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Phylogeny of Barnadesioideae (Asteraceae) inferred from DNA sequence data and morphology

Michael Gruenstaeudl [a,b,*], Estrella Urtubey [c], Robert K. Jansen [b], Rosabelle Samuel [a], Michael H.J. Barfuss [a], Tod F. Stuessy [a]

[a] Department of Systematic and Evolutionary Botany, Faculty Center of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria
[b] Section of Integrative Biology and Institute of Cellular and Molecular Biology, University of Texas, Austin, TX 78712, USA
[c] Instituto de Botánica Darwinion, Labardén 200 (esq. Estanislao Del Campo), B1642 HYD. Casilla de Correo 22, San Isidro, Buenos Aires, Argentina

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ABSTRACT

Subfamily Barnadesioideae (Asteraceae) consists of nine genera and 91 species endemic to South America. They include annual and perennial herbs, arching shrubs and trees up to 30 m tall. Presumed sister to all other Asteraceae, its intergeneric relationships are key to understanding the early evolution of the family. Results of the only molecular study on the subfamily conflict with relationships inferred from morphology. We investigate inter- and intrageneric relationships in Barnadesioideae with novel DNA sequence data and morphological characters using parsimony, likelihood and Bayesian inference. All results verify Barnadesioideae as monophyletic and sister to the rest of the family. A basal split within the subfamily is recognized, with *Chuquiraga*, *Doniophyton* and *Duseniella* in one clade, and *Arnaldoa*, *Barnadesia*, *Dasyphyllum*, *Fulcaldea*, *Huarpea* and possibly *Schlechtendalia* in another. The largest genus, *Dasyphyllum*, is revealed as biphyletic with the two clades separating along subgeneric and geographic lines. *Schlechtendalia*, suggested as the earliest diverging lineage of the subfamily by morphological studies and parsimony analyses, is found in a more derived position under model-based inference methods. Competing phylogenetic hypotheses, both previous and present, are evaluated using likelihood-based tests. Evolutionary trends within Barnadesioideae are inferred: hummingbird pollination has developed convergently at least three times. An early vicariance in the subfamily's distribution is revealed. $X = 9$ is supported as the ancestral base chromosome number for both Barnadesioideae and the family as a whole.

1. Introduction

Asteraceae constitute the largest family of flowering plants and comprise two monophyletic groups of markedly unequal size. Barnadesioideae (Bremer and Jansen, 1992), consisting of nine genera and 91 species, is the much smaller entity and entirely restricted to South America. It is distinguished from the rest of the family by axillary spines (reviewed in Ezcurra, 1985), a pubescence of unbranched three-celled hairs (barnadesioid trichomes) on floral and vegetative structures (Cabrera, 1959; Bremer, 1987; Bremer and Jansen, 1992; Erbar and Leins, 2000), peculiar types of testa epidermis (Grau, 1980) and various pollen features (Parra and Marticorena, 1972; Skvarla et al., 1977; Hansen, 1991; Urtubey and Telleria, 1998; Zhao et al., 2000). More diagnostic, however, is the presence of two chloroplast DNA inversions in all Asteraceae except the taxa of Barnadesioideae (Jansen and Palmer, 1987; Kim et al., 2005). Because related families also lack these rearrangements, their presence provides a synapomorphy that unites all Asteraceae excluding Barnadesioideae.

Though small in number, genera of Barnadesioideae display a broad range of habits and distinct geographic distributions. The four monotypic genera *Duseniella*, *Huarpea Fulcaldea* and *Schlechtendalia* range from annual herbs to arborescent shrubs and are endemic to isolated areas in Argentina, Brazil, Ecuador, Peru and Uruguay. *Doniophyton* comprises two herbaceous species (Katinas and Stuessy, 1997) that grow in xeric areas of the Patagonian steppe, the Puna and the Monte desert. The three species of *Arnaldoa* (Stuessy and Sagástegui, 1993; Ulloa et al., 2002) have shrubby habit and occur in southern Ecuador and northern Peru. *Chuquiraga*, a genus of 23 species of evergreen shrubs (Ezcurra, 1985; Harling, 1991; Sagástegui and Sánchez, 1991; Granda, 1997), is a prominent member of the xeric flora in high Andean elevations and in Patagonian semideserts. Members of the genera *Dasyphyllum* and *Barnadesia* are also distributed along the Andes, but additionally occur in tropical forests of Argentina, Brazil and Paraguay. *Barnadesia* consists of 19 species of shrubs and trees (Chung, 1965;

* Corresponding author. Address: University of Texas at Austin, Integrative Biology, 1 University Station C0930, Austin, TX 78713, USA. Fax: +1 512 232 5699.
E-mail address: michael.gruenstaeudl@mail.utexas.edu (M. Gruenstaeudl).

