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Revision of *Brighamia* (Campanulaceae: Lobelioideae), a Caudiciform Succulent Endemic to the Hawaiian Islands

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ABSTRACT. *Brighamia* is a genus of caudiciform succulents endemic to coastal cliffs on four of the Hawaiian Islands. Aside from its habit, the genus is also unusual among Lobelioideae in its salverform corolla and few-flowered axillary inflorescences. The four species and two non-autonymic infraspecific taxa previously recognized are reduced to two allopatric species: *Brighamia insignis* of Ni'ihau and Kaua'i, with deltate to ovate calyx lobes 0.2–1 mm long, pedicels 10–30 mm long, papillose seeds, and yellow to pale cream (rarely white) corollas; and *B. rockii* of Moloka'i and Maui (and possibly Lāna'i), with oblong to elliptic calyx lobes 2.5–8 mm long, pedicels 6–12 mm long, smooth seeds, and white corollas. The relationships of *Brighamia* to other genera are obscure. Possibly, it is most closely related to the endemic Australian genus *Isotoma*. The floral nectar is rich in sucrose, supporting suggestions based on floral morphology that the genus is pollinated by hawkmoths (Lepidoptera: Sphingidae).

The endemic Hawaiian genus *Brighamia* A. Gray has attracted much interest in recent years, especially among aficionados of succulent plants (Christensen 1979; Johnson 1986; Perlman 1979; Rauh 1981; Rowley 1983). Much of this interest is due to its caudiciform (cf. Rowley 1987) habit, unique among Lobelioideae. Certainly, it is one of the most unusual members of the Hawaiian flora, resembling as it does a "big cabbage-head stuck on a naked pole" (Hillebrand 1888, p. 235).

The genus was revised most recently by St. John (1969), who recognized four species and two non-autonymic infraspecific taxa. However, Rowley (1983) and Johnson (1986) have suggested that this is not the best possible classification of these plants. St. John's concepts of species and infraspecific taxa are extremely narrow and typological, resulting in the recognition of more taxa than would be consistent with contemporary taxonomic practice. Preparation of a taxonomic summary of all Hawaiian Campanulaceae for the forthcoming *Manual of the Flowering Plants of Hawai'i* (Wagner et al., in press) afforded an opportunity to revise *Brighamia*. Due to the abbreviated format necessary in this single-volume manual, the complete revision is presented here.

TAXONOMIC HISTORY

The indigenous Polynesians were familiar with these curious plants of coastal cliffs, which they called *ālula*, *hāhā*, *pua'ala*, and *pū aupaka*

(Degener et al. 1975; Rock 1919; St. John 1969). The hollow stems of dead plants were used as trumpets, in much the same way that conch shells were used (St. John 1969). Jules Rémy, a collector for the Muséum National d'Histoire Naturelle in Paris (Mann 1867–1868), first brought them to the attention of the outside world. Rémy collected specimens (labelled "Isotoma?") on Moloka'i, Maui, and Ni'ihau sometime between 1851 and 1855. Subsequently, William T. Brigham collected liquid-preserved specimens on Moloka'i during 1864–1865 (Mann 1867–1868, 1869). Asa Gray studied Brigham's spirit collection from Moloka'i and Rémy's dried specimens from Ni'ihau. Gray (in Mann 1867–1868) concluded that the plants represented a new genus, which he named for Brigham. The Moloka'i and Ni'ihau specimens were considered to represent a single species, which he christened *Brighamia insignis* A. Gray.

The genus was never again collected on Ni'ihau or Maui. All specimens collected during the next 50 years were white-flowered plants obtained on Moloka'i. Such plants came to be regarded as "typical" in the nomenclatural sense, even though the species had never been lectotypified formally. As a result, when yellow-flowered plants were discovered in the Hā'upu Range of Kaua'i, they were segregated by Forbes and Lydgate (in Forbes 1917) as *f. citrina* C. Forbes & Lydgate. St. John (1958) noted that these plants also differed by their shorter calyx lobes and papillose (vs. smooth) seeds, and elevated it to

specific rank as *Brighamia citrina* (C. Forbes & Lydgate) H. St. John.

