

Sharpening plant taxonomy in South Florida: *Baccharis* and *Melanthera* (Asteraceae), *Borreria* and *Chiococca* (Rubiaceae), and *Lantana* (Verbenaceae)

Alan R. Franck

Institute of Environment, Department of Biology, Florida International University, Miami, Florida, USA

George D. Gann

The Institute for Regional Conservation, Delray Beach, Florida, USA

Jimi Sadle

Everglades National Park, National Park Service, 950 Krome Avenue, Homestead, FL, USA

Arian Farid

Herbarium, Department of Cell Biology, Microbiology, and Molecular Biology, University of South Florida, Tampa, Florida, USA

Corresponding author email: afranck@fiu.edu

ABSTRACT

The varied habitats of South Florida (e.g. pine rocklands, prairies, coastal strands, and hammocks) harbor some exceptional biodiversity, including many endemics. Some plant taxa in South Florida can be difficult to distinguish from relatives, resulting in varying taxonomic opinions among authors with important conservation implications. Taxonomic concepts were revisited in five genera among three families: Asteraceae (*Baccharis* and *Melanthera*), Rubiaceae (*Borreria* and *Chiococca*), and Verbenaceae (*Lantana*). Based on field work and herbarium studies, *Borreria terminalis*, *C. parvifolia*, *C. pinetorum*, *M. angustifolia*, and *M. parviflora* are here recognized as species distinct from their more widespread relatives *B. verticillata*, *C. alba*, and *M. nivea*, contrasting with other treatments that have only recognized one species in each genus among these names. *Lantana depressa* is here restricted to the pine rockland species endemic to Miami-Dade County. The other native taxa previously considered varieties of *L. depressa* are segregated as a separate species with two varieties. *Baccharis dioica* is confirmed to be extirpated in the wild from Florida (and the USA) despite its occasional misapplication to plants in Florida and elsewhere. Lectotypes are designated for several names, especially in *Chiococca*. *Published online* www.phytologia.org *Phytologia* 103(2): 29-68 (June 21, 2021). ISSN 030319430.

KEY WORDS: botany, Caribbean, coastal, herbarium, pine rocklands, prairies, typification

The vascular plant species richness of South Florida (Charlotte, Glades, Martin cos. and south to the Florida Keys in Monroe Co.; Gann et al. 2020) is represented by about 1500 native species, of which approximately 270 species are not known elsewhere in the state. About half of Florida's endemic plants, about half of Florida's state endangered and threatened plants, and about one-third of Florida's federally listed plant species have been documented in South Florida (Gann et al. 2020; Wunderlin et al. 2020). The conservation status of the entire native flora has been assessed by The Institute for Regional Conservation (IRC) using Heritage/NatureServe criteria (Gann et al. 2002, 2020).

The biota of extreme southern Florida (ca. south of 26.25°N; Bolter 2014: Fig. 1.3) is probably relatively young since this region may have been completely submerged ca. 120 Ka ago when the sea level was about 6 m higher than current levels. About 80 Ka ago sea levels were similar to present-day levels.

Freshwater terrestrial habitats have then probably been in fairly continuous existence in some form only for the past 80–100 Ka in extreme southern Florida (Dillon 1956; Petuch 1987; Gleason & Stone 1994; Emslie 1998; Morgan 2002), while some local habitats may only be a few to several thousand years old (Willard et al. 2006; Willard & Bernhardt 2011). Consistent with this timeline, a clade of southern Florida haplotypes of the marsh rabbit *Sylvilagus palustris* was estimated to have diversified in the last 19–104 Ka (node 4 in Tursi et al. 2012). Probably, the taxa endemic to extreme southern Florida (Appendix 1) speciated sometime in the last 100 Ka. About 2% of the vascular plant taxa of extreme southern Florida are locally endemic, a proportion similar to the single island/island group endemism rate of the Bahamas Archipelago (Freid et al. 2014) and El Hierro of the Canary Islands (Steinbauer et al. 2012).

During the last glacial maximum ca. 14 Ka ago, sea levels were ca. 120 m lower, expanding the terrestrial area of South Florida. Since 14 Ka ago, sea levels have been rising, decreasing the terrestrial area (Emslie 1998: 95; Knorr 2006; Zong 2015). As far back as 10 Ka ago, the presence of humans and the extinction of several mammal species appear to coincide in South Florida (Morgan 2002: 22), possibly causing extinction and extirpation of other taxa. In the past 100 years, anthropogenic activity has caused five vascular plant taxa endemic to South Florida to presumably become extinct (Gann et al. 2002, 2020; Knapp et al. 2020; NatureServe 2020; Appendix 2), and an additional 34 taxa not found elsewhere in Florida to be presumably recently extirpated from South Florida (Gann et al. 2020; Appendix 3).

South Florida represents about 22.5% of the state's total land area (excluding perennial open water) but contains about 36% of the resident human population (U.S. Census Bureau 1994, 2010, 2020) and a significant amount of agriculture (USDA 2019). Drastic landscape-level changes in the past 100–150 years have destroyed more than 80% of the pine rocklands of Miami-Dade County (Shaw 1975; URS Corporation Southern 2007), a globally imperiled ecosystem dependent on fire (FNAI 2010; WWF 2020). While fires may have historically occurred about every 2–15 years in pine rockland and other pyrogenic communities (Taylor 1981; Lockwood et al. 2003; Huffman 2006; Harley et al. 2012), since about the 1950s, fire frequency has significantly decreased in South Florida (Albritton 2009; Kocis 2012), causing further degradation of the pine rockland ecosystem. Both fire regime disruption and major changes to the local hydrology affect marl prairies (Willard & Holmes 1997; Willard et al. 2006; Hanan et al. 2010; Richards & Olivás 2020), which often border pine rocklands and share many of the same taxa (Olmsted et al. 1983). Coastal uplands have been dramatically transformed by anthropogenic development and sea level rise (Saha et al. 2011). Ecotones between these ecosystems and hammocks are also important habitat for many South Florida plants.

To conserve and restore South Florida's flora, an accurate understanding of its biodiversity is necessary, requiring a wealth of taxonomic effort and field work (Gann et al. 2002). In particular, we address the taxonomy among select species of five plant genera in three families in South Florida: Asteraceae (*Baccharis* L. and *Melanthera* Rohr), Rubiaceae (*Borreria* G.Mey and *Chiococca* P.Browne), and Verbenaceae (*Lantana* L.). We recognize the species *Borreria terminalis* (a Florida endemic), *C. parvifolia*, *C. pinetorum*, *M. angustifolia*, and *M. parvifolia* (a Florida endemic). Some prior treatments have considered these five species synonyms of the more widespread species *B. verticillata*, *C. alba*, and *M. nivea* in their respective genera. Species rank is proposed for the pine rockland endemic *L. depressa*, while together *L. depressa* var. *floridana* and *L. depressa* var. *sanibelensis* are segregated as a new species (*L. sandersii*) separate from *L. depressa*. Comments are provided concerning the genus *Baccharis* L., particularly *B. dioica* which is extirpated from Florida (and the USA) and commonly confused with *B. halimifolia*. Several lectotypes are designated.

MATERIALS & METHODS

Herbarium specimens were studied in person (FNPS, FTG, USF) or through digital resources (A, ARCH, BM, C, CONN, DUKE, DWC, F, FLAS, FSU, G, GA, GH, HAL, L, LY, M, MA, NCU, NY, P,

PH, US, VT, WVA). Herbarium acronyms follow Thiers (2020). Many specimens were consulted through the Southeast Regional Network of Expertise and Collections (sernecportal.org). Plants of some taxa were cultivated at the greenhouse of the Department of Biological Sciences, Florida International University or outdoors in Goulds, both in Miami-Dade Co., Florida. In addition to herbarium specimens and field observations, observations on iNaturalist.org were studied.

TAXONOMIC TREATMENTS

BACCHARIS (ASTERACEAE)

Baccharis consists of about 400 species, predominantly of the neotropics. The genus is characterized by the usually dioecious plants, often gland-dotted leaves, discoid inflorescence heads, and pappus bristles often exerted beyond the phyllaries in fruit (Sundberg & Bogler 2006).

Species can be somewhat challenging to identify in Florida, due to the heterogeneity of leaf blade shape, size, and margins. Within the continental USA, *Baccharis dioica* was known only from the Miami area in Florida, but that native population is clearly extirpated from both Florida and the continental USA. Despite this, the name *B. dioica* continues to be misapplied to plants of *B. halimifolia*. Part of the confusion could be due to morphological variation within *B. halimifolia* or alleged hybrids and admixtures of *B. angustifolia* and *B. halimifolia* (Sundberg & Bogler 2006).

Key to *Baccharis* in Florida

1. Leaf blades mostly linear and mostly entire, rarely narrowly elliptic or toothed, 1–7(–11) mm wide
 *B. angustifolia*
1. Leaf blades obovate, rhombic, to elliptic, entire to toothed, (7–)10–80 mm wide (some blades smaller, especially distal ones or on immature plants) 2
2. Leaf blade entire or with sharply acute teeth, glands small and inconspicuous under magnification; synflorescence of sessile clusters subtended by normal-sized to slightly reduced leaves
 *B. glomeruliflora*
2. Leaf blade entire or with bluntly acute to obtuse teeth, sometimes somewhat lobate, glands large and usually conspicuous under magnification (less so in older specimens); synflorescence in paniculiform or umbelliform arrays, the arrays pedunculate and not appearing sessile, the individual heads sometimes sessile along the leafless or bracteate central rachis of the paniculiform or umbelliform array 3
3. All leaf blades entire (marginal teeth extremely rare), the apex broadly subtruncate to subacute or mucronulate, fairly uniform in size and shape, typically only a few markedly reduced immediately below the inflorescence; synflorescence umbelliform; involucre obconic; phyllaries often with a light midvein that bisects the base of the darker medial band; pappus 3–6 mm long in fruit *B. dioica*
3. Usually at least some leaf blades toothed or lobed, rarely all entire, sometimes the distal ones especially entire, the apex narrowly acute to rounded, size and shape typically not uniform, the leaves typically gradually reduced in size towards the inflorescence; synflorescence paniculiform; involucre campanulate; phyllaries without a light midvein or rarely present at the base of the darker medial band; pappus (6.5–)7–12 mm long in fruit *B. halimifolia*



Figure 1. *Baccharis*. A. Lectotype of *Baccharis dioica* (Reproduced with permission of the Natural History Museum of Denmark). B. *B. halimifolia* (Lakela 30376, Collier Co., USF), originally misidentified as *B. dioica*. C–D. Plant of *B. angustifolia* at Matheson Hammock, Miami-Dade Co. with some toothed, wide leaves on a sterile shoot (photos by A.R. Franck).

Baccharis angustifolia Michx., Fl. Bor.-Amer. 2: 125. 1803. Lectotype (designated here): USA, Carolina to Florida, *Michaux s.n.* (lectotype, P00755433; islectotype, P00755434).

Native to the southeastern USA and the Bahamas, this species is primarily found in coastal habitats. Its leaves are usually linear and entire with few to no glands, but infrequently they are toothed or densely glandular (e.g. Martin Co., *Popenoe 1580*, FTG). Its inflorescence head (with ca. 15–20 flowers) tends to be smaller than the other species in Florida. It probably hybridizes with *B. halimifolia* (Sundberg & Bogler 2006), and a few specimens have been identified as such hybrids (Miami-Dade Co., *Correll & Correll 40247*, FTG; Miami-Dade Co., *Franck 5048*, FTG; and Levy Co., *Judd et al. 8374*, FLAS).

Below are cited several specimens with one or more toothed leaves (Fig. 1C–D), which all appear to be identifiable as *B. angustifolia*. The presence of toothed and sometimes narrowly elliptic leaves in *B. angustifolia* seems to approach *B. halimifolia* (Fig. 1). It is unclear what extent of hybridization or introgression may be occurring between *B. angustifolia* and *B. halimifolia*.

Specimens of *B. angustifolia* with one or more toothed leaves. **BAHAMAS.** New Providence, Fort Montagne, 23 Aug 1904, *Britton & Brace 172* (NY); New Providence, Lake Cunningham, 30 Apr 1941, *Peggs s.n.* (FLAS). **USA. Florida.** Citrus Co.: W of Ozelto, 18 Mar 1990, *Hansen et al. 6890* (USF). Lee Co.: last rest stop on I-75, 18 Oct 1986, *Southerland s.n.* (USF); Lower Captiva Island, 30 Jan 1969, *Brumbach 6604* (FTG). Levy Co.: Cedar Key Airport, 1 Mar 1994, *Loconte & Walker 892* (FTG). Miami-Dade Co.: Elliott Key, 24 Jul 1959, *Ward & Ward 1596* (FLAS). Monroe Co.: Cudjoe Key, 20 Oct 1985, *Hansen et al. 10648* (USF); North Key Largo, 3 Jun 1981, *Zerba s.n.* (FLAS); Key Largo, 12 Jan 1941, *Woodbury s.n.* (FTG). Volusia Co.: Tomoka State Park, 22 Oct 2005, *Kunzer 1170* (FTG, USF).

Baccharis dioica Vahl, Symb. Bot. 3: 98. 1794. Lectotype (designated here): Montserrat, *Rohr s.n.* (lectotype, C1006974 [pistillate]; islectotypes, C1006973 [staminate], GH00003896, L0065805, PH00042343).

Baccharis dioica (Fig. 1A) is native to the West Indies, Mexico, and Florida (Sundberg & Bogler 2006). It is extirpated in the wild in Florida (Gann et al. 2002, 2020), but it can be found in cultivation in Florida, presumably sourced from populations in the Caribbean islands. It was previously only known from the Brickell Hammock area near present-day downtown Miami, where it may have been somewhat common given that 24 herbarium sheets exist from six separate collections, first collected in Mar 1904 (Small 1905) and the last in 1915.

In 1895, Miami's population was around 200–300. In 1896, John Sewell was quoted as saying “I found Miami all woods” and shortly thereafter the 1st train arrived in Miami (Carson 1956). In 1900, the population was around 1,500, by 1910 it was about 5,000, and in 1920 it nearly reached 30,000 (Tweed 1995). By 1931–1932, the Brickell Hammock was already noted as a “relict”, most of it “cleared or fenced in by big estates” (Young 1968; see also Small 1918 and Broun 1936). It is likely then that *B. dioica* had been extirpated from Florida by the 1930s, nearly coinciding with the sympatric extinction of *Tephrosia angustissima* Shuttlew. ex Chapm. var. *angustissima* (Robinson 1899; Gann et al. 2002). The Brickell Hammock area also supports the only known extant Florida locations for *Licaria triandra* (Sw.)Kosterm. and *Tropidia polystachya* (Sw.)Ames (Hammer 1997; Gann et al. 2002).

