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# Species tree phylogeny and character evolution in the genus *Centipeda* (Asteraceae): Evidence from DNA sequences from coding and non-coding loci from the plastid and nuclear genomes

Stephan Nylinder<sup>a</sup>, Bodil Cronholm<sup>b</sup>, Peter J. de Lange<sup>c</sup>, Neville Walsh<sup>d</sup>, Arne A. Anderberg<sup>a,\*</sup>

<sup>a</sup> Department of Phanerogamic Botany, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden

<sup>b</sup> Department of Molecular Systematics, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden

<sup>c</sup> Ecosystems and Species Unit, Department of Conservation, Private Bag 68908, Newton, Auckland 1145, New Zealand

<sup>d</sup> National Herbarium of Victoria, Birdwood Avenue, South Yarra 3141, Australia

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#### ABSTRACT

A species tree phylogeny of the Australian/New Zealand genus *Centipeda* (Asteraceae) is estimated based on nucleotide sequence data. We analysed sequences of nuclear ribosomal DNA (ETS, ITS) and three plasmid loci (ndhF, psbA-trnH, and trnL-F) using the multi-species coalescent module in BEAST. A total of 129 individuals from all 10 recognised species of *Centipeda* were sampled throughout the species distribution ranges, including two subspecies. We conclude that the inferred species tree topology largely conform previous assumptions on species relationships. *Centipeda racemosa* (Snuffweed) is the sister to remaining species, which is also the only consistently perennial representative in the genus. *Centipeda pleiocephala* (Tall Sneezeweed) and *C. nidiformis* (Cotton Sneezeweed) constitute a species pair, as does *C. borealis* and *C. minima* (Spreading Sneezeweed), all sharing the symplesiomorphic characters of spherical capitulum and convex receptacle with *C. racemosa*. Another species group comprising *C. thespidioides* (Desert Sneezeweed), *C. cunninghamii* (Old man weed, or Common sneeze-weed), *C. crateriformis* is well-supported but then include the morphologically aberrant *C. aotearoana*, all sharing the character of having capitula that mature more slowly relative the subtending shoot. *Centipeda elatinoides* takes on a weakly supported intermediate position between the two mentioned groups, and is difficult to relate to any of the former groups based on morphological characters.

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#### 1. Introduction

The genus *Centipeda* Lour. (Asteraceae) comprises 10 species (Walsh, 2001) with mostly Australian/New Zealand distribution, and are commonly known as "Sneeze-weeds". It is a genus of small, annual or perennating herbs (Fig. 1) with small, heterogamous, epaleate capitula, very small florets, the outermost tubular and female, the inner ones funnel-shaped and hermaphroditic, shortly tailed anthers, undifferentiated anther filament collar, and a lack of pappus. Interpretation of a number of reduced floral characters has made the genus difficult to place systematically, and it was at first included in the larger genus *Sphaeromorphaea* in Artemisiae under the Senecionidae by Candolle (1837). The systematic position of *Centipeda* has been much discussed since then, and different views on tribal affiliation have been put forward over the years (Bentham, 1873; Hoffmann, 1892; Heywood and Humphries, 1977; Skvarla et al, 1977; Bremer and Humphries,

\* Corresponding author. *E-mail address:* stephan.nylinder@nrm.se (A.A. Anderberg). 1993; Bremer, 1994; Nesom, 1994). Few large-scale molecular analyses of the Asteraceae including representatives of Centipeda have been made. Wagstaff and Breitwieser (2002) included Centipeda cunninghamii (DC.) A. Braun & Asch. in a single locus study using ITS sequences, which indicated a sister relationship to a group consisting of Athroisma DC., Blepharispermum DC., and Anisopappus Hook. & Arn. together with the genera of the Heliantheae tribal complex. Panero (2005) referred to unpublished data that placed *Centipeda* in the tribe Athroismeae (Panero and Funk, 2002) as the only genus of subtribe Centipedinae. The five genera of the Athroismeae (Athroisma, Blepharispermum, Leucoblepharis Arn., Anisopappus, and Centipeda) differ considerably from each other in several morphological respects and the group appears to be very heterogeneous (Panero, 2005), illustrating the difficulties of drawing conclusions on phylogenetic relationship in this group based on morphological characters only. Despite lack of detailed knowledge on the presumed closest relative to Centipeda it is feasible to consider one of the four remaining genera in Athroismeae to be the best sister genus candidate (Panero, 2005). A common feature for the representatives in Athroismeae is the presence of

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**Fig. 1.** Photographs of *Centipeda* (Asteraceae) representatives; Habit of (1) *C. minima* ssp. *minima*; and (2) *C. pleiocephala*; (3) an unearthed specimen of *C. elatinoides* showing the prolonged roots adapted for arid environments; (4) habit of *C. nidiformis*; (5) close-up of capitula of *C. pleiocephala*; and (6) habit of *C. racemosa* with camera lens cover indicating scale. All photographs by Neville Walsh.

a perennial woody habit, with a few species of *Anisopappus* and *Athroisma* being annual. However, this is clearly a secondarily derived character in both genera (Panero, 2005). Further information on morphology, palynology, and secondary chemistry in the other genera of the Athroismeae was presented and discussed by Panero (2006) and by Anderberg (2009).

Although the exact placement of Centipeda with respect to the genera putatively associated with it remains unclear, the genus itself is morphologically so distinct from the other four, and also fairly homogeneous with a number of unique character states, that it is plausible to assume its monophyly. Character variation within the genus was clarified in a detailed monograph by Walsh (2001). Walsh used informal groups to reflect morphological similarity among species, and one such group comprised C. borealis, C. minima, C. nidiformis, and C. racemosa sharing characters of spherical flowering and later disintegrating fruiting capitula, convex receptacles, and cypsela shape and trichomes. Associated with these species, but differing in some fruit aspects was C. pleiocephala. We refer to this assemblage as the "C. minima group". Another such informal group can be called the "C. crateriformis group" and comprises C. crateriformis, C. thespidioides, and C. cunninghamii, sharing persistent fruiting capitula and more or less linear cypselas with apically coiled trichomes. Two species, viz. C. aotearoana and C. elatinoides were considered difficult to place, either because of intermediate sets of characters as in C. aotearoana, or by just not matching any of the two informal groups and thus appearing isolated like C. elatinoides. Looking at growth habit it can be noted that C. pleiocephala, C. nidiformis and C. thespidioides are the only species appearing to be genuine annuals, while C. racemosa is the only species consistently perennial throughout its range. All other species exhibit facultative perennial habits to various degrees. Many of the character states in Centipeda appear to show some variation throughout the genus and sometimes variation within species. The task of character interpretation in Centipeda accentuates the difficulties in understanding species relationships based on its reduced morphology only, and highlights the need for using unbiased data for resolving systematic issues within the genus. The potential conflict of evaluating species relationships and character evolution based on the phylogenetic properties of individual specimens can be improved on by adopting a species centred approach drawing from multiple and possibly contradicting sources of genetic information. Evaluation of the species relationships conditioned on the taxonomic affinities of the individual specimens can provide a fruitful fundament for discussion on character evolution.

For the purpose of resolving relationships at and/or below species level investigation of rapidly evolving DNA spacers and intron sequences are usually required, and many such regions are readily amplifiable from both the plasmid (Shaw et al., 2005, 2007) and the nucleus (e.g. Hughes et al., 2005; Steele et al., 2008) using stanDownload English Version:

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