The only comprehensive monograph of the genus was prepared by St. John (1969), who recognized four species, each endemic to a single island. Of special importance was the typification of *Brighamia insignis*. Unable to locate the spirit specimen from Moloka'i, St. John designated Rémy's sheet from Ni'ihau as the lectotype. Consequently, that name was restricted to the plants of Ni'ihau. The plants of Moloka'i, long regarded as "typical" *B. insignis*, were judged specifically distinct and named *B. rockii* H. St. John; sporadic individuals with caudate corolla lobes were segregated as *f. longiloba* St. John. The plants of Kaua'i constituted two varieties of *B. citrina*: var. *citrina* of the Hā'upu Range and var. *napaliensis* H. St. John of the Nāpali Coast. The only known specimen from Maui was recognized as a fourth species, *B. remyi* H. St. John. Illustrations and distribution maps were provided for each taxon recognized.

SYSTEMATIC RELATIONSHIPS

Brighamia is characterized by a number of morphological features that are unusual in Lobelioideae: unbranched caudiciform habit, white or yellow salverform corollas, and few-flowered axillary inflorescences. The uniqueness of this suite of features makes assessing taxonomic relationships difficult. Data from cytology (Lammers 1988), palynology (Selling 1947), and wood anatomy (Carlquist 1969) similarly have not been helpful in resolving this question. Gray (in Mann 1867-1868) originally suggested a relationship with *Sclerotheca* A. DC., a small genus of trees and shrubs endemic to southeastern Polynesia. However, *Sclerotheca* differs from *Brighamia* by its branched and non-caudiciform habit, solitary axillary flowers, bilabiate corolla free from (vs. dorsally adnate to) the staminal column, anthers with apical tufts of white hairs on the lower two (vs. all five), and apically poricidal (vs. loculicidal) capsules.

Bentham (1876) grouped *Brighamia* with four other Hawaiian endemics (*Clermontia* Gaudich., *Cyanea* Gaudich., *Delissea* Gaudich., and *Rollandia* Gaudich.) on the basis of their woodiness, axillary inflorescences, and provenance. However, these four genera, treated by Wimmer (1943) as subtribe Cyaneinae F. Wimmer, differ by their non-caudiciform habit, bilabiate or uni-

labiate corolla, free staminal column (adnate to the corolla in *Rollandia*), anthers with apical tufts of white hairs on the lower two (all five in a few species of *Cyanea*), and baccate fruit. However, as regards the last, it should be noted that the pericarp of *Brighamia* is quite fleshy at first, and only later dries and dehisces.

Rock (1919) and Degener (1937) suggested that *Brighamia* might be derived from species of *Isotoma* (R. Br.) Lindl. A similar relationship was implied by Schönland (1889), who positioned *Brighamia* next to *Isotoma*. These authors apparently were impressed by the large white salverform corolla of *I. longiflora* (L.) K. Presl, a pantropical weed originally endemic to the West Indies. This species is now segregated as monotypic *Hippobroma* G. Don (Melville 1960). It differs from *Brighamia* by its annual or biennial herbaceous habit, solitary axillary flowers, and entire (vs. dorsally cleft) corolla tube. The similarity of the flowers probably is due to convergent adaptations for sphingophily (see below). The species currently accepted in *Isotoma* are endemic to Australia and differ from *Brighamia* by their annual (rarely perennial) herbaceous habit, solitary axillary flowers (rarely secund racemes), entire corolla tube, and anthers with a specialized pollen presentation mechanism (cf. Melville 1960). St. John's (1969) suggestion of a relationship to *Laurentia* Adans. (*nom. illeg.*, cf. Meikle 1979) is essentially an extension of this view. St. John apparently accepted the classification of Wimmer (1953), who included *Hippobroma* and *Isotoma* within *Laurentia*.

In the most recent monograph of the Lobelioideae, Wimmer (1953) emphasized the isolated position of *Brighamia* by treating it as the sole member of subtribe Brighamiiinae F. Wimmer. This subtribe was positioned next to the equally monotypic subtribe Apetahiinae F. Wimmer. However, *Apetahia* Baillon, endemic to Raiatea in the Society Islands, differs from *Brighamia* by its non-caudiciform and branched habit, solitary axillary flowers, unilabiate corolla, free staminal column, unilocular (vs. bilocular) ovary, parietal (vs. axile) placentation, and capitate (vs. bilobed) stigma.

