



## Origin and diversification of the *Milla* Clade (Brodiaeoideae, Asparagaceae): A Neotropical group of six geophytic genera



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### ABSTRACT

The *Milla* clade currently comprises six genera of geophytic plants distributed from Arizona to Guatemala. Three genera (*Behria*, *Jaimehintonia* and *Petronymphe*) are monotypic while the remaining genera (*Bessera*, *Dandya* and *Milla*) contain from two to ten (*Milla*) species. Parsimony, Maximum Likelihood and Bayesian Inference analyses were conducted with plastid and nuclear DNA sequences from a total of 181 plants belonging to 15 species in all six genera. Molecular dating was performed under a relaxed clock model. We examined the phylogenetic relationships of the genera and species, estimated origin-divergence times for the clade and genera and determined the ancestral distribution area of the clade by optimizing ancestral areas given current biogeographic distributions. The phylogenetic results suggest that final decisions on limits of the six genera in the *Milla* clade will have to be established until further taxonomic work is completed for *Milla*, in particular for the group of populations included under the name *M. biflora*. The later genus is rendered polyphyletic by other genera of the family. The origin of the *Milla* clade is estimated at 15.8 Ma. Ancestral area of the clade most likely was located in the California Floristic Province and dispersal occurred most likely to the Chihuahuan-Coahuila Plateaus and the Trans-Mexican Volcanic Belt and from there to Baja California and the Sierra Madre del Sur. Two hypotheses that need further testing are proposed to explain complex relationships of genera and polyphyly of *Milla*, one in relation to fragmentation of populations and pollinator shifts and another suggesting that populations remained in refugia in the Trans-Mexican Volcanic Belt.

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### 1. Introduction

The *Milla* Clade is a group of geophyte genera that has been previously included in Alliaceae, Amaryllidaceae or Themidaceae because its species have indistinguishable monocot floral and vegetative morphology (Moore, 1953; Fay and Chase, 1996; Pires et al., 2001; Pires and Sytsma, 2002) (see Fig. 1). At present the group is recognized as part of the subfamily Brodiaeodidae of Asparagaceae (APGIII, Chase et al., 2009). The clade contains six genera, each with only a few species: *Behria*, *Jaimehintonia* and *Petronymphe* are monotypic, *Bessera* comprises two species, *Dandya* comprises four species, and *Milla*, the largest genus, contains ten currently defined species (Moore, 1951, 1953; Lenz 1971a, 1971b; Ravenna, 1971; Turner, 1993; Howard 1999).

Each of the smaller genera within the *Milla* clade have restricted distributions to particular provinces within North and/or Central America, i.e. the Baja California Peninsula (*Behria*), the Chihuahuan

Desert (*Jaimehintonia*), the Pacific Slopes and (*Dandya* and *Petronymphe*), the Trans-Mexican Volcanic Belt (*Bessera*) and the Balsas River Basin (*Dandya*), from Arizona and Texas to Guatemala (Moore, 1953; Lenz, 1971b; Ravenna, 1971; Ramírez-Delgadillo, 1992; López-Ferrari and Espejo-Serna, 1992; Turner, 1993; Howard 1999). Most of the species are restricted to arid lands, or occur in temperate and tropical areas with a marked dry season. Only three species of *Milla* grow in more humid habitats.

Vegetative morphology in the group is uniform, consisting of coated membranous corms with up to 15 leaves. Floral morphology is variable, mainly in the position of pedicel (erect or pendant), the type of perianth, the size of the corolla tube, flower color, the degree of fusion of floral elements, and in the size of stamens (Moore, 1953; Pires et al., 2001; Gándara et al., 2009) (Fig. 1). Most species of the group have flowers with bright colors, attracting pollinators such as hummingbirds, butterflies, and bees, while a few taxa have nocturnal and fragrant white flowers that attract hawk moths (Pires and Sytsma, 2002; pers. obs.).

Previous phylogenetic analyses, based on plastid DNA sequences have consistently retrieved the *Milla* clade (containing

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**Fig. 1.** Morphological variation in the genera of the Milla Clade. (A) *Bessera elegans*. (B) *B. tuitensis*. (C) *Dandya hanibalii*. (D) *Milla biflora*. (E) *M. magnifica*. (F) *M. potosina*. (G) *Behria tenuiflora*. (H) *D. thadhowardii*. (I) *Jaimehintonia gypsophila*. (J) *Petronymphe decora*.

all six genera) as sister to the *Brodiaea* complex (Fay and Chase, 1996; Pires et al., 2001; Pires and Sytsma, 2002). The clade is supported by two synapomorphic character states: an ovary stipe adnate to the perianth tube and a membranous corm (Pires and Sytsma, 2002). Sampling in earlier phylogenetic studies of the Milla clade has, however, been incomplete. The selection of taxa in the study of *Brodiaea* by Pires and Sytsma (2002) was extensive but did not include eight species of *Milla*, three of *Dandya* and *Behria tenuiflora*. Moreover, analyses to establish the generic limits of *Behria* and *Bessera* included only a few taxa from the other genera in the Milla Clade (Gándara et al., 2009). The status of *Jaimehintonia* needs further clarification as the most recent studies indicate its position as nested within a clade of *Milla* species (Gándara et al., 2009). In contrast, diagnostic floral anatomical characters (Gutiérrez et al., 2010) indicate that *Dandya* is likely to retain its taxonomic position. *Milla* has been retrieved as polyphyletic group (Pires et al., 2001; Pires and Sytsma, 2002; Gándara et al., 2009). Thus, the Milla clade is in need of further phylogenetic analysis to clarify the limits of the genera, and to understand their biogeographic and floral evolution.

The diversification of a number of plant lineages from arid lands in North America has been correlated with events from different geological periods. For example, the rapid aridification that started during the Cenozoic allowed for the diversification of *Tiquilia* (Boraginaceae) at the Eocene/Oligocene boundary in the Chihuahuan Desert (Moore and Jansen, 2007), and habitat expansion from the Pliocene to the Pleistocene promoted speciation events in the North American species of *Ephedra* (Loera et al., 2012) and Baja California species of *Encelia* (Asteraceae) (Fehlberg and Ranker, 2009). Hence, lineages of the Milla clade that correspond to different arid

regions of North America offer an ideal group to further investigate timing of origin and diversification and to determine if speciation and dispersal events are associated with geological and/or climatic events.

Our study focuses on the evolutionary history of the Milla clade to (1) determine the phylogenetic relationships of the genera and species in order to identify monophyletic groups, (2) estimate the origin-divergence times of the clade and its lineages, and (3) determine the ancestral distribution area of the clade.

## 2. Materials and methods

### 2.1. Taxon sampling

For each species, three to ten plants were collected in the field or from herbarium specimens (vouchers and GenBank accessions are provided in Appendix S1). The ingroup contains 15 species belonging to the six genera of the Milla clade. *Dandya purpusii* and three species of *Milla* (*M. filifolia*, *M. mortoniana* and *M. rosea*) were not included because we were not able to find them in their type localities. *D. purpusii* is known from a single specimen in Sierra La Paila, Coahuila without a precise locality. The type of *M. filifolia* was collected in the east of Cuernavaca near Yautepec and Cuautla, which is currently an urban area and we were not able to find plants. *M. mortoniana* was described from Tierras Blancas, Guerrero, without an accurate location. *M. rosea* type comes from Cerro del Obispado in Nuevo León and at present it is a recreational park with the Bishopric Palace. Four species of *Dichelostemma* (*Brodiaea* clade) were used as outgroup and *D. volubile* was selected as the functional outgroup (Pires and Sytsma, 2002).

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