The Origin of *Trimeris* (Lobeliaceae) Is Illuminated by a Second Species, *T. anceps*

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Abstract. A new combination, *Trimeris anceps* (L. f.) E. B. Knox, is established for the species previously known as *Lobelia anceps* L. f. *Lobelia* L. is the "core" genus of the Lobeliaceae, which has more than 30 segregate genera that have been recognized based on their evolutionarily divergent reproductive morphology. *Wimmerella* Serra, M. B. Crespo & Lammers is a segregate South African genus with completely fused corollas (which affect pollinator access), yet one of its descendant lineages has somehow reverted to the *Lobelia*-like condition of the corolla split to the base on the back. Recent discovery that the St. Helena–endemic *T. scaevolifolia* (Roxb.) Mabb. is sister to *L. anceps* provides an established segregate genus into which both of these morphologically anomalous species can be placed.

Key words: Australia, Chile, Juan Fernández, *Lobelia*, New Zealand, South Africa, St. Helena, *Trimeris*, *Wimmerella*.

The island of St. Helena in the South Atlantic Ocean is well known as Napoleon's second place of exile after his defeat at the Battle of Waterloo in 1815. In 1813–1814, Dr. William Roxburgh (1816) compiled a list of plants he saw growing on St. Helena, which included *Lobelia scaevolifolia* Roxb. The genus *Trimeris* C. Presl was established to accommodate this unusual shrubby species, which Presl (1836) named *T. oblongifolia* C. Presl. (a legitimate name as *L. scaevolifolia* was not cited). De Candolle (1839) transferred *Trimeris* as a monotypic section within *Lobelia* L. and altered the spelling of Roxburgh's epithet, incorrectly, to *L. scaevolaefolia*. Mabberley (1974) reviewed the giant lobelias and excluded the St. Helena endemic from his revised sectional treatment in *Lobelia* (in part, because of the solitary, axillary flowers instead of terminal inflorescences) by making the new combination *T. scaevolifolia* (Roxb.) Mabb. Lammers (2007) preferred retention of this species in *Lobelia* but placed it in the monotypic section *Trimeris* (C. Presl) A. DC. (Lammers, 2011).

DNA-based research confirmed the hypothesized pantropical radiation of tetraploid giant lobelias (including species in *Lobelia* and related segregate genera; Knox et al., 1993; Antonelli, 2008; Knox, 2014; Chen et al., 2016; Knox & Li, 2017), but several other groups of robust herbaceous to woody lobeliads in various sections of *Lobelia* (Lammers, 2011) and segregate genera, such as *Burmeistera* H. Karst & Triana, *Centropogon* C. Presl, and *Siphocampylus* Pohl, evolved independently (Antonelli, 2008; Knox et al., 2008; Knox, 2014; Lagomarsino et al., 2014; Chen et al., 2016; Knox & Li, 2017). While the morphological evidence indicated that *Trimeris scaevolifolia* is not part of the pantropical radiation of giant lobelias (Mabberley, 1974), the question regarding its origin remained unanswered.

A tissue sample from the Paris herbarium of a specimen collected on St. Helena in 1856 by J. S. C. Dumont-d'Urville (P [barcode] 02867158) recently yielded a complete plastid genome, with the surprising result that it is sister to *Lobelia anceps* L. f., a relatively small, herbaceous species that originated in South Africa and subsequently established a circumaustral distribution along coastal areas of Madagascar, Australia, New Zealand, and Chile as well as the Juan Fernández and other South Pacific islands (Lammers, 2007, 2011). Although *Lobelia* forms the "core" genus of the Lobeliaceae (Knox et al., 2006), *L. anceps* is taxonomically problematic because it is the sole species of *Lobelia* (thus far discovered) that is not part of this core phylogenetic nexus, and is instead at least maternally derived from the segregate genus *Wimmerella* Serra, M. B. Crespo & Lammers (Knox et al., 2006; see also Knox, 2014). *Wimmerella* has completely fused corollas (Serra et al., 1999), whereas the common ancestral species of *L. anceps* and *Trimeris scaevolifolia* reverted to the *Lobelia*-like condition of having the corolla split to the base on the back, which provides a flexible opening for pollinators who enter the flower. The non-cave–dwelling species of *Wimmerella* have similar morphological attributes and ecological requirements as *L. anceps* except that *L. anceps* has long-pedunculate axillary flowers that are very similar to those of *Trimeris scaevolifolia*, which provides morphological evidence to support the plastid DNA-based phylogenetic results uniting these two species. Given the prehistoric long-distance dispersal capability of *L. anceps*, it is not surprising that the common ancestral species reached St.

Version of record first published online on 6 February 2024.
doi: 10.3417/2024863

Helena. What is surprising is that a presumably herbaceous, coastal species evolved into a 1–2 m tall shrub that occupies the highest peaks (600–795 m) of this oceanic island (Mabberley, 1974).

A detailed presentation of the DNA-based phylogenetic relationships and biogeographic reconstruction within this *Wimmerella–Trimeris* clade will be presented elsewhere. Floral fusion has occurred repeatedly in the Lobeliaceae, with extreme examples such as *Brighamia* A. Gray, *Hippobroma* G. Don, and *Isotoma* (R. Br.) Lindl., but it is not clear how floral fusion could revert to the ancestral condition seen in *Lobelia*. It is possible that *Trimeris* originated as a hybrid between a maternal *Wimmerella* species and a paternal *Lobelia* species, but this hypothesis cannot yet be evaluated. Therefore, inadequate molecular support exists for lumping *Trimeris* with the morphologically well-distinguished *Wimmerella*, and *L. anceps* should be transferred to *Trimeris*. In order to submit the plastid genomes to GenBank with the correct names, a new combination is provided here.

Trimeris anceps (L. f.) E. B. Knox, comb. nov. Basionym: *Lobelia anceps* L. f., Suppl. Pl.: 395. 1782. TYPE: South Africa. Cape Province, *C. P. Thunberg s.n.* (SBT [barcode] 13478 image!).

Notes. Because *Lobelia anceps* was discovered repeatedly on different continents and oceanic islands, this species has many homotypic and heterotypic synonyms that were carefully compiled by Lammers (2007) and are not repeated here.

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ISSN 1055-3177 (PRINT); ISSN 1945-6174 (ONLINE)