The remaining genera of Lobelioideae have even less in common with *Brighamia* than do the genera discussed here. Barring the possibility that extra-Hawaiian relatives are extinct, it is safe to say that the morphological changes

that have occurred since the ancestor of *Brighamia* colonized the archipelago have been truly spectacular. Until more definitive data can be brought to bear on this problem, it would be best to regard *Isotoma* as the extant genus most closely related to *Brighamia*. Both have loculicidal capsules and salverform corollas dorsally adnate to the staminal column. Further, axillary racemes occur in one species, *Isotoma hypocraeteriformis* (R. Br.) Druce. Finally, chromosome numbers are concordant if not informative: $n = 7$ or 14 in *Isotoma* (McComb 1968), $n = 14$ in *Brighamia* (Johnson 1984; Lammers 1988).

POLLINATION SYNDROME

Lammers and Freeman (1986) presented evidence from nectar sugar compositions that supported the hypothesis that most Hawaiian Lobelioideae were adapted for pollination by nectarivorous birds, i.e., ornithophily. However, on the basis of its floral morphology and fragrance, they suggested that *Brighamia*, for which they had no nectar data, might be adapted for pollination by hawkmoths (Lepidoptera: Sphingidae), i.e., sphingophily. Evidence supporting this suggestion has been provided by Herbert and Irene Baker of the University of California at Berkeley (pers. comm.). The Bakers analyzed nectar of greenhouse-grown *Brighamia insignis* and found it to be dominated by sucrose. Sucrose-dominant nectars are characteristic of sphingophilous flowers, while those pollinated by passerines produce hexose-dominant nectars (Lammers and Freeman 1986).

SYSTEMATIC TREATMENT

BRIGHAMIA A. Gray in H. Mann, Proc. Amer. Acad. Arts 7:185. 1867.—TYPE: *Brighamia insignis* A. Gray.

Unbranched caudiciform succulents, 1–5 m tall. Stems fleshy, thickened toward the base, light gray, glabrous, with numerous helically arranged leaf scars near the apex; pith chambered; latex white, viscous. Leaves simple, exstipulate, fleshy, obovate, light green to yellowish green, glabrous, sessile to subsessile, arranged in a dense apical rosette; margin entire or weakly and distantly toothed in the apical half; apex subacute to obtuse; base cuneate. Flowers resupinate, protandrous, fragrant, 3–8 in suberect or spreading axillary, bracteolate ra-

ces. Calyx synsepalous; tube 10-ribbed, adnate to the ovary, forming a hypanthium; lobes 5, free, valvate, shorter than the tube. Corolla salverform, white, pale cream, or yellow; tube slender, straight, entire at anthesis, later dorsally cleft for ca. $\frac{1}{2}$ its length; lobes 5, valvate, subequal, their margins finely erose. Stamens 5, connate, included within the corolla tube; filaments connate, adnate to the corolla tube below the middle, glabrous to pubescent; anthers dithecal, opening by introrse longitudinal slits, the three dorsal ones longer than the two ventral ones, all with apical tufts of white hairs; pollen tricolporate, prolate, ellipsoidal. Ovary inferior, 2-locular; placentation axile; style slender, exserted; stigma 2-lobed. Fruit a capsule, ellipsoid, compressed, at first fleshy, eventually drying, each locule dehiscent by two lateral longitudinal slits. Seeds numerous, pale, ovoid to ellipsoid, smooth to minutely papillose. $n = 14$ (Johnson 1984; Lammers 1988).

Brighamia comprises a series of isolated populations scattered over four of the Hawaiian Islands: Ni'ihau, Kaua'i, Moloka'i, and Maui. Examination of patterns of morphological variation among these populations suggests that they divide naturally into two clusters: 1) plants of the western islands, Ni'ihau and Kaua'i, with small calyx lobes, long pedicels, papillose seeds, and yellow to pale cream (rarely white) corollas (*Brighamia insignis*, including *B. citrina*); and 2) plants of the central islands, Moloka'i and Maui, with large calyx lobes, short pedicels, smooth seeds, and white corollas (*B. rockii*, including *B. remyi*). Because these two clusters of populations are each distinguished by a correlated suite of several morphological features, they are recognized here as distinct species. The populations comprising each species are sufficiently similar among themselves that the recognition of infraspecific taxa is not warranted.

