



## Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians

Charles D. Bell<sup>\*,1</sup>, Michael J. Donoghue

Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 065211, USA

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### Abstract

Species of Valerianaceae are a common component of the alpine flora throughout the Northern Hemisphere as well as the Andes of South America. Sequence data from three chloroplast markers (*psbA-trnH* intron, *trnK-matK* intron, and the *trnL-F* region) along with the internal transcribed spacer region (ITS) of nuclear ribosomal DNA were used to infer relationships within Valerianaceae. Both genomes, as well as a combined data set, provide support for the major clades within the group and do not support a monophyletic *Valeriana*. In addition, these data indicate that *Plectritis* is nested within South American *Valeriana*, as opposed to being sister to *Centhranthus* as previously hypothesized. Valerianaceae appear to have originated in Asia, probably in the Himalayas, and subsequently to have dispersed several times to Europe and to the New World. Our results imply that Valerianaceae colonized South America on multiple occasions from the north. In one of these cases there appears to have been a substantial and rapid radiation, primarily in the high elevation paramo habitat. A variety of methods were used to estimate divergence times to determine when Valerianaceae might have colonized South America. Regardless of the method and fossil constraints applied, our estimates suggest that Valerianaceae colonized South America prior to the formation of the Isthmus of Panama.

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### Introduction

Valerianaceae contains ca. 350 species distributed throughout much of the world (except Australia and New Zealand), mostly at high elevations and with many species in alpine zones. These plants are characterized by sympetalous, bilaterally symmetric, or sometimes highly

asymmetric flowers; inferior, three-carpelate ovaries, with one fertile carpel at maturity and a single anatropous ovule; achene fruits; and the absence of endosperm. The presence in many species of iridoids of the valepotriate type also characterizes the group (see Backlund and Moritz, 1998).

Valerianaceae exhibit considerable diversity in flower and fruit morphology. Perhaps the most impressive variation in flower morphology concerns the number of stamens, which ranges from four to one (five stamens have also been reported in *Patrinia*; Eriksen, 1989). The trend in the group has been toward reduction in the number of stamens. Donoghue et al. (2003) inferred that

\*Corresponding author.

E-mail address: [cbell3@xula.edu](mailto:cbell3@xula.edu) (C.D. Bell).

URL: <http://www.senckenberg.de/odes/05-09.htm>.

<sup>1</sup>Present address: Department of Biology, Xavier University of Louisiana, New Orleans, LA 70125, USA.

there was an initial reduction from the ancestral condition of four to three stamens in the core Valerianaceae, followed by further reduction to two stamens in *Fedia* and, independently, to a single stamen in *Centranthus*. The calyx in Valerianaceae can be persistent and leafy (as in *Nardostachys*), reduced to small teeth (as in *Fedia* and *Valerianella*), feathery and pappus-like (as in *Centranthus* and species of *Valeriana*), or completely lacking (as in species of *Valeriana*). Eriksen (1989) hypothesized that complete reduction of the calyx occurred independently on several occasions within Valerianaceae (e.g., within the Latin American species of *Valeriana*). The degree of reduction of the two sterile locules in the ovary is quite variable, from highly reduced to inflated (as in some *Valerianella* and *Valeriana*). Modifications of the calyx and of the sterile locules are related to dispersal mode.

Valerianaceae traditionally has been subdivided into three tribes (Graebner, 1906): Triplostegieae, Patrinieae, and Valerianeae. Many authors (see Weberling, 1970; Cronquist, 1988; Brummitt, 1992; Backlund, 1996) have recognized 14 genera: a single genus (*Triplostegia*) in the tribe Triplostegieae, two (*Patrinia* and *Nardostachys*) in the tribe Patrinieae, and 11 genera assigned to five subtribes within the Valerianeae. Six genera besides *Valeriana* have been recognized in South America (*Aretiastrum*, *Astrephia*, *Belonanthus*, *Phuodendron*, *Phyllactis*, and *Stangea*). However, recent treatments of the South American taxa have argued for placing these species in *Valeriana*, thus reducing the number of genera within Valerianaceae to eight (Borsini, 1944; Larsen, 1986; Eriksen, 1989).

