



Brunfelsia (Solanaceae): A genus evenly divided between South America and radiations on Cuba and other Antillean islands

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ABSTRACT

Hallucinogenic or toxic species of *Brunfelsia* (Solanaceae: Petunieae) are important in native cultures throughout South America, and the genus also contains several horticulturally important species. An earlier morphological revision of the c. 50 species recognized three main groups, one consisting of the 23 Antillean species, another of southern South American and Andean species, and a third of species from the Amazon Basin and Guiana Shield. Based on plastid and nuclear DNA sequences from up to 65 accessions representing 80% of the species, we generated a phylogeny and a calibrated chronogram for *Brunfelsia* to infer clade expansion and shifts in pollinators and fruit types. *Brunfelsia* flowers offer nectar, and attract lepidoptera, hummingbirds, or bees; the fruits are dry or fleshy. Our results imply that *Brunfelsia* is 16–21 Myr old and entered the Antilles from South America early during its history, with subsequent expansion along the island arc. The ancestor of the Antillean clade was hawk-moth-pollinated and had fleshy capsules, perhaps facilitating dispersal by birds. The only shift to hummingbird pollination occurred on Cuba, which also harbors the largest single radiation, with 11 species (10 included in our study) that apparently arose over the past 4 Myr. Jamaica, Hispaniola, and Puerto Rico each sustained smaller radiations. The data also reveal at least one new species.

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1. Introduction

The medium-sized family Solanaceae, with ca. 2500 species in 100 genera, most of them in the Neotropics, is well known for its many biologically active alkaloids and saponins. Among the most important hallucinogenic or toxic plants used by indigenous groups throughout South America are species in the genus *Brunfelsia* L. (Schultes, 1979; Bennett, 1992; Plowman, 1998; Kloucek et al., 2005; Singh et al., 2008), and a saponin from *B. grandiflora* has potent leishmanicidal activity (Fuchino et al., 2008). *Brunfelsia* also has horticultural importance, with species being sold under the names “lady of the night” or “yesterday–today–tomorrow” for their nocturnally scented and color-changing flowers, which during anthesis turn from dark purple over mauve to white (Fig. 1E). The decrease in anthocyanin concentration in these flowers is extremely rapid and occurs at a specific and well-defined stage (Vaknin et al., 2005). In total, *Brunfelsia* comprises some 50 species that occur between Panama and northernmost Uruguay and on the Greater and Lesser Antilles. Most are medium-sized shrubs. Molecular data place the genus in the tribe Petunieae (Olmstead et al., 2008), which besides *Petunia* L. (14 species)

includes *Bouchetia* Dunal (3 species), *Calibrachoa* La Llave & Lex (24 species), *Fabiana* Ruiz & Pav. (15 species), *Hunzikeria* D'Arcy (3 species), *Leptoglossis* Benth. (7 spp.), *Nierembergia* Ruiz & Pav. (20 species), and *Plowmania* Hunz. & Subilis, a monotypic genus.

Brunfelsia has two centers of species diversity. One is in South America, especially south-central and eastern Brazil, where about half the species are native. The other is in the Antilles, with 23 species overall, distributed in Cuba, Jamaica, Hispaniola, and Puerto Rico. The *Flora de Cuba* lists 13 species, two cultivated and 11 endemic (León and Alain, 1974). Jamaica has six endemic species (Adams, 1972), Hispaniola two endemics and two widespread species (Liogier, 1994), Puerto Rico three endemics and the same two widespread species (Liogier, 1995), and the Lesser Antilles are thought to share a single species from St. Lucia to Hispaniola (Plowman, 1979). Most Antillean brunfelsias occur in specialized habitats, such as serpentine outcrops in Puerto Rico (*B. densifolia*), limestone at sea level in northern Jamaica (*B. undulata*), or cloud forest in the Blue Mountains of eastern Jamaica (*B. jamaicensis*).

Besides the Antillean species group (section *Brunfelsia*), a revision of the genus in South America recognized two other sections differing in flower morphology, *Franciscea* with 24 species in the eastern Andes and southeastern Brazil and *Guianenses* with six species in the Amazon basin and the Guayana region (Plowman, 1978, 1979, 1998). The three species occurring in coastal Ecuador, the Pacific Colombian Chocó region, and Panama have different flower