The name *Baccharis dioica* has continuously been misapplied to specimens of *B. halimifolia* (Fig. 1B; Lance 2004), or possibly hybrids of *B. angustifolia* and *B. halimifolia*. The leaf blades of *B. dioica* are often rather uniform in shape, obovate-spatulate with a subtruncate to broadly rounded apex. The leaf blades are also nearly uniform in size on a plant, often with only a few reduced in size below the inflorescence. The involucre is obconic and the pappi of the cypselae are 3–6 mm long. These characters help to distinguish *B. dioica* from the other species.

In the protologue, Vahl cited specimens of Julius Philipp Benjamin von Rohr and John Ryan. Two specimens attributed to Rohr reside at the C herbarium. One is a pistillate plant and the other is a staminate plant. They can be considered part of one gathering (Deng 2016; Art. 8.2). They are here lectotypified. These specimens have precedence over the protologue's cited illustration (Art. 9.12) which was taken by Howard (1989) to be the type.

Representative specimens examined. **BAHAMAS.** Abaco, 21 Dec 2005, *Freid 05-030* (FTG); Andros, Mangrove Cay, 8 May 1973, *Popenoe 203* (FTG); Cat Island, Dumphries, 20 Oct 1999, *Richey 99-963* (FTG); Cat Island, north of Stevenson, 21 Nov 1975, *Correll 46152* (FTG); Eleuthera, The Current, 21 Dec 1969, *Lewis 7421* (FTG). **CAYMAN ISLANDS.** Little Cayman, 30 Aug 2003, *Strittmatter & Mulligan 115* (FTG). **JAMAICA.** St. Ann Parish, 1.5 mi. W of Runaway Bay, 1 Aug 1976, *Proctor 36366* (FTG). **USA. Florida.** Miami-Dade Co.: rocks, shore of bay, south of Miami, 19 Mar 1904, *Britton 72* (F, NY); hammocks, Miami, 5–21 May 1904, *Small & Wilson 1651* (NY); Brickell Hammock, near Miami, 24 Oct–26 Nov 1906, *Small & Carter 2751* (CONN, NY); *ibid.*, Feb 1911, *Small et al. 3286* (FTG, GH, NY, TENN, US); *ibid.*, 26 Nov–20 Dec 1913, *Small & Small 4838* (DUKE, FTG, FLAS, GH [2 sheets], S, U, US [2 sheets], WVA [2 sheets]); *ibid.*, 19 Feb–22 Mar 1915, *Small 5449* (FTG, NY, S).

Baccharis halimifolia L., Sp. Pl. 2: 860. 1753. Lectotype (designated by Reveal 1993): Virginia, LINN 992.4 (lectotype, LINN).

Baccharis halimifolia is native to the southeastern and eastern USA, West Indies, and Mexico (Sundberg & Bogler 2006). It is a rather common shrub in Florida. Plants usually have relatively larger leaf blades with coarse teeth, being sometimes somewhat lobate. The leaf blades leading to the inflorescence are reduced in size and can often be entire and narrowly elliptic-obovate. The involucre is campanulate and pappus bristles of mature fruits are 8–12 mm long.

It is not uncommon for herbarium specimens to exhibit mostly or only entire leaf blades, but it is often unclear if toothed leaves might have been present on more basal portions of these plants. Several of these specimens have been misidentified as *B. dioica* (Fig. 1B). Most of these misidentified specimens are from coastal habitats along the gulf coast of Florida, and some are of a short stature (ca. 1 m or less tall). Perhaps, these specimens have a history of hybridization with *B. angustifolia*, a species generally restricted to coastal habitats.

Below are cited several specimens of *B. halimifolia* that were misidentified as *B. dioica*. Further research would be useful to reveal if these fit within the variation of *B. halimifolia*, bear some taxonomic consideration, and if these are evidence of hybridization occurring with *B. angustifolia*.

Specimens of *B. halimifolia* misidentified as *B. dioica*. **USA. Florida.** Collier Co.: Marco Island, 14 Mar 1964, *Brass 33188* (ARCH); *ibid.*, 23 Oct 1964, *Lakela & Brass 27755* (FLAS, NY, USF); *ibid.*, colonies less than 1 m high, 23 Oct 1964, *Brass 33368* (ARCH); *ibid.*, 22 Nov 1966, *Lakela 30369* (USF); *ibid.*, 22 Nov 1966, *Lakela 30376* (FLAS, FTG, NY, USF). Hillsborough Co.: Double Branch River, E side of bridge, FL 580, 24 Dec 1962, *Lakela 25609* (USF); *ibid.*, 1 Mar 1964, *Lakela 26865* (GH). Lee Co.: near NW end of Sanibel Island, 29 Dec 1953, *Thorne 13846* (NCSC); Sanibel Island, 21 Feb 1954, *Cooley 2513* (USF); western Sanibel Island, 23 Dec 1969, *Brumbach 7020* (FTG). Okaloosa Co.: Fort Walton Beach, 11 Aug 1954, *Ford 4037* (FLAS); near Wynnhaven Beach, 25 Oct 1964, *Burch 471* (FLAS, USF). Pinellas Co.: Boca Ciega Bay, 29 Dec 1939, shrub 3 ft. high, *Uhler s.n.* (NCSC); New Port Richey, 3 Jan 1970, *Genelle & Fleming s.n.* (USF); *ibid.*, 1 Feb 1970, *Genelle & Fleming 50* (USF).

MELANTHERA (ASTERACEAE)

Melanthera Rohr consists of herbs to subshrubs with opposite leaves, lacking ray florets, with white disc corollas, and 4-angled obpyramidal cypselae (Parks 2006). Plants of *Melanthera* can be an important source of nectar for insects in Florida, such as the federally endangered *Cyclargus thomasi bethunbakeri* (Cannon et al. 2010). In South Florida, Small (1913: 1251, 1372, 1933: 1419) recognized five species (*M. angustifolia*, *M. deltoidea* Small, *M. ligulata* Small, *M. parvifolia*, and *M. radiata* Small), while his *M. hastata* DC. occurred north of South Florida. Parks (1973) recognized *M. angustifolia*, *M. aspera* (Jacq.) Steud. ex Small (2 varieties), *M. ligulata*, and *M. parvifolia* for South Florida. Parks (2006) later revised this into three species for South Florida (*M. angustifolia*, *M. nivea*, and *M. parvifolia*), while Wunderlin (1998) recognized only one widely delimited species, *M. nivea*.

Parks (1973) indicated that “vigorous F1 offspring were recovered from all interspecific crosses and many of these were grown to flower. As the potential for interbreeding exists among all species, ecological differences appear to be most important in maintaining the identity of *Melanthera* taxa in nature.” Parks (1973) also discussed cases of intergradation between taxa in situ and annotated some herbarium specimens with similar such judgements. Nonetheless, we concur with the species concepts of Parks (2006) and find it important to recognize three species in South Florida, given the ecological and morphological differences (Figs. 2–5). Plants of *M. nivea* with provenance from Orange Co. and a plant of *M. parvifolia* from Miami-Dade Co. were both cultivated in Goulds, Miami-Dade Co. and maintained their stark differences. From our field observations, we generally find the species distinguishable, but it is unclear how often or to what extent the three taxa might intergrade, given the observations by Parks (1973). Fragmentary specimens consisting of only the upper portion of the plants can be more difficult to identify.

Key to *Melanthera* in Florida

1. Fertile plants 0.5–2.2 m tall; main stems (2–)4–15 mm wide at the base of the plant; petiole (2–)5–40 mm long; larger leaf blades (2.5–)4–12 cm wide; inflorescence head 0.8–3.2 cm wide with 30–100 florets; larger phyllaries (2.5–)3–4 mm wide; corollas 7–9 mm long ***M. nivea***

1. Fertile plants 0.2–1 m tall; main stems 2–5(–7) mm wide at the base of plant; petiole 0–5 mm long; larger leaf blades 0.5–4 cm wide; inflorescence head 0.6–1.8 cm wide with 18–75 florets; larger phyllaries 1.5–3 mm wide; corollas 4.5–6.5 mm long. **2**

2. Leaf blades linear to elliptic (lower ones sometimes broadly elliptic or rarely all short and broadly elliptic), unlobed or scarcely lobed, usually 5–13 times long as wide; peduncles (2–)5–20 cm long; phyllaries 4–5.5 mm long; paleae 4–5 mm long ***M. angustifolia***

2. Leaf blades ovate to 3-lobed, rarely elliptic, 1–4 times long as wide; peduncles 2.5–10 cm long; phyllaries 4.5–7 mm long; paleae 5.5–7 mm long. ***M. parvifolia***

Melanthera angustifolia A. Rich. in Sagra, Hist. Fis. Cuba, Bot. 11: 54. 1850. Lectotype (designated by Parks 1973): Cuba, Isla de Pinos, *de la Sagra s.n.* (lectotype, P02140219).

This species is found in Florida, Cuba, Hispaniola, Mexico, and Central America. In Florida, it is typically found in pyrogenic, seasonally flooded prairies and occasionally in wetter pine rocklands (Fig. 2C and Fig. 3). North of Collier and Broward counties, *M. angustifolia* is found in a variety of prairie and pineland habitats. It is ranked as rare in South Florida by IRC (Gann et al. 2020). The species is characterized by its linear to elliptic leaf blades and sparse growth habit. In the Everglades region, it may intergrade with *M. parvifolia* according to Parks (1973; e.g. *Lakela* 27442). Two rather odd plants with short, somewhat broadly elliptic leaf blades are tentatively placed here, but perhaps they are hybrids with

M. nivea (i.e. *Bridges et al.* 24196 and *Campbell & Dickman* 973). Many of the specimens under the name *M. ligulata* (Parks 1973) seem best placed with *M. angustifolia*.

Representative specimens examined. **USA. Florida.** Broward Co.: Hillsboro Pineland, 17 Mar 1998, *Gann et al.* 55 (FTG); Crescent Trail Natural Area, 2 Apr 2019, *Lange & Angelo* 111 (USF); Ft. Lauderdale, 29 Mar 1897, *Curtiss* 5846 (FLAS). Charlotte Co.: Peace River Preserve, 2 Oct 2011, *Franck* 2860 (USF). Collier Co.: along Tamiami Trail W of Oasis gas station, 30 May 1977, *Correll et al.* 48644 (FTG); E of Monroe Station, 4 Mar 1967, *Lakela* 30656 (USF); Big Cypress, 23 Aug 2012, *Strong* 4128 (USF); W of Immokalee, 25 Sep 1964, *Lakela* 27442 (USF). Hernando Co.: Chinsegut Hill, 3 Sep 1959, *Ray Jr.* 9384 (USF). Hillsborough Co.: Cypress Creek Preserve, 10 Oct 2016, *Campbell* 437 (USF); Double Branch Bay Preserve, 2 Nov 2017, *Campbell & Dickman* 973 (USF). Lee Co.: ca. 9 air mi. NE of Bonita Springs, 28 Nov 1995, *Bridges et al.* 24196 (FTG); Caloosahatchee Creeks Preserve, 3 Aug 2006, *Woodmansee & Green* 1909 (FTG). Miami-Dade Co.: 8 mi. WSW of Homestead General Airport, 1 Feb 1975, *Correll et al.* 44251 (FTG); Everglades National Park, near fire tower SW of road to Anhinga Trail, 29 Dec 1973, *Correll & Long* 40969 (FTG). Monroe Co.: Big Cypress National Preserve, 15 Feb 1978, *Avery et al.* 1820 (FTG); 10 mi. SSW of Monroe Station, 13 Mar 1992, *Reveal et al.* 7240 (USF). Okeechobee Co.: ca. 11.8 air mi. W of Fort Drum, 21 Oct 1994, *Orzell & Bridges* 23365 (FTG, USF). Palm Beach Co.: NW of Loxahatchee on route 98, 26 Aug 1966, *Parks* 90 (FTG); NW of Loxahatchee, 3 Sep 1957, *Kral* 5642 (FSU). Pasco Co.: 0.3 mi. W of Zephyrhills, 14 Oct 1979, *Saulea* 3082 (USF). Polk Co.: 4.5 mi. E of Haines City, 1 Nov 1963, *Conard s.n.* (GA). Sarasota Co.: Churchill Ranch, 23 Aug 2007, *Franck* 329 (USF).

***Melanthera nivea* (L.)** Small, Fl. S.E. U.S. 1251, 1340. 1903. *Bidens laevis* L., Sp. Pl. 2: 833. 1753. Lectotype (designated by Parks 1973): Dillenius, Hort. Eltham. tab. 47, fig. 55, *Bidens scabra flore niveo, folio trilobato*. 1732.

Melanthera nivea is primarily found throughout Caribbean Basin, but it also ranges as far north as Illinois and Kentucky in the USA (Parks 1973, 2006) and as far south as Brazil (GBIF 2020b). In South Florida, it is most commonly found in coastal thickets and open areas, including disturbed sites. Compared to the other two species in Florida, *M. nivea* is typically a taller, erect plant with larger leaves, larger inflorescence heads, and larger corollas (Figs. 2A–B and 4).

This concept of *M. nivea* follows Parks (2006), which includes in synonymy two species previously recognized by Parks (1973), *M. aspera* and *M. ligulata*. Parks (1973) restricted *M. nivea* s.str. to central Florida and northward, excluding it from South Florida. *Melanthera aspera* was applied to plants mainly of coastal habitats, while *M. ligulata* was used for plants in interior habits of South Florida by Parks (1973). Parks (2006) concluded that these entities were better treated as one species given field observations of intermediate plants and crossing experiments. Many of the specimens of *M. ligulata* (Parks 1973) appear identifiable as *M. angustifolia*, though Parks (2006) listed *M. ligulata* as a synonym of *M. nivea*. The type of *M. ligulata* (Small & Wilson 1775, NY) is rather robust like *M. nivea* but has mostly linear blades like *M. angustifolia*.

Representative specimens examined. **BAHAMAS.** Eleuthera, 14 May 1975, *Correll & Hill* 45064 (FTG); Long Island, 26 Apr 1975, *Correll* 44868 (FTG); San Salvador Island, 2 Jan 1970, *Gillis* 8826 (FTG). **USA. Florida.** Collier Co.: Marco Island, 14 Mar 1964, *Brass* 33196 (USF). Lee Co.: Sanibel Island, 17 Feb 1967, *Cooley* 11842 (USF). Miami-Dade Co.: Key Biscayne, 15 Mar 1969, *Gillis* 7674 (FTG). Monroe Co.: Bush Key, 17 Jan 1991, *Imhof* 12 (USF). Putnam Co.: Deep Creek, 7 Nov 1990, *Orzell & Bridges* 15720 (FTG). Sarasota Co.: Longboat Key, 29 Aug 1966, *Parks* 125 (FTG). Volusia Co.: Tomoka State Park, 22 Oct 2005, *Kunzer* 1164 (FTG). Wakulla Co.: W side of Newport, 30 Aug 1966, *Parks* 135 (FTG); ca. 3 mi. S of Sopchoppy, 5 Jul 1979, *Hansen & Richardson* 5829 (USF).