KEY TO THE SPECIES OF BRIGHAMIA

- Calyx lobes deltate to ovate, 0.2–1 mm long; pedicels 10–30 mm long; seeds papillose; corolla yellow to pale cream (rarely white) 1. *B. insignis*
 Calyx lobes oblong to elliptic, 2.5–8 mm long; pedicels 6–12 mm long; seeds smooth; corolla white, the tube green to yellowish green .. 2. *B. rockii*

1. BRIGHAMIA INSIGNIS A. Gray in H. Mann, Proc. Amer. Acad. Arts 7:185. 1867.—TYPE:

Hawaiian Islands, "Kauai ou Nihau" [Ni'ihau, fide St. John], 1851–1855, *J. Rémy 309ter* (lectotype, designated by St. John 1969, p. 192: GH!; isolectotypes: P [3]!).

Brighamia insignis forma *citrina* C. Forbes & Lydgate, Occas. Pap. Bernice Pauahi Bishop Mus. 6:203. 1917. *Brighamia citrina* (C. Forbes & Lydgate) H. St. John, Pacific Sci. 12:182. 1958—TYPE: Hawaiian Islands, Kaua'i, Hā'upu Range near Nāwiliwili Bay, 31 Oct 1916, C. N. Forbes 706.K (holotype: BISH!; isotypes: MO [2]!, NY!, P!, US!).

Brighamia citrina var. *napaliensis* H. St. John, J. Linn. Soc., Bot. 62:194. 1969—TYPE: Hawaiian Islands, Kaua'i, Nāpali Trail, between Ho'olulu and Waiahuakua valleys, 650 ft, 15 Sep 1957, W. J. Newhouse & J. Hewett s.n. (holotype: BISH!).

Leaves 12–20 cm long, 6.5–11 cm wide. Peduncles (including rachis) 4–12 cm long; pedicels 1–3 cm long. Hypanthium 10–12 mm long, 4.5–7 mm wide. Calyx lobes deltate to ovate, 0.2–1 mm long. Corolla yellow to pale cream (rarely white); tube 7–14 cm long, 0.3–0.4 cm wide; lobes elliptic, 1.3–2.2 cm long, 0.7–1.1 cm wide. Anthers glabrous or pubescent along the connectives. Capsules 13–19 mm long, 9–13 mm wide, 4–5 mm thick. Seeds 0.8–1.2 mm long, papillose. *n* = 14 (Johnson 1984; Lammers 1988).

Distribution. Endemic to the Hawaiian Islands. Basaltic cliffs near the ocean, at elevations up to 400 m. Known only from Ni'ihau (Ka'ali Cliff) and Kaua'i (Nāpali Coast and Hā'upu Range). The only specimens from Ni'ihau are those collected by Rémy in the 1850's. However, it was subsequently observed there in 1912 (Forbes 1913) and 1947 (St. John 1969).

Representative specimens. HAWAIIAN ISLANDS. **Kaua'i:** Waiahuakua Valley, Hā'ena-Kalalau trail, *Degener 21553* (B); SE face of Mt. Hā'upu, Kipūkai, Kipū, Lane 57-150 (BISH); Hanakoa sea cliffs between Ho'olulu Str. & Waiahuakua Str., Lane & St. John 57-154 (BISH, US); sine loc., *Lydgate s.n.* (BISH [2]); headland E of Waiahuakua Valley, Hanakoa, St. John et al. 23156 (US, W), St. John et al. 23158 (DUKE); Kalalau Trail, E of Hanakoa Valley, W of Hanakāpī'ai Valley, Stone 1475 (BISH); Pacific Tropical Botanical Garden, Lāwa'i, cultivated, *Lammers & Flynn 5386* (DUKE, OS).