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Urtubey, 1999), most of which are restricted to elevations of 1800–3400 m. The largest genus of the subfamily, *Dasyphyllum*, has 40 species (Cabrera, 1959, 1962, 1977, 1997; Sagástegui, 1980; Sagástegui and Dillon, 1985; Zardini and Soria, 1994), occurs at lower elevations and shows a disjunct distribution matching its subgeneric delimitation: The arborescent subgenus *Archidasyphyllum* is confined to the relict *Nothofagus* forests of central Chile and the southwest of Argentina, whereas the shrubs of subgenus *Dasyphyl-*

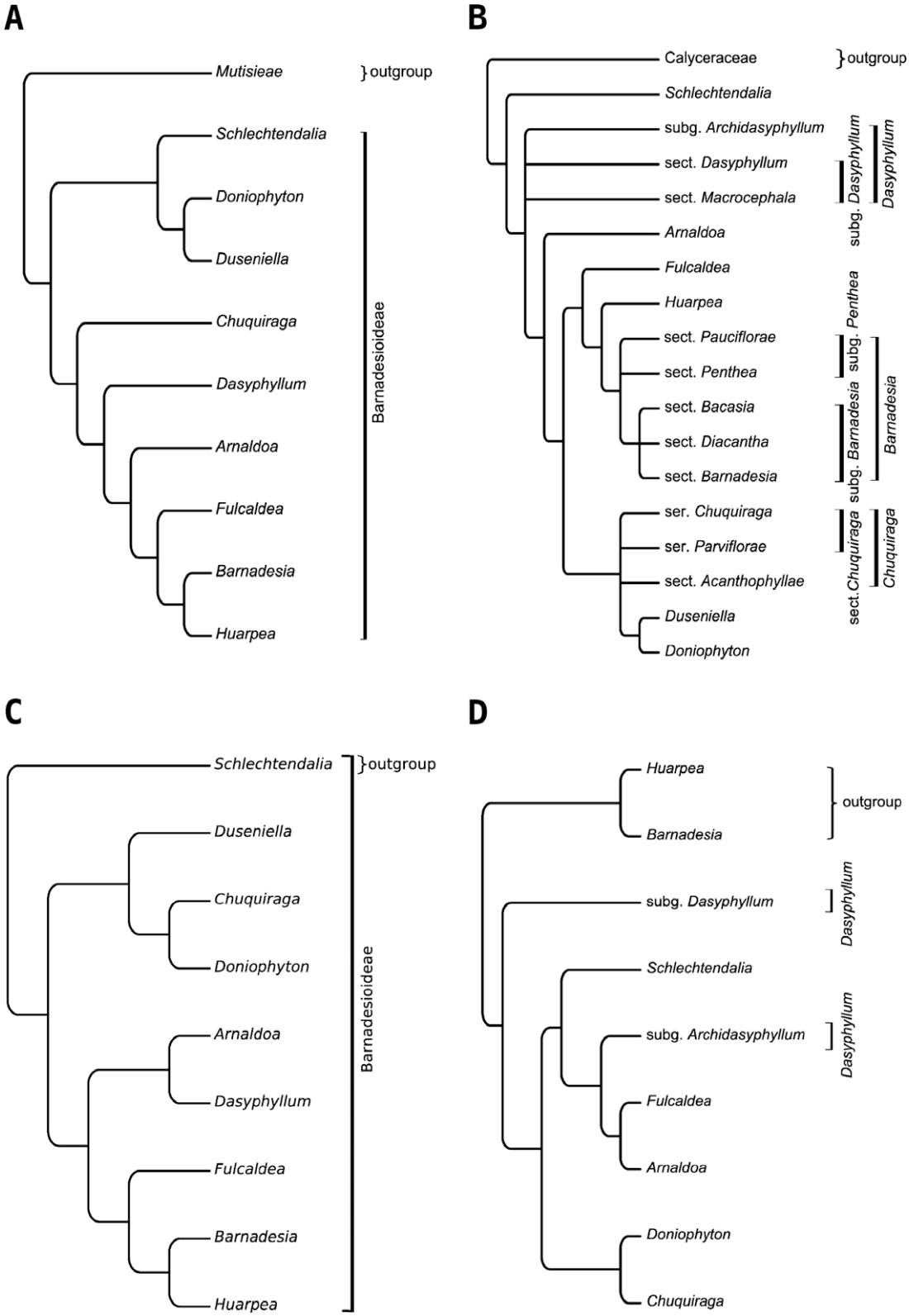

Fig. 1. Previously proposed relationships among genera of subfamily Barnadesioideae. (A) Bremer (1994); (B) Stuessy et al. (1996); (C) Urtubey and Stuessy (2001); (D) Gustafsson et al. (2001).