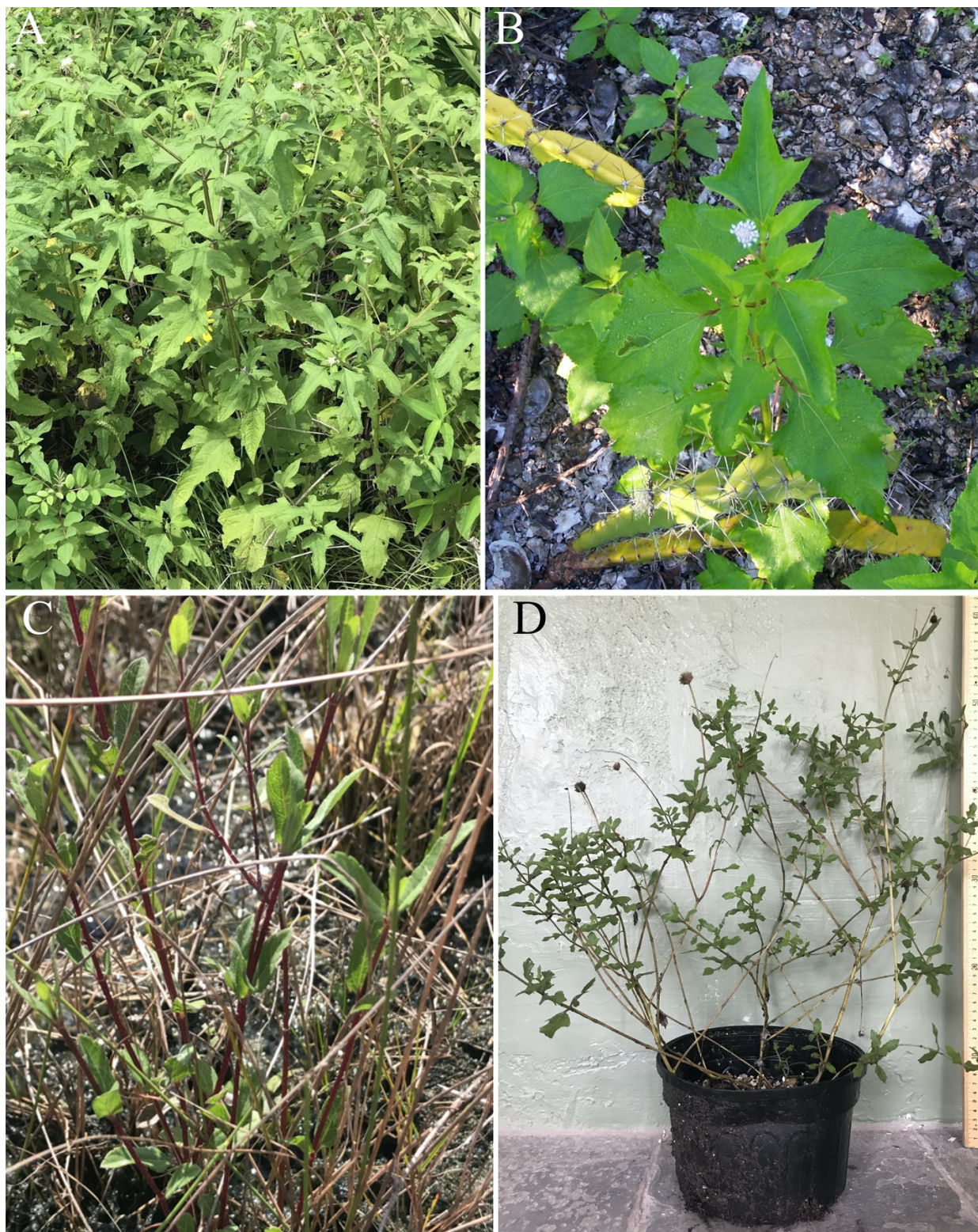


Figure 2. Habit of three species of *Melanthera*. A. *M. nivea*, Orange Co. B. *M. nivea*, Russell Key (ca. 7 km WSW of Everglades City), Collier Co. (photo by J. Sadle). C. *M. angustifolia*, Long Pine Key, Miami-Dade Co. D. *M. parvifolia*, cultivated (with meter stick), with the main stems mostly spreading-ascending but being propped up by the edges of the container, provenance from Goulds, Miami-Dade Co. A, C, and D photos by A.R. Franck.

Melanthera parvifolia Small, Fl. S.E. U.S. 1251, 1340. 1903. Type. USA, Florida. Monroe Co., Pine Key, *Blodgett s.n.* (holotype, NY00215046; isotype, GH00010087).

This Florida endemic is characterized by its short stature and relatively small, ovate leaf blades (Figs. 1D and 5). Plants are often sprawling with ascending to procumbent stems. The species generally prefers drier habitats than *M. angustifolia*. *Melanthera parvifolia* is mostly restricted to pine rocklands of Collier, Miami-Dade, and Monroe Cos., although a Broward County specimen (*Small & Small 4441*) presumably outside of pine rockland habitat was identified as this species. According to Parks (1973), it may intergrade with *M. angustifolia* in parts of the Everglades (e.g. *Long 1731*). *Melanthera parvifolia* is ranked as rare in South Florida by IRC (Gann et al. 2020).

Representative specimens examined. **USA. Florida. Broward Co.:** near the South New River Canal, 11-25 Nov 1913, *Small & Small 4441* (NY). **Collier Co.:** Big Cypress National Preserve, Platt Island, 23 Jun 2004, *Woodmansee & Sadle 1489* (FNPS). **Miami-Dade Co.:** corner of SW 57th Court and SW 116th St., 20 Oct 1967, *Barrick 49* (FTG); W of Old Cutler Road just S of Cutler Hammock, 15 Sep 1973, *Correll & Correll 40044* (FTG); back of Fairchild Gardens Research Center, 18 Sep 1970s, *Brackman 13* (FTG); Long Pine Key, 11 Oct 1962, *Cooley et al. 9189* (USF). **Monroe Co.:** near Miles City, 21-24 Oct 1965, *Long 1731* (USF); Big Pine Key, 27 Sep 1999, *Koptur et al. 882* (FTG); Big Pine Key, 10 Nov 1999, *Koptur et al. 881* (FTG); Big Pine Key, Aug 1999, *Liu 403* (FTG).

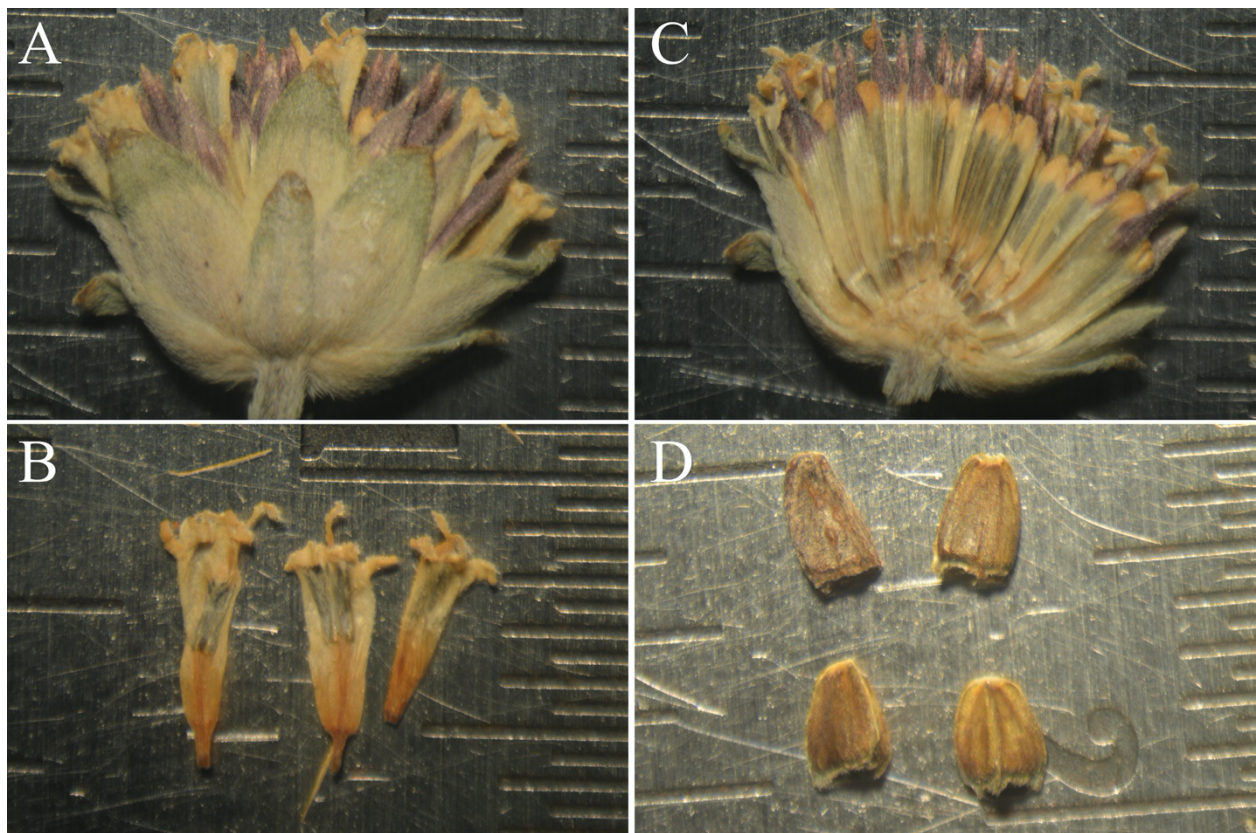


Figure 3. *Melanthera angustifolia*, with right side of ruler metric with the finer increments being 0.5 mm (photos by A. Farid). A–C. Inflorescence and flowers of *Jennings & Jennings s.n.* (Dec 1929), Miami-Dade Co. D. Cypselae of *Cooley et al. 9171*, Monroe Co.



Figure 4. *Melanthera nivea*, Orange Co., with ruler in mm increments (photos by A.R. Franck). A. View of the outer phyllaries. B. Longitudinal section of the inflorescence. C, E. Cypselae. D. Individual flowers.



Figure 5. *Melanthera parvifolia*, Goulds, Miami-Dade Co., with ruler in mm increments (photos by A.R. Franck). A. Longitudinal section of the inflorescence. B, D. View of the outer phyllaries. E. Individual flowers. C, F. Cypselae.

BORRERIA (RUBIACEAE)

Borreria s.str. is composed of herbs characterized by exserted stamens and styles, fruits with both mericarps dehiscent, and smooth, foveolate, or fissured seeds with a ventral longitudinal groove (Rogers 2005; Miguel & Cabral 2013; Wiersema et al. 2017). A DNA phylogeny based on ITS and ETS supports the recognition of *Borreria* as a genus distinct from the *Spermacoce latifolia* Aubl. clade and the clade of *Spermacoce* L. s.str. (Florentín et al. 2017). In *Spermacoce* s.str. the stamens and styles are included, the fruits indehiscent or dehiscent in only one mericarp, and the seeds ventrally flat (Miguel & Cabral 2013). The *S. latifolia* clade is similar to *Borreria* s.str., except that in the *S. latifolia* clade the seeds are densely papillose (Sobrado & Cabral 2015; Wiersema et al. 2017).

Borreria terminalis has been considered an endemic species restricted to South Florida (Herndon 1987; Kartesz & Gandhi 1992; Wunderlin et al. 2018) or synonymized with *B. verticillata* (Wunderlin 1979). *Borreria terminalis* is undoubtedly a species distinct from *B. verticillata*. We present a revised key with additional morphological characters to separate *B. terminalis* from *B. verticillata* (Fig. 6). Erroneously placing the southern Florida endemic taxon *B. terminalis* into synonymy under the introduced *B. verticillata* and viewing the combined entity as nonnative is particularly troublesome as it could lead to land managers unwittingly exterminating the endemic *B. terminalis*, further confounding conservation efforts.

Key to *Borreria terminalis* and *B. verticillata*

1. Stems and branches many from the base of the plant; deltoid prickles (0.1–0.5 mm long) along leaf blade midvein usually absent or 1–2 at the blade base; terminal inflorescence typically with 15–30 flowers; base of calyx ca. 1 mm wide; corolla tube 1.25–2.5 mm long; corolla limb (2.2–)2.5–4.5 mm wide; corolla lobe ca. 1.5 mm wide at base, ca. 2 mm long; stamen exserted to 1.5–2 mm beyond tube apex (base of lobe); anthers 0.5–1 mm long; ovary (1.4)2–3.5 mm long, 1.0 mm wide; fruit (including persistent calyx lobe) 2.5–4 mm long ***B. terminalis***

1. Stems single or many (especially when mowed) from the base of the plant, typically few to unbranched in the basal ½ of the plant; deltoid prickles (0.1–0.5 mm long) along leaf blade midvein present throughout the blade; terminal inflorescence typically with 30–115 flowers; base of calyx ca. 0.5 mm wide; corolla tube 0.6–1.0 mm long; corolla limb 1.3–2.2 mm wide; corolla lobe ca. 1 mm wide at base, < 1.5 mm long; stamens exserted to 1.5 mm beyond tube apex (base of lobe); anthers <0.6 mm long; ovary 1–2 mm long, 0.7 mm wide; fruit (including persistent calyx lobe) 2–2.5 mm long ***B. verticillata***

Borreria terminalis Small, Bull. Torrey Bot. Club 51: 387. 1924. *Spermacoce terminalis* (Small) Kartesz & Gandhi, Brittonia 44: 370. 1992, nom. illeg. (non *S. terminalis* Vell. 1829). *Spermacoce neoterminalis* Govaerts, World Checkl. Seed Pl. 2: 18. 1996. Lectotype (designated by Kartesz & Gandhi 1992): USA, Florida, Miami-Dade Co., pinelands about Ross Hammock, 23 Jun 1915, Small et al. 6502 (NY00130910).

=*Borreria podocephala* DC. var. *pumila* Chapm., Fl. South. U.S. 175. 1860. Lectotype (designated here): USA, Florida, Monroe Co., woods, Pine Key, Blodgett s.n. (NY03492751).

Borreria terminalis is endemic to South Florida and restricted to pyrogenic habitats, primarily pine rocklands and marl prairie. It is ranked as imperiled in South Florida by IRC (Gann et al. 2020). Its flowers are a source of nectar for insects, including the federally endangered *Strymon acis bartrami* (Salvato & Salvato 2008).