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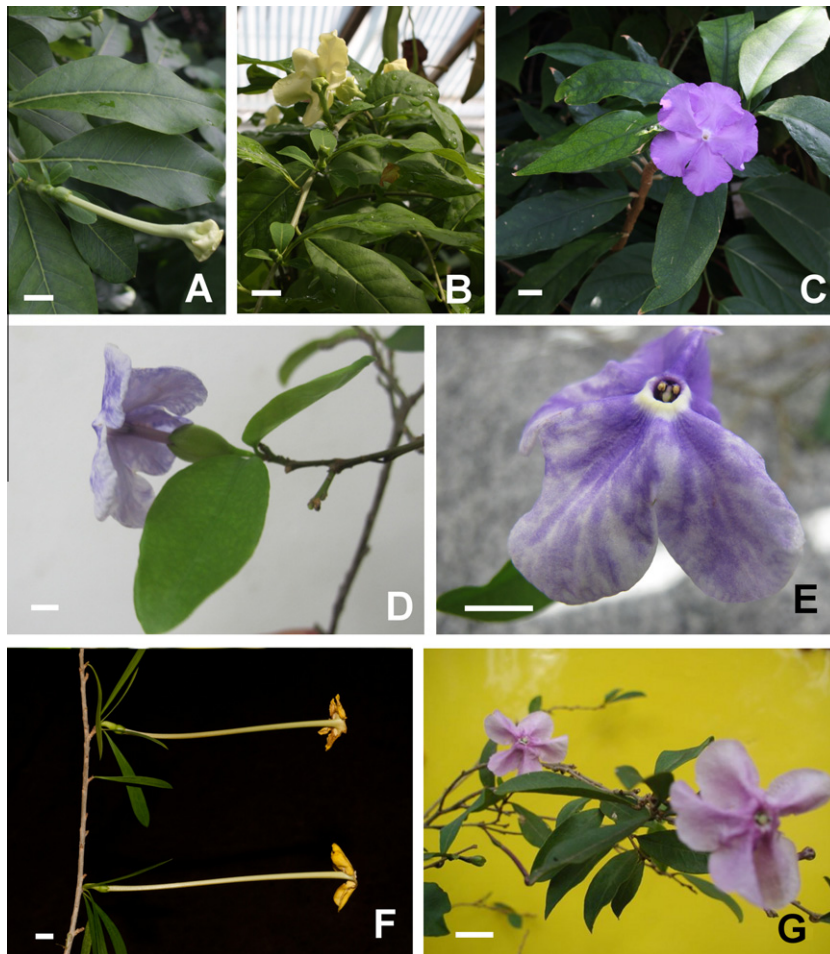


Fig. 1. Flowers of *Brunfelsia*. The scale bar corresponds to 1 cm. (A) *B. americana* bud, (B) open flower, Lesser Antilles; (C) *B. pauciflora* 1st-day flower, coastal lowland forest from Espiritu Santo to Santa Catarina; (D and E) *B. uniflora* 2nd or 3rd day flowers changing color from violet to pale lavender; eastern coast of Brazil; (F) *B. densifolia* endemic to Puerto Rico; (G) *B. cestroides* endemic to Cuba. Photographs by: N. Filipowicz (A–C), R. Teixeira de Queiroz (D and E), M. Nee (F), V. Fuentes (G). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

shapes and were therefore partly assigned to section *Franciscea*, partly to section *Guianenses*. The typical *Brunfelsia* habitat in South America is lowland rain forest, but a few species grow in riverine habitats, *Araucaria* forests, or the Brazilian shrub savanna “cerrado” (Plowman, 1998). Based on fieldwork and hundreds of herbarium specimens, Plowman (1979, 1998) hypothesized that the range of *Brunfelsia* in South America was once much wider and that climatic deterioration led to the disjunctions in the genus range seen today (our Fig. 2, inset B). He also thought that *Brunfelsia* arrived from South America to the Lesser Antilles and did not re-disperse to South or Central America. These hypotheses are now testable with a dated molecular phylogeny.

Besides Plowman’s explicit hypotheses about the geographic history of *Brunfelsia*, his classification indirectly points to a role of flower size and morphology, and hence pollinator shifts, in the evolution of the genus. This is apparent from Plowman’s use of flower structure as a sectional character, while fruit morphology was judged too labile for grouping species. The capsular fruits of *Brunfelsia* can be dehiscent or indehiscent, thin-walled or thick-walled, fleshy or dry, with brown or orange colors (Plowman, 1998). The flowers are salverform and differ in the relative proportions of corolla tube length and calyx size (Fig. 1A, D, and F). Most South American species have flowers with narrow, medium-length tubes with a circular nectar guide near the tube opening (Fig. 1C, and E), diurnal anthesis, and petals that change color during anthesis. Most Antillean species, by contrast, have long-tubed flowers

that are pale colored, open at night, and are strongly scented (Fig. 1A, B, and F; Cocucci, 1995; Plowman, 1998). Two Cuban species, however, have purplish flowers with medium-length corolla tubes (Fig. 1G; Plowman, 1998).

We here use plastid and nuclear DNA sequences for some 80% of the *Brunfelsia* species (sampling multiple populations for widespread species), molecular clock dating, and ancestral trait and area reconstruction to (i) infer species relationships in *Brunfelsia*, (ii) date the biogeographical events that led to the group’s disjunct distribution, and (iii) infer shifts in pollination and fruit type in a biogeographic context. *Brunfelsia* is among the few genera that have almost as many species in the Antilles as in South America (see Francisco-Ortega et al., 2007), making it an interesting system for addressing questions about the time and direction of clade expansion into or out of the Antilles or among islands. Given the group’s distribution and Plowman’s work (1998), our expectation was that the Antillean clade would be nested inside one of the two South American sections, *Franciscea* or *Guianenses*.

2. Materials and methods

2.1. Taxon sampling

Table 1 provides a list of the material used, with species and author names, voucher information, geographic origin, and

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