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Higher level phylogeny and evolutionary trends in Campanulaceae subfam. Lobelioideae: Molecular signal overshadows morphology

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Abstract

Relationships within the subfamily Lobelioideae in Campanulaceae are inferred from DNA sequence variation in the *rbc*L and *ndh*F genes, and the *trn*L–F region including the *trn*L intron and the *trn*L–F intergenic spacer. Results derived from Bayesian and parsimony analyses provide evidence for the long-suspected paraphyly of the genus *Lobelia*, comprising over 400 species as presently circumscribed. The perennial dwarf herbs belonging to the Andean genus *Lysipomia* are sister to a group comprising the Neotropical shrubs *Burmeistera*, *Centropogon*, and *Siphocampylus*. Giant lobelioids from the Hawaiian Islands, Brazil, Africa, and Sri Lanka form a strongly supported group. Character optimizations on the phylogenetic tree reveal that shifts in fruit types and lignification have occurred much more commonly than generally assumed. The main clades in the subfamily are outlined, which largely contradict previous classifications based on morphology.

Keywords: Campanulaceae; Lobelioideae (Lobeliaceae); *rbc*L; *ndh*F; *trn*L–F; Fruit evolution; Bayesian inference; SH test; Systematics

1. Introduction

The Campanulaceae Jussieu is a well-known group of plants comprising 84 genera and nearly 2400 species (Lammers, 2007). The family has a cosmopolitan distribution and is present in a wide array of habitats, from tropical rain forest to tundra. The variety of life forms ranges from dwarf herbs shorter than 2 cm to trees up to 15 m tall (Fig. 1). There are at least three synapomorphies that characterize the family: laticifers producing milky sap, stamens attached to a disk at the apex of the ovary, and (usually) epigynous flowers (Judd et al., 2002). Other useful features that make the family easy to identify in the field include estipulate, simple, alternate, and entire leaves; flowers with secondary pollen presentation; 5-lobed, synsepalous calyces that form a hypanthium; 5-lobed, sympetalous, and often blue or violet corollas; solitary styles; and small and numerous seeds (Lammers, 2007).

As currently circumscribed (Lammers, 1998b), the family is divided into five subfamilies: Campanuloideae Burnett, Lobelioideae Burnett, Nemacladoideae Lammers, Cyphioideae (A. DC.) Walp., and Cyphocarpoideae Miers. Of these, Lobelioideae is the largest subfamily, comprising about 1200 species, half of which are native to South America. It is distinguished by having resupinate flowers with zygomorphic corollas and connate anthers (for a three-dimensional model of a typical lobelioid flower, see the on-line version of this article). The only taxonomic treatment covering all species in the subfamily is that of Wimmer (1953, 1968), who recognized two tribes, eleven subtribes, and five rami (Table 1). The delimitations of these groups were mainly based on reproductive characters, such as floral shape, juxtaposition of the ovary, fruit type, and number and mode of dehiscence of the capsules, but also habit and geographic distribution were sometimes employed. Still largely based on Wimmer's monography, Lammers (2007) recognizes 29 genera in the Lobelioideae (reduced to 28 by Koopman and Ayers, 2005) (Table 2). It is