The earliest collection of *B. terminalis* in Florida may be that of Blodgett, who resided in Key West from 1838–1853 (Wunderlin et al. 2000). From this Blodgett specimen, Chapman was perhaps the first to

recognize this endemic taxon under the name *B. podocephala* var. *pumila*, which only has priority at the varietal rank and is blocked at the species rank by *B. pumila* DC.; consequently, Small's name *B. terminalis* is adopted at the species rank. Steyermark (1972) considered *B. podocephala* DC. a synonym of *B. verticillata*, but did not include *B. terminalis* nor *B. podocephala* var. *pumila* in synonymy.

The flowers and fruits of *B. terminalis* are consistently larger than those of *B. verticillata* (Fig. 6). There are typically several somewhat lax stems and branches arising at the base of plants of *B. terminalis*, even in cultivation. *Borreria terminalis* is restricted to relatively undegraded pinelands and prairies, while *B. verticillata* is found primarily in degraded habitats. These features are reliable for identifying *B. terminalis* in South Florida. The leaf blades of *B. verticillata* are variable and sometimes linear like the blades of *B. terminalis*.



Figure 6. Side-by-side comparison of *Borreria terminalis* and *B. verticillata*, provenance both from Goulds, Miami-Dade Co., with meter stick in mm increments (photos by A.R. Franck). A. Inflorescence. B. Section of inflorescence. C. Dehiscent fruits. D–F. Individual flowers. G. Leaves and stem. H. Habit, both rooted in the same pot.

Some preliminary microscopic examinations suggest other potentially reliable differences. In a cross-section of fresh leaf material from the Everglades, the blades of *B. terminalis* were rather succulent, about two times thicker than those of *B. verticillata*. Abundant raphides were present in *B. terminalis* but unapparent in *B. verticillata*. The epidermal cells of the blade surfaces of *B. terminalis* were relatively large

and created a smooth to coarsely sinuous margin while those in *B. verticillata* were smaller and created a finely crenate to smooth margin (Fig. 7).

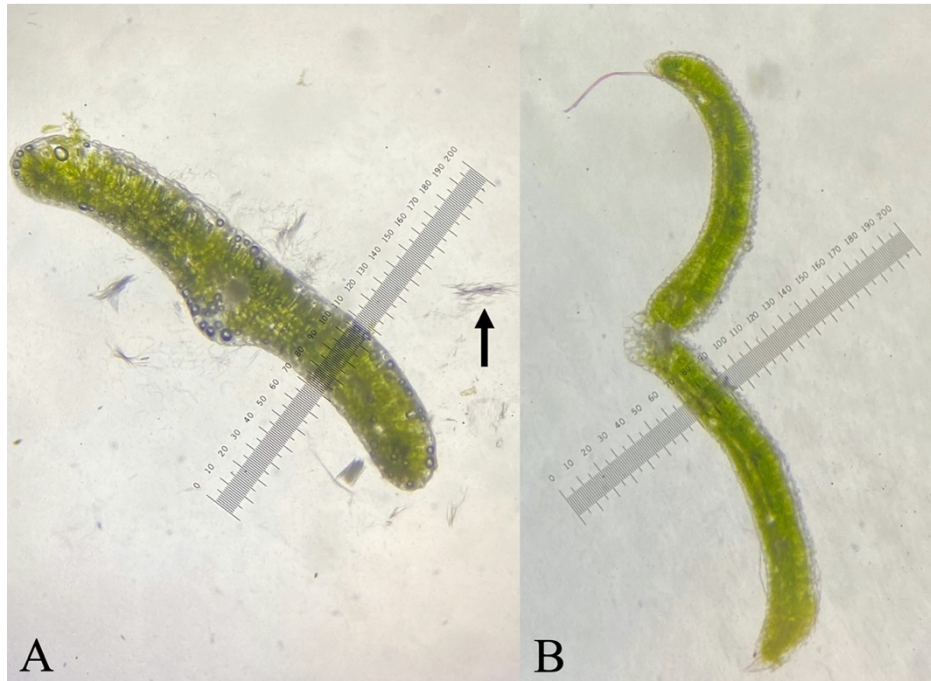


Figure 7. Transverse section of leaf blades of *Borreria* from Long Pine Key, Everglades National Park, Miami-Dade Co., collected on the same day. A. *Borreria terminalis* from a wet pine rockland, Long Pine Key, the black arrow indicating a clump of raphides. B. *Borreria verticillata* from a parking lot, ca. 3 km WSW of the *B. terminalis* collection.

There is no evidence that *B. terminalis* is interfertile with *B. verticillata*. As far as is known, their ploidy levels differ (Herndon 1987). *Borreria terminalis* is a hexaploid ($2n=84$) based on a Collier Co. specimen, *Godfrey & Reinert 61001* (Lewis 1962). We have observed numerous areas where the two species are sympatric, with *B. verticillata* being present because of significant substrate disturbance. Never is there the appearance of plants intermediate between the two, as specimens and plants always fit clearly into one of the species.

Representative specimens examined. **USA. Florida. Collier Co.:** 6 mi. W of Miles City, 14 Jan 1946, *Brass 15879* (ARCH, US); Alligator Alley, 30 May 1979, *Black & Black 384* (FTG); Big Cypress National Preserve, 10 Feb 1999, *McCartney Jr. 60* (FTG); along Route 839, E of Jerome, 12 May 1981, *Correll et al. 51768* (FTG); Miles City Prairie, 9 May 1990, *Orzell & Bridges 13426* (FTG); South Fla 846, E of Cocohatchee River, 29 Jul 1967, *Lakela 30906* (FTG); 10 mi. N of Jerome, 10 Jun 1961, *Godfrey & Reinert 61001* (FLAS, US); Big Cypress, 30 May 2016, *Burch 2940* (USF). **Hendry Co.:** Indian Reservation, 15 Jan 1942, *Davis s.n.* (FLAS). **Miami-Dade Co.:** Miami, Jun-Jul 1877, *Garber s.n.* (FLAS, US); Long Pine Key, 6 Nov 1983, *Herndon 964* (FTG); road leading to Long Pine Key Camp, 23 Mar 1985, *Seavey & Seavey 54* (FTG); entrance to Everglades National Park along US 27, 23 Oct 1983, *Herndon 949*; Coral Gables, 3 May 1935, *Buswell s.n.* (FTG); Costello [Castellow] Hammock, 28 Feb 1920, *Young 245* (US); Miami, 9 May 1904, *Tracy 9248a* (US); Miami, Jun-Jul 1877, *Garber s.n.* (US); between Everglades and Biscayne Bay, Jun 1880, *Curtiss 1114* (US); W of Coconut Grove, 15 May 1918, *Small 8798* (NY); Hole-in-the-Doughnut, 14 Mar 1974, *Willson s.n.* (USF); Hole-in-the-Doughnut, 29 Dec 1973, *Long & Wunderlin 4095* (USF). **Monroe Co.:** Big Pine Key, 8 Feb 1977, *Correll & Popenoe 48080* (FTG); Big Pine Key, 21 Feb 1936, *Killip 31544* (US); Big Pine Key, 18 May 1963, *Gilbert s.n.* (USF); Big Pine Key, 3 Oct 1962, *Craighead s.n.* (USF).

***Borreria verticillata* (L.) G. Mey, Prim. Fl. Esseq. 83. 1818. *Spermacoce verticillata* L., Sp. Pl. 1: 102. 1753. Lectotype (designated by Rendle J. Bot. 72 1934: 331): "*Spermacoce verticillis globosis*" in Dillenius, Hort. Eltham., 2: 369, t. 277, f. 358, 1732.**

Borreria verticillata is a weedy and sometimes invasive species (FLEPPC 2019) found throughout the Neotropics and western Africa, and apparently is further spreading into the Paleotropics (GBIF 2020a). It is not native to Florida. The earliest introduction in Florida appears to be centered around Martin Co. in 1950 (e.g. *Brass 21156*), and it has since spread as a weed nearly throughout peninsular Florida and in parts of the panhandle. The species is diploid, $2n=28$ (Lewis et al. 1967; Borgen 1980; Corrêa & Forni-Martins 2004). Since *B. verticillata* is clearly non-native, diploid, and morphologically distinct from *B. terminalis* in Florida, it is illogical to consider it synonymous with *B. terminalis*.

Representative specimens examined. **USA. Florida. Highlands Co.:** Archbold Biological Station, 25 May 1965, *Herndon 1216* (FTG). **Lee Co.:** Six Mile Cypress Preserve, 15 Aug 1997, *Bradley & Woodmansee 521* (FTG). **Martin Co.:** Hobe Sound, 23 Dec 1950, *Brass 21156A* (ARCH); N of Port Salerno, 4 May 1962, *Lakela 25033* (FTG, USF); Jupiter Island [possibly in Martin or Palm Beach Co.], 28 Jul 1956, *Cooley et al. 4912* (USF); S of Salerno, 21 Apr 1962, *Lakela 24977* (USF). **Miami-Dade Co.:** Florida International University, Tamiami Campus, 21 Feb 1983, *Herndon 681* (FTG); SW 160 St., 108 Ave, 2 Mar 1980, *Herndon 327* (FTG); SW 120th Ave. and SW 232nd Street, 1 Jan 2015, *Franck & Alexander 3689* (USF). **Monroe Co.:** Big Pine Key, 8 Sep 1981, *Brumbach 9730* (USF). **Osceola Co.:** Cyrils Drive, 19 Mar 2015, *Longbottom & Williams 22206* (USF). **Palm Beach Co.:** 28 Jul 1984, *Herndon 1091* (FTG).

***CHIOCOCCA* (RUBIACEAE)**

The genus *Chiococca* consists of shrubs, subshrubs, or vines with valvate corolla lobes, stamens inserted near the base of the corolla tube, a 2–3-locular ovary with one pendulous and apically attached ovule per locule, and white drupes (Moore & Rendle 1936; Rogers 2005). Birds are probably important consumers of the fruits and dispersers of the seeds (Carlo & Morales 2016). The taxonomic diversity of *Chiococca* can be difficult to assess due to the paucity of discrete characters to separate taxa (Standley 1934; Lorence 2012).

In Florida, there are three species of *Chiococca* (Figs. 8–10). The growth form, plant size, color of the bark, and the size of the larger leaves are reliable characters for identification. The most common species is *C. alba*, which develops relatively thick, rigid trunks with light gray bark and larger leaves and inflorescences. The other two species, *C. parvifolia* and *C. pinetorum* generally lack trunk-like stems, and have smaller leaves and inflorescences relative to *C. alba*. In pine rocklands occurs *C. pinetorum*, having the smallest leaves and smallest overall plant size, and in various habitats occurs *C. parvifolia* with purplish gray bark and its leaves intermediate in size among the prior two species.

It may be surprising to think that three species of *Chiococca* occur in Florida, since previous works have recognized two species (Small 1933; Long & Lakela 1971; Rogers 2005) or only *C. alba* (Wunderlin 1998; Taylor et al. 2004; Acevedo-Rodríguez & Strong 2012). We must emphasize that we feel very confident that there are indeed three species in Florida and that presently we have not found any evidence that these three species hybridize. Herbarium specimens often poorly represent the differences among the three species, especially specimens consisting of only young stems and young leaves or specimens that lack description of the whole plants.

Chiococca alba is frequently sympatric with the other two other species (*C. parvifolia* and *C. pinetorum*), and yet the taxa do not intergrade. If these all represented one species and were interfertile, these morphologically divergent forms would doubtfully be maintained in sympatric conditions, especially for plants that are quick to flower with short generation times. In cultivation in a common garden (Goulds, Miami-Dade Co.), the three remain distinctive. As the taxa can be sympatric, and herbarium labels do not make note of this, it is possible that label descriptions could be describing one taxon and collecting a different one. While we have studied numerous herbarium specimens outside of Florida to characterize the

species concepts employed here, additional work is surely needed to better understand *Chiococca* outside of Florida.



Figure 8. Habit of *Chiococca* (photos by A.R. Franck). A. *C. alba* with a dense high-climbing habit, Goulds, Miami-Dade Co. B. Basal part of plant of *C. alba*, Crandon Park, Miami-Dade Co. C. Basal part of plant of *C. parvifolia*, North Key Largo, Monroe Co. D. Sprawling plant of *C. parvifolia*, North Key Largo, Monroe Co. E. Much larger and taller mature *C. alba* next to procumbent, mature plant of *C. pinetorum* at Tropical Research & Education Center, Homestead, Miami-Dade Co.

Key to *Chiococca* in Florida

1. Mature plant 1–4 m tall, compact or scandent shrubs to high-climbing vines, rarely rooting where stems touch the ground; the central stem 1.2–5.4 cm wide at the plant base, trunk-like and becoming much wider than distal stems, strongly rigid; bark of older stems becoming light gray below newer green (rarely purplish) growth; leaves to 10 cm long and 4 cm wide, the petiole usually distinct and to 15 mm long, the secondary veins 3–6 on each side of the midrib, the secondary veins often relatively conspicuous on the upper surface and discoloured (whitish to yellow-green) from the green blade surface, reticulate veins sometimes apparent, the upper blade surface lustrous; peduncle, rachis, pedicel, and ovary green; peduncle 7–25 mm long, the peduncle+rachis 2–9 cm long; calyx and corolla (4)5-merous; corolla yellow to whitish ***C. alba***

1. Mature plant 0.1–3.5 m tall, sprawling, procumbent, to scandent subshrubs to vines, commonly rooting where stems touch the ground; the central stem 0.1–1(–2) cm wide at the plant base, not much wider than

distal portions of the stems, weakly stiffened; bark of older stems becoming dark purplish gray to gray-black below newer green to purplish growth or if gray then the mature plant <1 m tall; leaves to 6 cm long and 1.8 cm wide, the petiole often indistinct or to 4 mm long, the secondary veins unapparent or 1–3 on each side of the midrib and sometimes concolorous with the blade surface, reticulate veins usually unapparent, the upper blade surface dull; peduncle, rachis, pedicel, and ovary green to purplish; peduncle 2–10 mm long, the peduncle+rachis 0.5–4 cm long; calyx and corolla 4–5-merous; corolla yellow to purplish **2**

2. Plant 0.1–3.5 m tall; longer stems usually >1.5 m long; larger leaves >3 cm long, >13 mm wide, mostly 2.5–5 cm long; inflorescence peduncle+rachis 0.5–4 cm long; of hammocks, swamps, pinelands, and prairies ***C. parvifolia***

2. Plant 0.1–0.5(–1) m tall; longer stems <1(1.5) m long; larger leaves $\leq 3.1(3.8)$ cm long, ≤ 13 mm wide, mostly 1–3 cm long; inflorescence peduncle+rachis 0.5–2 cm long; of pine rocklands ***C. pinetorum***

Chiococca alba (L.) Hitchc., Rep. (Annual) Missouri Bot. Gard.) 4: 94. 1893. *Lonicera alba* L., Sp. Pl. 1: 175. 1753. Lectotype (designated here): Jamaica, St. Catherine Parish, savanna, towards Two-Mile-Wood, “Jasminum forte”, Sloane, Voy. Jamaica 2: tab. 188, fig. 3. 1725. Epitype (designated here): Jamaica, *Sloane s.n.* (epitype, BM000594058).