On the western islands of the archipelago, populations of *Brighamia* are found in three geographically distinct areas: 1) Ka'ali Cliff,

Ni'ihau, 2) Nāpali coast, western Kaua'i, and 3) Hā'upu Range, southeastern Kaua'i. These populations are characterized by deltate to ovate calyx lobes 0.2–1 mm long, pedicels 1–3 cm long, papillose seeds, and yellow to pale cream (rarely white) corollas. On this basis, they are treated here as a single species. The name *Brighamia insignis*, as typified by St. John (1969), has priority and must be used for the species thus circumscribed. On the basis of minor differences in staminal column vestiture, prominence of seed papillae, calyx lobe lengths, and leaf margins, St. John (1969) recognized the populations in each area as a distinct taxon: *Brighamia insignis*, *B. citrina* var. *napaliensis*, and *B. citrina* var. *citrina*, respectively. However, the variation in these characters is such that I prefer not to recognize infraspecific taxa on these bases.

2. **BRIGHAMIA ROCKII** H. St. John, J. Linn. Soc., Bot. 62:196. 1969.—TYPE: Hawaiian Islands, Moloka'i, peninsula east of Wailau Valley, rock crevices, 50 m, 4 Jul 1933, F. R. Fosberg 9643 (holotype: BISH!).

Brighamia remyi H. St. John, J. Linn. Soc., Bot. 62:201. 1969.—TYPE: Hawaiian Islands, Maui, 1851–1855, *J. Rémy 309bis* (holotype: P!).

Brighamia rockii forma *longiloba* St. John, J. Linn. Soc., Bot. 62:201. 1969.—TYPE: Hawaiian Islands, Moloka'i, sea pali of Wailau, both sides of Wy Ehu [Wai'ehu], Sep 1912, C. N. Forbes 519a.Mo (holotype: BISH!; isotype: MO!).

Leaves 6–22 cm long, 5–15 cm wide. Peduncles (including rachis) 3.5–7.5 cm long; pedicels 0.6–1.2 cm long. Hypanthium 9–12 mm long, 5–8 mm wide. Calyx lobes oblong to elliptic, 2.5–8 mm long. Corolla white; tube 8–13 cm long, 0.2–0.4 cm wide; lobes elliptic, 1.7–3.7 cm long, 0.8–1.3 cm wide. Anthers glabrous. Capsules 13–20 mm long, 7–10 mm wide, 3–4 mm thick. Seeds 1.1–1.2 mm long, smooth.

Distribution. Endemic to the Hawaiian Islands. Basaltic cliffs near the ocean, at elevations up to 470 m. Currently known only from the windward coast of Moloka'i between Kalau-papa and Hālawā. Inclusion of Maui in its range is based upon the single specimen collected by Rémy in the early 1850's. This species may also occur on Lāna'i, for in 1910, Joseph Rock ob-

served several inaccessible individuals of *Brighamia* on cliffs near the head of Maunalei Valley (Rock 1919). In the absence of specimens, the identity of this population must remain unknown.

Representative specimens. HAWAIIAN ISLANDS. **Moloka'i:** Wailau Valley, coastal cliffs, *Degener 3328* (MASS, NY [3], US [2]), *Degener 3328a* (B), *Degener & Nitta 7868* (MASS, MO, NY); Sea pali of Wailau, *Forbes 519.Mo* (BISH, NY, P, US, W); pali of Hālawā Valley, *Hillebrand s.n.* (B); Hālawā Valley, *Rock 8817* (BISH); Kalaupapa-Waikolu cliffs, *Rock 8817a* (BISH); Kalaupapa pali, *Rock 8817b* (BISH); sine loc., *Faurie 474* (P), *Hillebrand s.n.* (B, E, GH), *Mann & Brigham s.n.* (BISH), *Rémy 316* (P).

St. John (1969) distinguished *Brighamia remyi* and *B. rockii* on the basis of minor differences in vestiture of the filament tube and shape of the calyx lobes. Although the sole specimen of *Brighamia remyi* lacks capsules and the color of the corolla is uncertain ("apparently white," fide St. John), it is here regarded as conspecific with *B. rockii* on the basis of its oblong to elliptic calyx lobes 4.5–8 mm long and its pedicels 6–12 mm long. Plants with the distinctive corolla lobes of *Brighamia rockii* f. *longiloba* apparently occur as sporadic individuals within populations of typical plants (St. John 1969). As such, they do not merit formal nomenclatural recognition.

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