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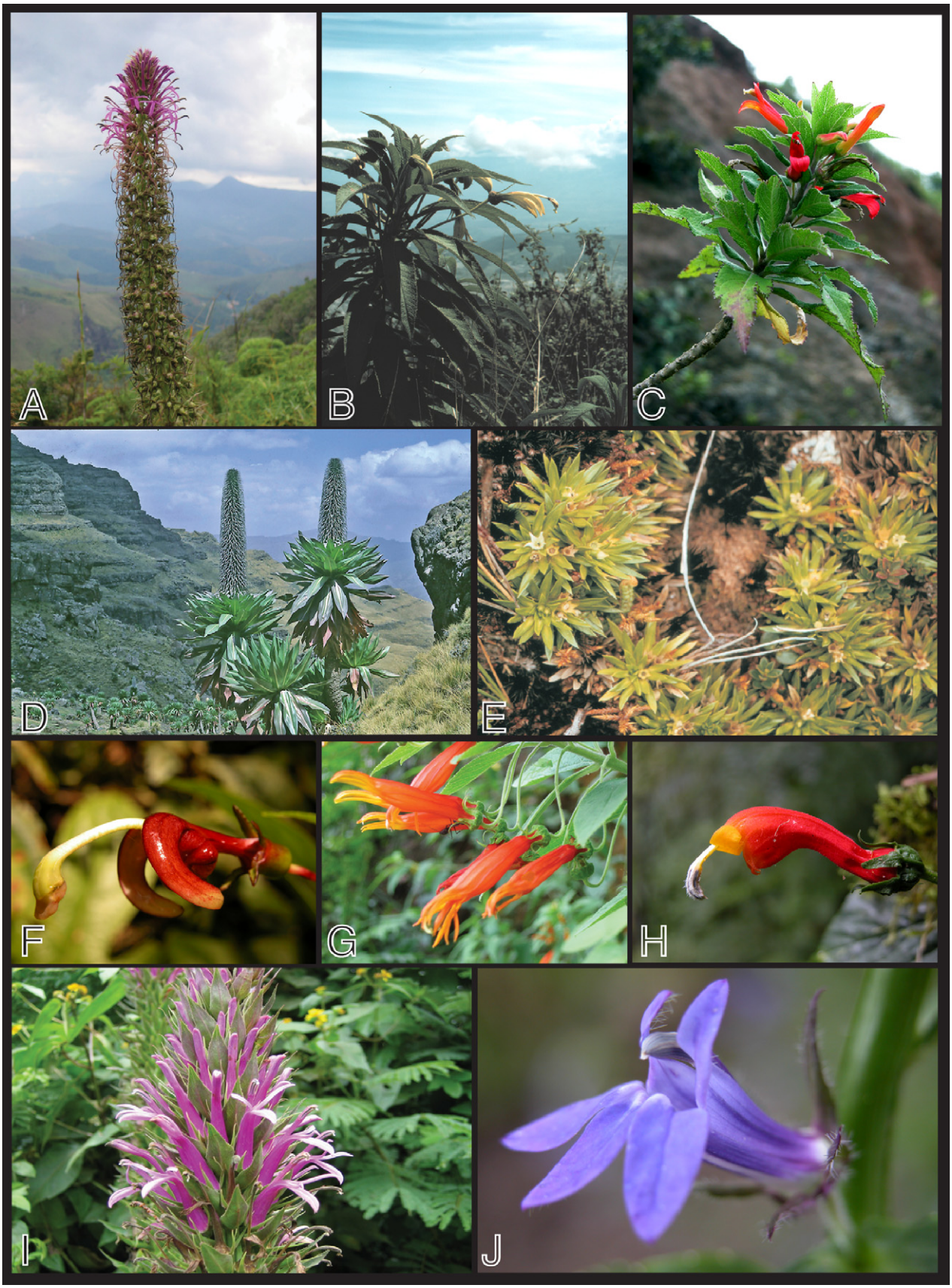

Fig. 1. Variation in floral morphology and habit within Campanulaceae subfam. Lobelioideae. (A) *Lobelia thapsoidea*, (B) *Siphocampylus giganteus*, (C) *Lobelia laxiflora*, (D) *Lobelia rhynchopetalum*, (E) *Lysipomia* sp., (F) *Burmeistera cyclostigmata*, (G) *Siphocampylus macropodus*, (H) *Centropogon granulosus*, (I) *Lobelia fistulosa*, (J) *Lobelia siphylitica*. Photos by Alexandre Antonelli (A, C, F, G, H, I, and J), Lennart Andersson (B and E), and Christian Puff (D).