=*Chiococca brachiata* Ruiz & Pav., Fl. Peruv. 2: 67. 1799. Lectotype (designated here): Peru, “in nemoribus Chinchao Quebrada ad Macora praedium [from the protologue]” (lectotype, MA815658; islectotype, MA815659).

=*Chiococca racemosa* L. var. *scandens* Persoon, Syn. Pl. 1: 209. 1805. Syntypes: Jamaica, Barbados.

=*Chiococca parviflora* Humb. & Bonpl. ex Roem. & Schult., Syst. Veg., 5: 202. 1819. Lectotype (designated here): Venezuela, Cumana, *Humboldt & Bonpland s.n.* (lectotype, B-W04140-010; probable islectotypes, B-W04140-020, HAL0113824).

=*Chiococca densifolia* Mart. var. *cubensis* DC., Prodr. 4: 482. 1830. Lectotype (designated here): Cuba, Havana, *de la Sagra s.n.* (lectotype, G00389833).

=*Chiococca racemosa* L. var. *floridana* DC., Prodr. 4: 482. 1830. Lectotype (designated here): “*Chiococca* Ici se termine les Plantes des climats froids et des climats chauds des Amériques 5-1” [Here is the end of the plants from the cold climates and from the warm climates of the Americas]. “arbriss. rampant f. oppos., fruits blancs en grappes, comprimé inférieus, cal. a5 divis., cal 5-fid., stam 5, fructus inferus” [creeping shrub opposite leaves, white fruits in bunches, basally compressed, calyx 5-parted, stamens 5, fruit inferior], *Chiococca racemosa*, *Michaux s.n.* (lectotype, P00320364; probable islectotype, P03920880).

=*Chiococca racemosa* L. var. *laxiflora* DC., Prodr. 4: 482. 1830. Lectotype (designated here): “v.s. cult. in hort. Calc.” [from protologue], 1819, *Wallich s.n.* (lectotype, G00666534).

=*Chiococca racemosa* L. var. *longifolia* DC., Prodr. 4: 482. 1830. Lectotype (designated here): Guadeloupe, *Badier 127* (lectotype, G00666535; islectotype, P00308513).

=*Chiococca floridana* Raf., Alsogr. Amer. 75. 1838. Lectotype (designated here): USA, Florida, *Ware s.n.* (lectotype, PH00025417).

=*Chiococca latifolia* Raf., Alsogr. Amer. 75. 1838. Lectotype (designated here, or perhaps holotype): Cuba, ex Durand, “468”, “*Chiococca racemosa*”, “latif Raf Cuba” [in Rafinesque’s handwriting], *Jalambic s.n.* [according to the protologue] (lectotype, DWC).

=*Chiococca trisperma* Hook. f., Trans. Linn. Soc. London 20: 219. 1847. Lectotype (designated by Porter 1980): Ecuador, Galápagos, Chatham Island, *Darwin 109* (lectotype, CGE; isotype, K000432644).

=*Chiococca micrantha* J.R. Johnst., Proc. Amer. Acad. Arts 40: 696. 1905. *Chiococca alba* (L.) Hitchc. var. *micrantha* (J.R. Johnst.) Steyerl., Acta Bot. Venez. 6: 139. Lectotype (designated by Howard 1989): Venezuela, Margarita Island, 27 Jul 1903, *Johnston 115* (lectotype, GH00057576; isotype, NY00099439).

=*Chiococca bermudiana* S. Br., Proc. Acad. Nat. Sci. Philadelphia 61: 493. 1910. Type: Bermuda, North Shore, 31 Aug–20 Sep 1905, *Brown & Britton 181* (holotype, PH00005273; isotypes, A00057578, F203773, GH00057577, PH00005272).

Chiococca alba is here applied to robust plants with thick trunk-like bases, light gray bark, relatively long leaves and long inflorescences, usually 5-merous flowers, and generally lacking purplish coloration on the stems and inflorescences (Figs. 8–10). Plants can be compact shrubs to high-climbing scandent vines. Trunks of old plants can become quite large and the older stems can be rather tough and woody. Many authors have characterized *C. alba* as having inflorescences longer than or as long as the leaves, but this is not reliable for identification. Relative to the other species, *C. alba* tends to have longer inflorescences, but it is not uncommon for plants of *C. alba* that exhibit all the typical characters emphasized here to have an inflorescence clearly shorter than the subtending leaf.

The name *C. alba* is widely applied to plants of southern Texas and Florida southward to Brazil. In Florida, it ranges from Monroe County north to Hendry and Polk counties in the interior, and Duval and Dixie counties along the coast. The species generally occurs in edges, thickets, hammocks, forest ecotones, and fire-suppressed areas in Florida.

Chiococca alba is based on a plant from Jamaica, as here lectotypified and epitypified (Fig. 11A). The lectotype illustration of *C. alba* is supported by a mirror-image typotype specimen, here designated the epitype, that allows for more detailed morphological scrutiny. Numerous synonyms were investigated here, the types of which all fall within the *C. alba* concept. As defined here, *C. alba* remains a morphologically variable, wide-ranging species and other taxa worthy of recognition could be obscured in the species concept employed here. The list of synonyms here should only be considered provisional.

Without species names, Browne (1756) described the “very common” *Chiococca* of Jamaica as becoming as large as “from four to seven or eight feet, sometimes more”. He described the root as “bitter acrid” and that it was frequently used to ease “very stubborn complaints” (similarly for Barbados, the roots were said to be used as a purgative or abortifacient; Gooding et al. 1965). Browne listed a second *Chiococca* in Jamaica, calling it the “climbing Snow-berry” and stating “I have seen one plant of this kind in the woods between St. Thomas’s and Mangeneel; it grew to a considerable height among the trees, and threw down some of its slender twigs again to the ground: I am apt to think it a different species, tho’ the leaves are very like those of the former plant.” There is a Browne specimen (233.1) of *Chiococca* at LINN. Persoon’s description of *C. racemosa* var. *scandens* repeated the Latin description of Browne’s second *Chiococca*. All of the above apply to *C. alba*.

Though *C. brachiata* is tentatively placed under *C. alba* here, Williams & Cheesman (1928) stated that the “Peruvian *C. brachiata* is distinct” without further explanation. A drawing of *C. brachiata* was

made by José Brunete (MA-AJB04-D-0441), who died 14 May 1787 (Dahlgren 1940: 218). The lectotype of *C. brachiata* has a label annotated in the handwriting of José Pavón as “*Chiococca brachiata* Sp. Pl. Fl. Per.” and the isolectotype bears a similar label. Ruiz mentioned the description for the name “*Chiococca ovata*” from Peru had burned in the fire at Macora (Dahlgren 1940: 203–204), and probably any specimens associated with this name were lost at sea near the coast of Portugal (Dahlgren 1940: 166, 198, 215, 219). It is impossible to know the true identity of “*Chiococca ovata*”.



Figure 9. Leaves, stems, and flowers of *Chiococca* (photos by A.R. Franck). A. Four-lobed corollas of *C. pinetorum*, Camp Owaissa Bauer, Miami-Dade Co. B. Five-lobed corollas of *C. alba*, Chekika, Everglades National Park, Miami-Dade Co. C. Side-by-side of *C. alba* (left - young stem green maturing to light gray) alongside *C. parvifolia* (right - young stem green maturing purplish dark gray), North Key Largo, Monroe Co. D. Four- or five-lobed corollas of *C. parvifolia* North Key Largo, Monroe Co. E. Three largest leaves of mature plants of each species all grown at first author's property in Goulds, Miami-Dade Co with a metric ruler along the bottom with mm increments; left - *C. alba* provenance from Goulds, middle - *C. parvifolia* provenance from North Key Largo, and right - *C. pinetorum* provenance from Goulds.

For the possible type specimens of the name *C. parviflora*, Humboldt appears to have written the label notes “1232 Pent lia Cumana” while Schlechtendal wrote “(Humboldt)”. Willdenow wrote “Pentandria Monogynia[,] *Chiococca parviflora*[,] foliis subrotundo-ovatis acuminatis, racemis paniculata axillaribus[,] Habitat in Cumana” which is nearly verbatim of the protologue. Possibly Bonpland wrote “*Chiococca*?” The note “Maragnon” (Peru?) and the flower description are in a hand unknown to us. With

“Cumana” written by both Humboldt and Willdenow, it is likely this is original material and is appropriate for a lectotype. All types at B and HAL appear to be from the same collection, having a similar morphology and development. *Chiococca parviflora* (= *C. alba*) should not be confused with *C. parvifolia*, a different species.

For the name *C. racemosa* var. *floridana*, Candolle gave the distribution as maritime Florida and Mexico, with the annotation “v.s.”, implying that specimens from both Florida and Mexico were seen. Only Michaux was further cited by Candolle, and in agreement with the varietal epithet, his Florida specimen is designated the lectotype (Fig. 11C). This Michaux lectotype was probably collected in 1788 from northeast Florida from Brevard County northward, since Michaux never went further south than this (Taylor & Norman 2004). Perhaps this *Chiococca* specimen was among the tropical plants mentioned by Michaux around 27 Mar 1788 from Mount Tucker (Sargent 1889). The lectotype of *C. floridana* was probably collected by Ware in the same general area, somewhere along coastal east-central/north-central Florida in Oct–Nov of 1821 (Nuttall 1822).

Chiococca trisperma Hook. f. was described from the Galápagos and distinguished by its trilobed stigma and 3-seeded fruits. The name was considered a synonym of *C. alba* by Porter (1980), tentatively followed here. Whether plants with 3-seeded fruits are distinct from those with 2-seeded fruits deserves further scrutiny. In Florida, plants of *Chiococca* only appear to be 2-seeded.

Chiococca micrantha was considered a variety of *C. parvifolia* by Steyermark (1971) and a synonym of *C. parvifolia* by Howard (1989). It was described as a shrub with 3 m long, decumbent stems, ca. 3-flowered inflorescence, 4–5-merous flowers, and a puberulent calyx. The profusely branched specimens with somewhat distinct petioles, acute leaf blade tips, and long peduncles are much more like *C. alba* rather than *C. parvifolia*, and as such it is placed here with *C. alba*.

Representative specimens examined. **ANTIGUA.** 4–16 Feb 1913, *Rose et al.* 3431 (US). **BAHAMAS.** Abaco: Wood Cay Settlement, 5 Aug 1979, *Sauleda et al.* 2858 (FTG). Acklin’s Island: 21 Dec 1905–6 Jan 1906, *Brace* 4327 (US). Eleuthera: 21 Dec 1969, *Lewis* 7408 (FTG). Great Abaco: 4 Jul 1974, *Correll & Popenoe* 42540 (FTG). New Providence Island: 27 Jun 1979, *Correll & Popenoe* 50775 (FTG); 2 Nov 1973, *Correll & Popenoe* 40376 (FTG). **BERMUDA.** Jan 1881, *Farlow s.n.* (USF). **COLOMBIA.** *Cospi, Llanos s.n.* (FTG). **CUBA.** Oriente, Caletones Road, Gibara, 28 Dec 1954, *Díaz-Piñer s.n.* (FTG); Las Villas, Abneus, 21 May 1895, *Combs* 57 (US); district of Cienfuegos, 21 May 1895, *Taylor* 213 (US). **DOMINICA.** Grande Savane, 13 Aug 1964, *Wilbur et al.* 8346 (US). **DOMINICAN REPUBLIC.** Peravia Province, Arroyo de Parra, 6 Sep 1980, *Mejía & Zanoni* 8098 (FTG). **HAITI.** Massif de la Hotte, 21 Jul 1927, *Ekman* H-8645 (US). **JAMAICA.** Potsdam, 9 Sep 1907, *Britton* 1269 (US); Peckham Woodland, 23 May 1912, *Harris* 11083 (US). St. Elizabeth Parish, Lititz, Jan 1847, *Wolle s.n.* (USF); St. Andrew Parish, 2 mi. NE of Kingston, 15 Jun 1963, *Crosby et al.* 157 (USF). **PUERTO RICO.** near Bayamon, 18 Jul 1901, *Underwood & Griggs* 907 (US); Cayey, 20 Sep 1885, *Sintenis* 2483 (G). **ST. THOMAS.** 1877, *Eggers* 21 (FTG). **TURKS & CAICOS.** Parrot Cay, 22 Oct 1990, *Neis s.n.* (FTG). **USA.** **Florida.** Collier Co.: Chokoloskee Bay, Ten Thousand Islands, 15 Aug 1967, *Lakela & Barilotti* 30999 (USF). Indian River Co.: 6 mi. S of Vero Beach County Park, 22 Jun 1972, *Long et al.* 3619 (USF); *ibid.*, *Long et al.* 3578 (USF). Lee Co.: Lower Captiva Island, 5 Jan 1977, *Brumbach* 9145 (USF); North Captiva Island, 28 Feb 1991, *Johnson* 8828 (FSU); Sanibel Island, 23 Jan 1967, *Cooley* 11905 (USF). Martin Co.: South County Park, 27 Jul 1998, *Bradley & Woodmansee* 1155 (FTG). Miami-Dade Co.: Deering Estate, 26 Aug 1978, *Correll & Popenoe* 50091 (FTG). Monroe Co.: North Key Largo, 18 Jan 1969, *Long et al.* 2808 (USF); No Name Key, 16 Sep 1979, *Hansen & Hansen* 6350 (FTG); South Key Largo, 4 Aug 1979, *Krauss & McMahon* 637 (FTG); Lignum Vitae Key, Jul 1974, *Schmitt* 3 (FTG); Key Largo, 8 Jul 1968, *Gillis* 6830 (FTG). St. Lucie Co.: Jack Island, 15 Feb 1969, *McCart* 10561 (FTG).

Chiococca parvifolia Wulfschl. ex Griseb., Fl. Brit. W.I. 337. 1861. *Chiococca alba* (L.) Hitchc. var. *parvifolia* (Wulfschl. ex Griseb.) Urb., Symb. Antill. 8: 675. 1921. *Chiococca alba* (L.) Hitchc. subsp. *parvifolia* (Wulfschl. ex Griseb.) Steyermark, Acta Bot. Venez. 6: 138. 1971. Lectotype (designated here): Jamaica, Manchester Parish, Fairfield, Blüht gelb [flowers yellow], Strauch 3 Fuß hoch [shrub 3 feet tall], 1849, *Wulfschlaegel* 856 (lectotype, M0187133).