Since the early 1990s, but especially since 2000, a variety of molecular and morphological phylogenetic analyses have shed light on the relationships of Valerianaceae within the Dipsacales and on relationships among the major lineages within Valerianaceae (Donoghue et al., 1992; Downie and Palmer, 1992; Backlund and Donoghue, 1996; Pyck et al., 1999; Pyck and Smets, 2000; Bell et al., 2001; Donoghue et al., 2001; Pyck et al., 2002; Bell and Donoghue, 2003; Donoghue et al., 2003; Zhang et al., 2003; Bell, 2004a, b; Hidalgo et al., 2004). Regarding relationships within Dipsacales, these studies have concluded that Valerianaceae is the sister group of a clade that includes *Triplostegia* (often treated as a member of Valerianaceae) and the Dipsacaceae. The Valerianaceae/Dipsacaceae clade in turn is most closely related to Morinaceae, together forming an herbaceous group that Donoghue et al. (2001) called the Valerina clade. In turn, Valerina is linked with the Linnaeae of the former Caprifoliaceae in the Linnina clade of Donoghue et al. (2001).

Regarding relationships within Valerianaceae, it appears (based on all data sets except *matK*) that the first split separates *Patrinia* from a clade containing all the other species. Within this remaining clade the first

split is between *Nardostachys* and a core Valerianaceae clade. These results demonstrate that the traditional Patrinieae (Graebner, 1906), consisting of *Patrinia* and *Nardostachys*, is paraphyletic. Within core Valerianaceae, *Valeriana*, *Centranthus*, and *Plectritis* form a clade that is sister to a clade containing *Fedia* and *Valerianella*. Most recently, Bell (2004a), based on a combined analysis of chloroplast and nuclear DNA sequences, found support for a South American valerian clade.

Overall, the distribution of Valerianaceae matches that of other Dipsacales clades (e.g., *Viburnum*, *Lonicera*). It is primarily found around the Northern Hemisphere, and probably originated in Asia and later moved into Europe and the New World (Bell et al., 2001; Donoghue et al., 2003; Bell, 2004a, b). Although its center of origin may be Asia, the present-day center of Valerianaceae species diversity is in South America, where many different morphological forms—from rosette plants (*V. rigida*) to microphyllous shrubs (*V. microphylla*) to annual vine-like species (*Valeriana chaerophylloides*)—occupy a wide range of habitats. Species of Valerianaceae are abundant and diverse in the Andes, especially in the paramo, scattered along the crests of the highest ranges in the northern Andes or on isolated mountaintops from 3000 to 5000 m.

Eriksen (1989) hypothesized that the diversity of Valerianaceae in South America represents three separate invasions (Fig. 1). She suggested that *Valeriana* twice entered South America through the Isthmus of Panama. One such movement was by the single species *V. chaerophylloides* (sect. *Astrephia* subgen. *Valeriana*), the other gave rise to subgen. *Phyllactis*, with some 160 species. In the case of *Phyllactis* this conclusion was based on the presence of the derived bisporangiate anther condition. Eriksen (1989) envisioned a separate invasion into Venezuela for sect. *Porteria*, using the Caribbean islands as stepping stones.

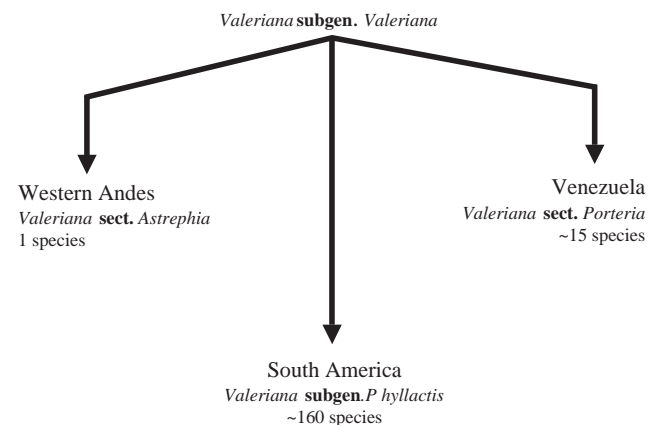


Fig. 1. The assumed pathways of *Valeriana* into the South American continent as proposed by Eriksen (1989).

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