Around this enormous core genus swirled a cloud of largely monotypic genera with unusual and distinctive morphologies that made it difficult to relate these taxa to those with the more common morphological ground plan of the tribe. For example, *Stokesia*, a monotypic endemic of the southeastern US, is the only member of the tribe with zygomorphic florets. Similarly, the monotypic *Pacourina edulis* from northern South America has an unusual head morphology and is the only truly aquatic member of the family, while *Hesperomannia* from the Hawaiian Islands has become so modified by adaptation to bird pollination that it was until recently (Kim et al., 1998) thought to belong to the tribe Mutisieae. Out of the 121 recognized genera in the Vernonieae 48 are monotypic and another 30 have only two species, leaving most species even now in only a few genera (Robinson, 1999a,b, 2007). Studies by Robinson and Kahn (1986) and Robinson and Funk (1987) pointed out the paraphyly of *Vernonia s.l.*, a finding supported by Keeley and Jansen (1994) in a chloroplast DNA (cpDNA) restriction site study. Robinson (1999a,b, 2007) made sweeping changes in the circumscription of *Vernonia*, limiting the genus to a small group of eastern North American species that includes the type species for the tribe (*Vernonia noveboracensis* (L.) Willd.). The remaining taxa were placed in newly created genera which were in turn placed into one of approximately 20 subtribes (Robinson, 2007). Few relationships were suggested among subtribes and genera, however, leaving relationships among tribal members unresolved as has been the case since the tribe's original description.

One of the few distinctions generally noted within the tribe has been that of two geographically separate lineages, one in the Old World and the other in the New World. This subtribal dichotomy, initially proposed by Gleason (1906), was extended by Jones (1977) in an overview of the tribe, followed by synoptic treatments of *Vernonia* in the New World (Jones, 1979) and the Old World (Jones, 1981). The Old World species of *Vernonia* were placed into the subgenus *Orbisvestus* and the New World species into subgenus *Vernonia.* In a treatment of African species, Jeffrey (1988) noted features of morphology, chemistry and pollen that also suggested separate lineages for New and Old World species. Despite the inclusion of most species in the genus *Vernonia s.l.*, Jeffrey (1988) proposed that the closest relationships were among taxa within each hemisphere, again suggesting two separate evolutionary lines within the tribe. Following this tradition, Robinson (1999a,b, 2007) erected separate subtribes for Old and New World Vernonieae in the most complete taxonomic treatments of the tribe to date.

Despite emphasis on the differences between the New and Old World subtribal lineages, cross-hemisphere relationships have been proposed. Turner (1981) suggested a possible connection to the Old World for the Central American Leiboldia (Leboldiinae) group. Their morphologies, chromosome numbers and chemistry did not entirely fit with other New World species, but were similar to some taxa in the Old World. Keeley and Turner (1990), in a cladistic analysis of morphological characters, and Keeley and Jansen (1994), using cpDNA restriction site data, found clades containing both New and Old World species suggesting a connection between the hemispheres. In his recent treatments Robinson (1999a,b, 2007) also pointed out cases where the New/Old World dichotomy did not seem to hold. For example, the Old World genus *Manyonia* was postulated to be close to the New World genus *Heterocypsela*, and conversely the New World genera *Telmatophila, Acilepidopsis* and *Mesanthophora* were placed in the Old World subtribe Erlangeinae.

The overall goal of this study was to provide a phylogeny for the Vernonieae for the first time and with it to clarify New and Old World subtribal relationships. Within this framework, additional goals were to gain a better understanding of the potentially important role of Meso/Central America in connecting the two hemispheres (Keeley and Jansen, 1994), to ascertain the derived position of the North American taxa, and to further explore the role of Brazil in the origin of New World taxa, as suggested by Keeley and Jones (1979). Three phylogenetic markers (the chloroplast non-coding *trn*L-F and coding *ndh*F) and the nuclear rDNA ITS region were chosen to resolve relationships within the Vernonieae. We also examined congruence and resolution of these three markers for the tribe worldwide.

2. Materials and methods

2.1. Choice of taxa and regions to be sequenced

Vernonieae taxa from 90 species and 35 genera were sampled across as wide a geographical range as possible in the Old and New Worlds. These taxa are listed in Table 1 with GenBank Accession Numbers. Nomenclature is according to Robinson (1999a,b, 2007). Revision of the Old World Vernonieae has not yet been completed (Robinson, pers. comm.), however. Consequently, a number of Old World species have yet to be formally transferred from *Vernonia s.l.* and thus must retain that genus name here despite the fact that *Vernonia s.s* is entirely New World (Robinson, 1999a).

The chloroplast gene *ndh*F has been used in a variety of phylogenetic studies at several taxonomic levels (Olmstead