Chiococca parvifolia is characterized by its purplish gray bark, long stems that scarcely become thicker towards the base, and leaves intermediate in size between the other two species (Figs. 8–10). In open spaces, plants often form dense, sprawling colonies, the stems rooting along the ground and flowering near the ground, while in the same population plants will climb to 3.5 m high if adjacent to other species of shrubs or trees. Many authors have distinguished *C. parvifolia* by an inflorescence subequal to or shorter than the subtending leaf, but this is not reliable as *C. alba* can also exhibit this feature. Reliance on the relationship between the inflorescence size relative to the leaves likely caused authors to misapply *C. parvifolia* to specimens of *C. alba* (e.g. Steyermark 1971).

Based on the specimens studied here, *C. parvifolia* is found in Florida and the Caribbean Islands. We have not investigated its possible occurrence elsewhere in the Neotropics. In Florida, *C. parvifolia* is found on limestone keys, sandy barrier islands, and in inland areas (including inundated swamps) that generally lack fire, but occasionally it is found in thickets and edges along fire-prone areas. The type of *C. parvifolia* is from Jamaica, where natural wildfires were not a common disturbance (Robbins et al. 2008). Careful field work is needed to fully characterize *C. parvifolia* in Florida and the Caribbean, especially since *C. alba* can co-occur with it.

Chiococca parvifolia was credited to Wulfschlaegel, who worked in Antigua and Jamaica. Grisebach also cited specimens collected by March on Jamaica and Crueger on Trinidad, and he also parenthetically included specimens from Martinique, Panama, Puerto Rico, Venezuela without mentioning the collectors. Steyermark (1971: 138) indicated the type was from Jamaica and collected by Wulfschlaegel, but did not indicate a specimen nor a herbarium. With the name credited to Wulfschlaegel, it is appropriate to first consider his specimens for lectotypification. Those that may have been at B or DR were probably destroyed during World War II. A specimen at BR is too ambiguous, having two different labels for what appears to be only one collection, the two stem fragments with nearly the exact same phenology and overall condition. A specimen at M collected by Wulfschlaegel from Jamaica matches the description of *C. parvifolia* and concurs with cited collections in Urban (1898); it is here lectotypified (Fig. 11B). The sheet of March at NY (00099444) may be a mixed collection, with the fragment on the left having wide leaves with distinct petioles like *C. alba* while the fragment on the right with only a few leaves appears to be *C. parvifolia*.

For Florida, some prior treatments recognized a wider species concept of *C. pinetorum* that at least partly encompassed *C. parvifolia*, and never mentioned the name *C. parvifolia* (Small 1933; Long & Lakela 1971; Rogers 2005). Both the names *C. alba* (e.g. Lakela 27085, 27515) and *C. pinetorum* (e.g. Lakela 27891, 29036) were partly misapplied to plants of *C. parvifolia* by Lakela, while Small misapplied *C. pinetorum* (e.g. Small & Small 4999, 5069) to plants of *C. parvifolia* (although the name is penciled in and appended with a question mark). Under *C. pinetorum*, Small wrote “On the Lower Keys a form grows in the hammocks which is more robust than the typical form” [of *C. pinetorum*] and that “Marked forms occur in the hammocks of the lower eastern coast, in the Big Cypress Swamp, and on the Florida Keys”, which pertain to *C. parvifolia*.

Several Caribbean floras have recognized *C. parvifolia*. For the Lesser Antilles, Howard (1989: 398) wrote “field observations suggest two distinctive populations, with *C. alba* more vigorous and a higher climbing vine than the lower sprawling or weakly climbing *C. parvifolia*.” For Trinidad and Tobago, *C. parvifolia* (mistakenly as “*C. parviflora* Wulfschl.”) was described as a “Shrub, branches slender” which

contrasts with their description of *C. alba* as a “climbing shrub” (Williams & Cheesman 1928). For the Bahamas, the description of *C. parvifolia* by Correll & Correll (1982) was nearly verbatim of the protologue of *C. pinetorum*, which was included in synonymy.

In the protologue of *C. parvifolia*, the habit was described as a “high climber” and attributed to Browne, but Browne’s description probably applied only to *C. alba*. The specimen *Barcelona et al. 1137* from Jamaica is very consistent with the type of *C. parvifolia* and was described as 0.5 m tall. For Jamaica,

Adams (1972) described *C. parvifolia* as a rather common climbing shrub to 3 m or more high with leaves 1–3.5 cm long. Elsewhere, other authors gave the following descriptions for *C. parvifolia*: “Arbusto trepador” (Liogier 1962), “a climbing shrub like [*C. alba*]” (Proctor 1984, 2012), “shrub, sometimes climbing” (Liogier 1985), and “Trepadora leñosa de hasta 3 m, las ramas cortas” (Liogier 1995).

Steiermark (1971) wrote that many specimens “are transitional between” *C. alba* and *C. parvifolia*, basing this on inflorescence and leaf size, and cited 18 such specimens from the Greater Antilles, Antigua, and Margarita Island. Of his cited specimens that we could locate, they all seemed to fit *C. alba*, having relatively large leaves with distinct petioles and venation. Urban (1921) treated *C. parvifolia* as a variety of *C. alba*, but gave no further discussion. Evidence that *C. alba* and *C. parvifolia* intergrade is lacking.

The similar specific epithets of *Chiococca parvifolia* and *C. parviflora* are sometimes confused (e.g. Williams & Cheesman 1928; Paudyal et al. 2018). The type of *C. parviflora* is from Venezuela, here considered a synonym of *C. alba*.

The type of *C. stricta* Correll (Correll 46265, A, FTG29947, NY) is similar to *C. parvifolia*, with rather short leaves with obscure venation, their close relationship also being mentioned by Correll in the protologue. *Chiococca stricta* is distinguished by being a strictly erect shrub to 2 m with puberulent pedicels (Correll & Correll 1982).

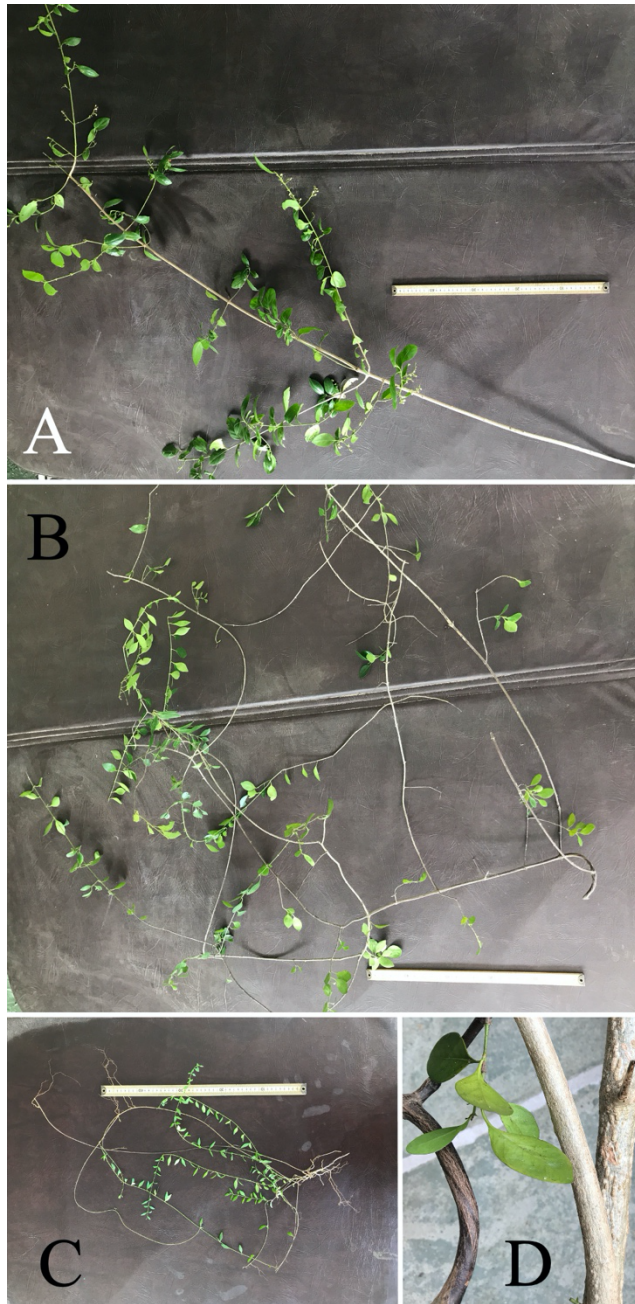


Figure 10. Habit of mature plants of *Chiococca* with the same 50 cm ruler in photos A, B, and C (photos by A.R. Franck). A. Distal portion of an ascending-arching shrub of *C. alba* ca. 2 m tall, from a hammock edge, North Key Largo, Monroe Co., sympatric with *C. parvifolia*. B. Distal portion of a vining plant of *C. parvifolia* ca. 2 m tall, from a hammock edge, North Key Largo, Monroe Co., sympatric with *C. alba*. C. Whole plant of *C. pinetorum*, Goulds, Miami-Dade Co., from a fire-suppressed pine rockland.

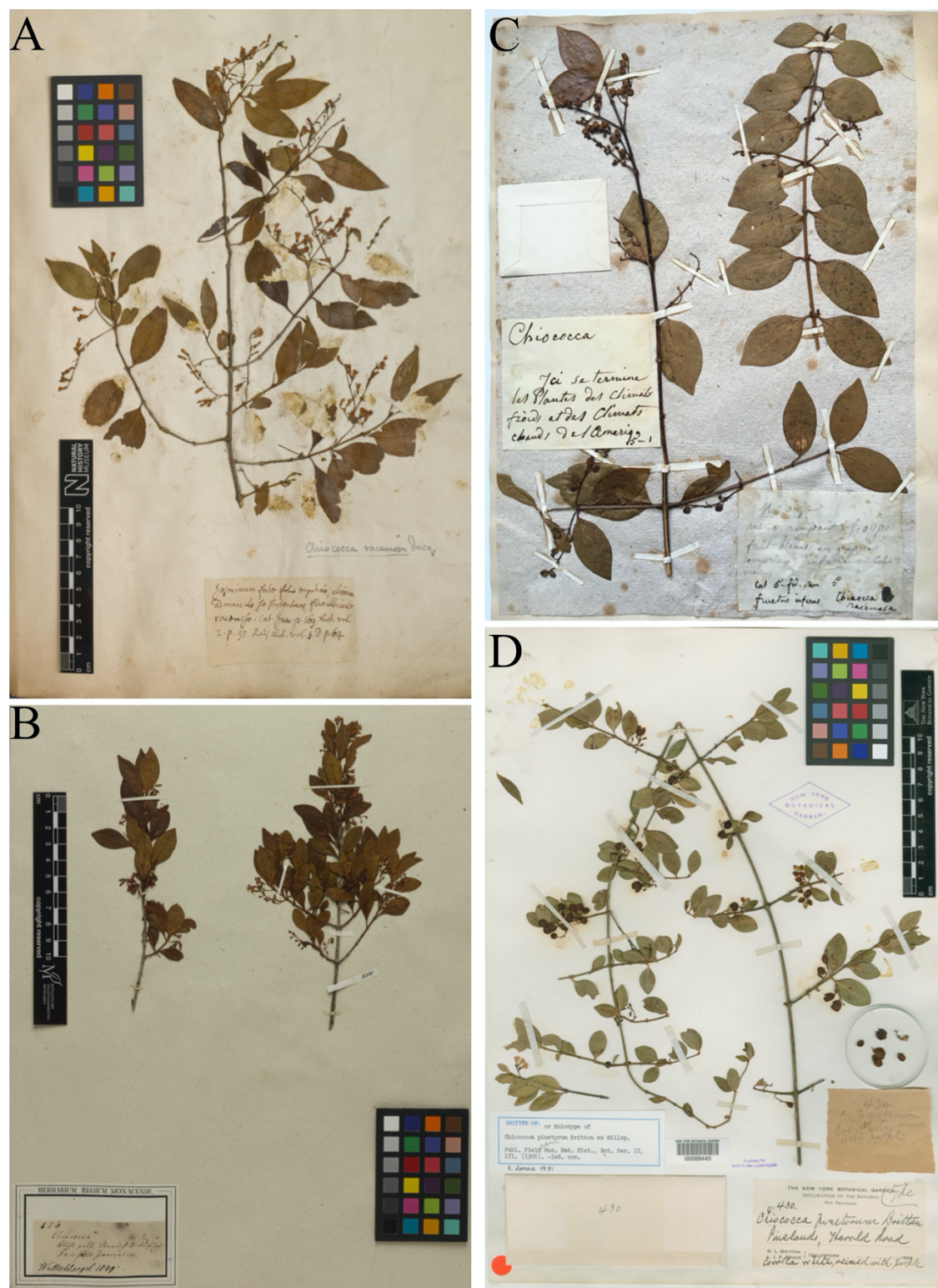


Figure 11. Type specimens of *Chiococca*. A. Epitype of *C. alba* (BM; copyright holder The Trustees of the Natural History Museum, London). B. Lectotype of *C. parvifolia* (M; copyright holder Botanische Staatssammlung München). C. Lectotype of *C. racemosa* var. *floridana* (P; courtesy of Muséum National d'Histoire Naturelle). D. Lectotype of *C. pinetorum* (NY; Image courtesy of the C. V. Starr Virtual Herbarium of the New York Botanical Garden, <http://sweetgum.nybg.org/science/vh/>).

Representative specimens examined. **ANTIGUA.** Wallings, 23 Sep 1937, *Box 1098* (US). **BAHAMAS.** Andros: 2 mi. E of San Andros, 10 Jul 1975, *Hill 3346* (FTG, VT). Cat Island: between Dolphin Head and Old Bight, 19 Nov 1975, *Correll 46114* (FTG); New Bight Airport, 15 Dec 1979, *Wunderlin et al. 8398* (USF); 2 mi. E of McQueens, 15 Jul 1968, *Byrne 524* (FTG); 7 mi. S of Fresh Creek, 15 Oct 1976, *Saulea 1243* (USF). Crooked Island: Sandrail Point, 9-23 Jan 1906, *Brace 4676* (US). Grand Bahama: detour N to Queens Hwy, 19 Mar 1971, *Austin & Conroy 4631* (FTG). Great Abaco: 10 Jul 1952, *Roberston Jr. 352* (FTG); 2.9 mi. S of Wilson City road, 16 Dec 1979, *Wunderlin et al. 8559* (USF). Long Island: 28 Nov 1998, *Richey & Freid 98-265* (FTG). New Providence: along Village Road, 2 Nov 1973, *Correll & Popenoe 40377* (FTG). San Salvador Island: 24 Nov 1975, *Breitbarth et al. 4* (FTG); 29 Nov 1977, *Smith 4717* (FTG); 1 Jan 1970, *Gillis 8767* (FTG); 19 Nov 1974, *Correll 43765* (FTG); 3 Jan 1970, *Gillis 8851A* (FTG). South Bimini Island: 12 Jul 1964, *Stimson 710* (FTG, USF). **CAYMAN ISLANDS.** Grand Cayman, 15 Dec 1971, *Chevalier 395* (USF). **CUBA.** Camaguey, Cayo Sabinal, Ganado, 17-18 Mar 1909, *Shafer 857* (US). **DOMINICA.** Bluffs leading down to L'Anse Noir, 16 Jul 1964, *Wilbur et al. 7516* (US); NE of Pont Casse, 29 Sep 1971, *Long & Norstog 3370* (USF); S side of Cochrane Road, 3 Aug 1992, *Hill & Wagenseil 24108* (USF). **GADELOUPE.** St. Rose, *Stehle 5938* (US). **HAITI.** Port de Paix, 22 Jan 1929, *Leonard & Leonard 12243* (US); Massif de la Selle, 17 Jul 1983, *Zanoni 26307* (FTG). **JAMAICA.** *March s.n.* (NY00099444, right-hand specimen); Trelawny Parish, near Barbecue Bottom, 14 Aug 1963, *Crosby & Anderson 1197* (US, USF); Wait-a-bit and Albertown, 20 Jul 1997, *Barcelona et al. 1173* (US); Clarendon Parish, E of Reckford, 8 Oct 1976, *Proctor 36409* (FTG). **PUERTO RICO:** San Juan Municip., Montes de San Patricio, 16 Nov 1981, *Hansen et al. 9013* (FTG, USF); Maricao Municip., along highway 120, 30 Nov 1981, *Hansen et al. 9481* (USF); Bosque Insular de Maricao, 10 Jul 1959, *Webster et al. 8869* (US). **TRINIDAD & TOBAGO.** Tobago, near Easterfield, 17 Mar 1910, *Broadway 3524* (US). **TURKS & CAICOS.** North Caicos, 30 Mar 2006, *Hamilton et al. MH510* (FTG); Parrot Cay, 11 Oct 1990, *Neis s.n.* (FTG). **USA.** **Florida.** Edge of Big Cypress Swamp (provenance), Edison Garden, Fort Myers, Oct 1929, *Buswell s.n.* (NY). Broward Co.: along Holmberg Road, 1.8 mi. W of US 441, 2 Jul 1981, *Hansen et al. 8392* (USF); along Hillsboro Canal, just S of Palm Beach Co. border, May 1981, *Bennett s.n.* (FTG). Charlotte Co.: Port Charlotte Beach State Recreation Area, 5 Mar 1991, *Erickson PC0026* (USF); Don Pedro Island State Recreation Area, 16 Sep 1998, *Braem DP0023* (USF); Little Gasparilla Island, 21 Feb 1980, *Fehling 67* (USF). Collier Co.: Percy Brown Ranch, 26 Jul 1978, *Popenoe 1316* (FTG); 1.5 mi. S of Monroe Station, 2 May 1958, *Cooley et al. 6183* (USF); vicinity of Fort Myers, 21 Feb 1916, *Standley 12592* (US); Golden Gate Estates, 8 Aug 1967, *Lakela 30969* (USF); N of Golden Gate subdivision, 20 Jul 1965, *Lakela 29036* (USF); below Bonita Springs, Apr 1927, *Buswell s.n.* (FTG); *ibid.*, 2 Jul 1930, *Buswell s.n.* (FTG); Marco Island, 27 Sep 1964, *Lakela 27515* (USF); ca. 5 mi. E of Naples, 10 Oct 1962, *Cooley et al. 9118* (USF); ca. 12.5 air mi. E of Naples, 16 Jun 1992, *Orzell & Bridges 19654* (FLAS, USF); Krehling Tract, *Tabb s.n.* (FTG); Marco Island, 31 Jul 1976, *Linker s.n.* (FTG); Willoughby Acres, 1 Feb 1987, *Burch 141* (USF). Hendry Co.: Green Glades West, 29 Jan 2021, *Franck et al. 5126* (USF). Lee Co.: Caloosahatchee Creeks Preserve, 19 Oct 2006, *Woodmansee & Hodges 1974* (FTG); western Sanibel Island, 24 Oct 1968, *Brumbach 6480* (FTG). ca. 1.6 mi. W of US 41 and 0.5 mi. E of Estero Bay, ca. 4.5 mi. N of Bonita Springs, 12 Sep 1990, *Orzell & Bridges 15184* (FTG, USF); Sanibel Island, 28 Oct 1978, *Wunderlin et al. 6136* (USF); Sanibel Island, 15 Feb 1954, *Cooley 2636* (USF); *ibid.*, 2 Jan 2021, *Franck 5067* (FTG); Bonita Springs, 21 Apr 1964, *Lakela 27085* (USF); Middle Captiva, 10 Oct 1977, *Brumbach 9288* (USF). Miami-Dade Co.: Key Biscayne, 25 May 1971, *Gillis 10876* (FTG); Biscayne National Park, Meigs Key, 9 Nov 2001, *Bradley et al. 1520* (FNPS). Monroe Co.: Pinecrest Road, 1 Mar 1952, *Cooley 1118* (USF); N end of Big Pine Key, 13 Nov 1964, *Lakela 27891* (USF); Cape Sable Road, 3 Nov 1934, *Buswell s.n.* (FTG); Road to Cape Sable, 22 Feb 1941, *Buswell s.n.* (FTG); Big Pine Key, 17 Dec 1913, *Small & Small 5069* (NY); Big Pine Key, 17 Jul 1971, *Sreemadhavan 5108* (USF); vicinity of Pinecrest, 11 Oct 1962, *Cooley et al. 9159* (NY, USF); Big Pine Key, 21 May 1976, *Poppleton 806* (USF); Sugarloaf Key, 11 Feb 1967, *Long et al. 2499* (USF); Big Pine Key, 11-20 Apr 1963, *Stern 3031* (USF); Big Pine Key, intersection of US 1 and FL 940, 6 Aug 1966, *Long et al. 2075* (USF); No Name Key, 16 Sep 1979, *Hansen & Hansen 6350* (USF); Little Torch Key, 4 Mar 2012, *Stalter s.n.* (USF); Key Largo, 19 Jul 1971, *Sreemadhavan 5125* (USF); Big Torch Key, 28 Mar-3 Apr 1970, *Stern et al. 2877* (FTG); Key Largo, 23

Aug 2012, *Strong* 4127 (FTG, USF); Big Pine Key, 11 Oct 1999, *Koptur et al.* 1122 (FTG); Key Largo, NE of Surprise Lake, 8 Jul 1968, *Gillis* 6830 (FTG); 2 mi. W of Pinecrest, S of Loop Road, 15 Nov 1968, *Garbarini* 48 (FTG); Middle Torch Key, 31 Dec 1972, *Fanning* KF256 (FTG); Big Pine Key, 14 Dec 1951, *Dickson s.n.* (FTG); No Name Key, 28 Mar-3 Apr 1970, *Stern et al.* 2843 (FTG); Sugarloaf Key, 15 Sep 1979, *Hansen & Hansen* 6324 (USF); Big Coppitt Key, 11 Nov 1985, *Southerland s.n.* (USF); W end of Ramrod Key, 20 Oct 1982, *Hansen et al.* 10698 (USF); N end of Big Torch Key, 20 Oct 1985, *Hansen et al.* 10715 (USF); Bahia Honda Key, 11 Dec 1980, *Brumbach* 9645 (USF); S of Card Sound Road, 25 Nov 1967, *Hetzell* 36 (USF). Palm Beach Co.: Route 441, between road and West Palm Beach Canal, 26 Dec 1972, *Meagher* MM692 (FTG, USF); NW corner of intersection of Southern Boulevard and US 441, West Palm Beach, 8 Mar 1995, *Austin s.n.* (FTG). **VIRGIN GORDA.** 5 Dec 2002, *Pollard et al.* 1165 (FTG).

Chiococca pinetorum Britton ex Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 171. 1906. Lectotype (designated here): Bahamas, New Providence, Harold Road, pinelands, corolla white, veined with purple, 1904, *Britton & Brace* 430 (lectotype, NY00099443; isolectotypes, F171854, K000432652, US00138520).

Chiococca pinetorum is a low-growing plant endemic to the pine rocklands of South Florida and the northwestern Bahamas (Figs. 8–10). Based on the revised taxonomy adopted here, it is ranked as imperiled in South Florida by IRC (Gann et al. 2020). Its leaves are typically 3 cm long or less and its stems are 4 mm wide or less at the base of the plant. Plants of *C. pinetorum* are smaller than *C. alba* or *C. parvifolia*, and these two latter species do not have the consistently small leaves throughout, as does *C. pinetorum*. The branches of *C. pinetorum* can arch and clamber over underlying vegetation, but rarely does *C. pinetorum* ever reach 1 m high.

Chiococca pinetorum and *C. alba* can grow sympatrically but they are clearly distinguishable. The two species were found immediately adjacent to each other in fire-suppressed pine rocklands invaded with hammock taxa (Fig. 8). They were also found next to each other in pine rockland-hammock ecotones (e.g. Long Pine Key in Everglades National Park, Camp Owaissa Bauer, and Fuchs Hammock). Near the town of Goulds, *C. pinetorum* was found in the midst of a frequently burned, open-canopied pine rockland, ca. 100 m from a typical plant of *C. alba* in a weedy thicket. When grown from seed in identical conditions, the two species retained their differences. There is absolutely no evidence of intergradation in the field. The previous use of the name *C. parvifolia* for plants of *C. pinetorum* (Correll & Correll 1982) is here regarded as a misapplication.

After 1894, Millspaugh's main herbarium was at F while Britton was based at NY. Millspaugh indicated a collection as type for *C. pinetorum*, but did not specify the herbarium. The specimen at NY is here lectotypified (Fig. 11D).

Representative specimens examined. **BAHAMAS.** Abaco: N of Marsh Harbour, 22 May 2000, *Freid* 00-158 (FTG). Andros: 4 m. S of south entrance to Autec, 7 Jun 1975, *Hill* 3175 (FTG, VT). Grand Bahama: along Queen's Highway, 19 Aug 1974, *Correll & Kral* 43045 (FTG); along Queen's Highway, 23 May 1975, *Correll & Popenoe* 45398 (FTG); 8 Mile Rocks, 5-13 Feb 1905, *Britton & Millspaugh* 2408 (NY). Great Abaco: ca. 1.5 mi. NW of Marsh Harbour, 13 Mar 1975, *Correll & Meyer* 44624 (FTG); a little N of Marsh Harbour Airport, 5 Jul 1974, *Correll & Popenoe* 42630 (FTG). New Providence: 18 Aug 1948, *Ledin* 310 (FTG); N of entrance to Coral Harbour, 10 Sep 1978, *Correll* 50210 (FTG, NY, US); S of Nassau on East Road, 2 Jan 1969, *Gillis* 7462 (FTG); near W end of island, 2 Jan 1969, *Gillis* 7453 (FTG); N side of Corry Sound, 18 Jul 1960, *Webster et al.* 10541 (US); 22 Feb 1888, *Eggers* 4195 (US); near Nassau, 17 Apr 1903, *Curtiss* 159 (LY, US, VT). **USA. Florida.** Miami-Dade Co.: S of SW 176 St., just S of Cutler Hammock and canal off Old Cutler Road, 21 Sep 1973, *Correll & Correll* 40100 (FTG); Grossman Drive, 6 km E of Cherika [Chekika] Recreation Area, 27 Mar 1994, *Loconte & Walker* 1020 (FTG); along SW 237th Ave, ca. 5 mi. S of Grossman Drive, *Orzell & Bridges* 18185 (FTG, USF); Everglades National Park,

12 Oct 1962, *Cooley et al.* 9220 (FSU, USF); SW of Sunset Drive, South Miami, 26 Oct 1969, *Lakela et al.* 31932 (USF); Navy Wells Pineland, 12 Aug 1992, *Orzell & Bridges* 20417 (USF); Everglades National Park, 11 Oct 1962, *Cooley et al.* 9183 (USF); corner of SW 117th Ave and Killian Drive, 17 Jun 1980, *Sauleda* 3603 (USF); E of Homestead General Airport, ca. 0.6 mi. W of C-111 canal, ca. 0.25 mi. N of SW 269 St., 11 Oct 1997, *Bradley* 929 (FTG); corner of SW 177 Ave. and 264 St., 12 Oct 1997, *Bradley* 952 (FTG); Coral Gables, 23 Jul 1936, *Buswell s.n.* (FTG); *ibid.*, 25 Jun 1942, *Buswell s.n.* (FTG); *ibid.*, 25 Aug 1944, *Buswell s.n.* (FTG); Miami, 14 Sep 1934, *Buswell s.n.* (FTG); intersection of SW 67 St. and SW 75 Ct., 9 Mar 1975, *Hill* 2548 (FTG, USF); 2 blocks N of Kendel [Kendall] Drive and Dixie Highway, 21 Nov 1967, *Cika* 35 (FTG); SW 107 Ct., at approx. 122-124 Streets, 1967, *Owens s.n.* (FTG); North Kendall Drive between US 1 and Palmetto X-way, 2 Feb 1965, *Metzger* 10 (FTG, USF); Aerojet road off US 1, Florida City, 4 Jun 1966, *Long* 1649 (USF); Coconut Grove, Dec 1925, *Small s.n.* (USF); Homestead, 13 Mar 1964, *Lakela* 26886 (USF); 100 ft. from corner of SW 57 Ct. and Red Road, 18 Jan 1968, *Barrick III* 39 (FTG, USF); *ibid.*, *Barrick* 31 (USF); Everglades National Park, S of pinelands trail, 29 Oct 1967, *Sullivan* 1077 (FTG); SW 178th Terrace off Old Cutler, 9 Feb 1974, *Hewes s.n.* (FTG); along SW 72 Ave., 6 Nov 1971, *Fanning & Gunzelman* 273 (FTG); Luiz Martinez United States Army Reserve Station, 12 Sep 2006, *Wendelberger* 509 (FTG); Pine Island, 2 Jul 1971, *Skinner s.n.* (FTG); Kings Highway, W Homestead, 7 Jul 1966, *Long* 1951 (USF); 3 mi. E of Royal Palm State Park, 14 Dec 1917, *Safford & Mosier* 322 (US); Coconut Grove, Dec 1925, *Small s.n.* (NY); Costello [Castellow] Hammock, 26 Jun 1966, *Long et al.* 1892 (USF); Telford, 9 Aug 1929, *Mulvania s.n.* (USF); USDA Subtropical Research Station, 24 Jul 2002, *Kabat & Kabat* 1015 (FLAS); Tropical Park, 26 Jul 1990, *Tan & Raymond* TP53 (FLAS). Monroe Co.: Big Pine Key, N end, 12 Dec 1974, *Poppleton & Shuey s.n.* (USF); Big Pine Key, 8 Feb 1977, *Correll & Popenoe* 48069 (FTG); close to Key Deer Boulevard, 16 Oct 1997, *Koptur et al.* 1125 (FTG); W of Nut Farm, 7 Feb 2000, *Koptur et al.* 1123 (FTG); S of Dogwood Summer, 27 Sep 1999, *Koptur et al.* 1124 (FTG); N spur of west mangrove fire trail, 16 Oct 1997, *Koptur et al.* 1126 (FTG); Big Pine Key, 12-18 Feb 1935, *Killip* 31368 (US); Big Pine Key, 11 Aug 1992, *Orzell & Bridges* 20393 (FLAS, USF); Big Pine Key, *Radford & Leonard* 45811 (NCU); Big Pine Key, 6 Nov 1978, *Correll & Correll* 50351 (FTG); Big Pine Key, Mar 1999, *Liu* 300 (FTG); Big Pine Key, 17 Feb 1991, *Orzell & Bridges* 15991 (FTG).

LANTANA (VERBENACEAE)

Lantana L. comprises aromatic shrubs with capitate inflorescences, five-lobed corollas lacking staminal tubes, and 2-seeded drupes (Sanders 2001; Marx et al. 2010). Three taxa of *Lantana* sect. *Lantana* are native to peninsular Florida, recently treated as varieties of *L. depressa* (Sanders 2006, 2012). These native taxa are diploids (Sanders 1987) and generally have light green, often involute leaf blades (Fig. 12) and relatively uniformly bright yellow-orange corollas, the oldest, outermost corollas of the inflorescence sometimes becoming slightly darker or more orange (Fig. 13). These taxa are primarily found in coastal habitats along the eastern and western coasts, in interior regions of central and southwest Florida, and in the pine rocklands of Miami-Dade Co. Their nectar is a food source for insects (Graenicher 1930) and their drupes are consumed by birds (Laessle 1944).

We propose to treat the native taxa of *Lantana* sect. *Lantana* as two species (similar to Small 1933; Long 1970), instead of as three varieties of *L. depressa* (as done by Sanders 2006, 2012). Plants of the pine rocklands of Miami-Dade Co. are the most distinct group, and the name *Lantana depressa* should be restricted to these plants with short leaves and a mostly decumbent habit. This more restricted species concept of *L. depressa* is consistent with previous authors (Small 1933; Long 1970; Wunderlin & Hansen 2011). The other two taxa previously classified as varieties of *L. depressa* are here placed as varieties of a new species *L. sandersii*; these plants are generally erect with larger leaves. The recognition of two species (*L. depressa* and *L. sandersii*) has the added benefit of providing more conservation attention, as varieties often attract less concern in conservation assessments. Previously, these native *Lantana* taxa were often treated as *L. ovatifolia* (e.g. Small 1933; Long 1970), but Sanders (1987) determined *L. ovatifolia* is endemic to the Bahamas.



Figure 12. Habit of *Lantana*. A. *Lantana depressa*, Camp Owaissa Bauer, Miami-Dade Co. B. *L. sandersii*, Crandon Park, Miami-Dade Co. C. *L. strigodepressa*, Goulds, Miami-Dade Co. D. *L. sanibelensis*, Sanibel Island, Lee Co. (photo by Karen M. Rogers). A–C. photos by A.R. Franck.

The non-native cultigen *Lantana strigocamara* (Fig. 13) readily hybridizes with the Florida native taxa (Sanders 2006, 2012), a threat to the persistence of the native taxa (Maschinski et al. 2010). Distinguishing the native and introduced taxa from each other is severely compromised by the history of hybridization and introgression (Maschinski et al. 2010). Since these hybrids can be rather common, it is useful to name them (which is done below) so they can be more easily communicated and recognized (Weakley et al. 2011: 441). It is notable that type specimens of the three native *Lantana* taxa lack stem prickles, whereas prickles are usually present in *L. strigocamara* or its hybrids.

The non-native *Lantana strigocamara* is tetraploid, the Florida native taxa are diploids, and the hybrids between the native and non-native taxa are triploids (Sanders 1987, 2006). Studies of *Lantana* triploids have shown they can produce a significant amount of fertile pollen (Spies & du Plessis 1987; Czarnecki II et al. 2014), indicating that triploid hybrids are not sterile and the triploids contribute to further admixture, which is supported by the commonness of hybrids and introgressant forms (Maschinski et al.

2010). Of the various cultivated forms of *Lantana* in Florida, diploid, triploid, tetraploid, pentaploid, and hexaploid plants were found (all as the misapplied *L. camara* L., Czarnecki II et al. 2014), some of which probably pertain to lineages of *L. strigocamara*.

Non-native *Lantana* plants had apparently arrived quite early to Florida, given the observations by Bartram in the 1770s in northeastern Florida (Bartram 1792: 101–102). One possible introduction route could have been through St. Augustine, the primary Florida settlement of the Spanish from 1565–1763 (Boniface 1971). Spanish St. Augustine received ballast-laden ships (Keith 2006; Gifford 2008) and castaways from the neotropics such as Veracruz, Mexico and Havana, Cuba that carried goods, visitors, immigrants, convict laborers, and enslaved laborers (Boniface 1971; Corbett 1974). *Lantana camara*, *L. hirusta* M. Martens & Galeotti, and *L. scabrida* Sol. are native to the Veracruz area and *L. camara*, *L. scabrida*, *L. splendens* Medik. are native to Cuba, while *L. nivea* Vent. is native to Brazil (Sanders 2012). These are possible taxa speculated to be involved in the creation of *L. strigocamara* (Sanders 2006).

The name *L. camara* is entrenched in worldwide usage and still widely misapplied to various taxa of *L. sect. Lantana* including *L. sandersii* and *L. strigocamara*. The continued misuse of *L. camara* hampers the recognition and conservation of the native diversity of *Lantana* throughout Florida and the Neotropics. Within *L. sect. Lantana*, Sanders (2012) recognized 20 species with 13 subspecies and five varieties.

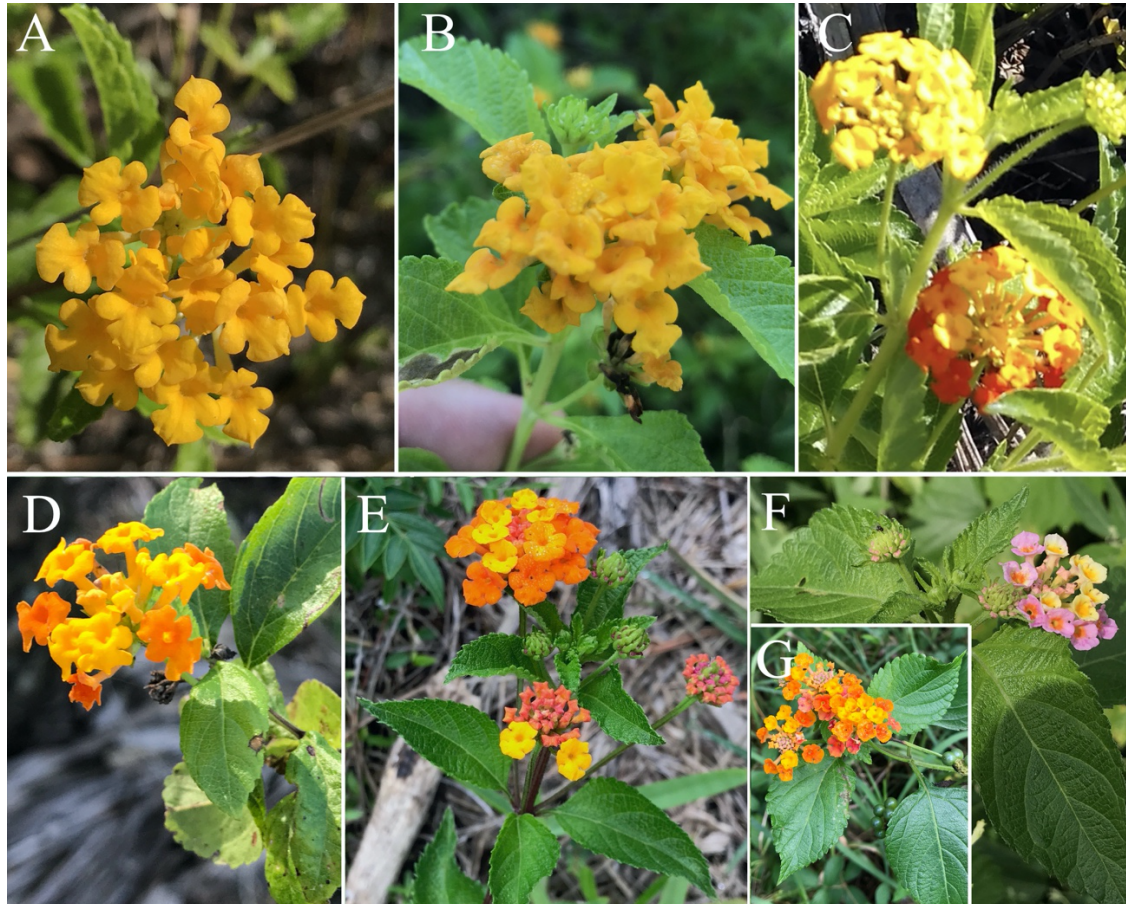


Figure 13. Corollas of *Lantana*. A. *Lantana depressa*, Camp Owaissa Bauer, Miami-Dade Co. B. *L. sandersii* var. *sandersii*, Crandon Park, Miami-Dade Co. C. *L. sandersii* var. *sanibelensis*, Sanibel Island, Lee Co. (photo by Karen M. Rogers). D. *L. sandersii* var. cf. *sandersii*, Green Glades West, Hendry Co. E. *L. strigodepressa*, Goulds, Miami-Dade Co. F–G. *L. strigocamara*, Celebration, Osceola Co. (both plants in same habitat on same day within 30 m of each other). A, B, D–F. photos by A.R. Franck.

Key to taxa of *Lantana* sect. *Lantana* in Florida

1. Stems without prickles; leaf blades generally light green, often involute, (1.5–)1.7–2.5(–3) times longer than wide, corollas fairly uniformly colored within each inflorescence, yellow to yellow-orange from bud, opening, and to the older flowers, occasionally the outermost ring of flowers turning a dark orangeish . . . **2**
1. Stems often with prickles, the prickles sometimes weak and sparse, sometimes prickles absent; leaf blades generally dark green, mostly plane, 1–1.7(–1.9) times longer than wide; corollas a mixture of contrasting colors within each inflorescence, differently colored from bud, opening, and/or to the older flowers, rarely the corollas nearly uniform in color, colors of the corolla may include various combinations and intergradations of white, yellow, orange, pink, to reddish orange **4**
2. Stems prostrate to decumbent, 0.1–0.3(–0.6) m tall; leaf blades 1–3(–4.5) cm long, mostly 3–10 teeth per side; fruit mostly 3–4 mm wide ***L. depressa***
2. Stems mostly erect to ascending, sometimes spreading or partly clambering, 0.5–2(–3) m tall; leaf blades 3–6.5 cm long, mostly 8–15 teeth per side; fruit mostly 4–5 mm wide **3**
3. Young stems glabrate, pubescent to moderately antrorsely pilose, the trichomes to 1.0(1.3) mm long ***L. sandersii* var. *sandersii***
3. Young stems densely spreading to antrorsely pilose, the trichomes to 2.0 mm long ***L. sandersii* var. *sanibelensis***
4. Larger blades usually >4 cm wide, mostly 1–1.5 times longer than wide, the base usually cordate, truncate, to subacute, usually shortly and narrowly cuneate into the petiole, usually not nigrescent upon drying ***L. strigocamara***
4. Larger blades usually <4 cm wide, mostly 1.4–1.7 times longer than wide, the base acute to subtruncate, often gradually tapering from the outer blade base margin to the petiole, younger ones sometimes nigrescent upon drying **5**
5. Shrubs mostly >60 cm tall; stems ascending to erect; larger leaf blades (often more proximal on the stems) usually >2.9 cm long, >1.8 cm wide; peninsular Florida ***L. ×floridana***
5. Shrubs mostly <1 m tall; stems spreading to ascending; larger leaf blades (often more proximal on the stems) mostly <4 cm long, <2.2 cm wide; Miami-Dade County ***L. ×strigodepressa***

Lantana depressa Small, Bull. New York Bot. Gard. 3: 436. 1905. Lectotype (designated here): Florida, Miami-Dade Co., between Cocanut Grove and Cutler, near the unfinished railroad grade, 31 Oct–4 Nov 1903, *Small & Carter 747* (lectotype, NY00137591; isolectotype, F172460).

Lantana depressa is a low-growing shrub with prostrate to decumbent stems and leaf blades usually to 3 cm long (Figs. 12A and 13A). Curiously, two mature plants in cultivation in Miami-Dade Co. of separate provenance both completely lost their leaves in February 2020 but leafed out in March. It is unknown if this is a consistent behavior in this species. *Lantana depressa* is a fire-adapted species endemic to the pine rocklands of Miami-Dade Co., from the Brickell Hammock area to Long Pine Key. The native populations are now presumably extirpated from the northeastern part of its range, i.e., the areas of Brickell Hammock, Coconut Grove, and Coral Gables (Gann et al. 2020). *Lantana depressa* is ranked as critically imperiled in South Florida by IRC (Gann et al. 2020).

Small only mentioned the “type specimens” were *Small & Carter 707* but did not specify a herbarium. In accordance with Arts. 7.11 and 9.23, the NY specimen is designated the lectotype.

Representative specimens examined. **USA. Florida. Miami-Dade Co.:** Miami, 4 May 1928, *Fisher 58* (US); south of Miami River, 20 Nov 1912, *Small 3845* (NY); Brickell Hammock, 5 Jul 1915, *Small & Small 6824* (NY); Long Pine Key, 21 Jun 1975, *Hill & Harvey III 3236* (FTG); Coconut Grove, 1910, *Rodham s.n.* (A); Brickell Hammock, 27 Apr 1920, *Rehder 811* (A); vicinity of Miami, 16 Jan 1919, *Hunnewell 5858* (GH); Homestead, 28 Apr 1958, *Traverse 646* (GH).

Lantana sandersii A.R. Franck & Gann, nom. nov. *Lantana bahamensis* Britton, var. *floridana* Moldenke, Phytologia 31: 373. 1975 (non *L. ×floridana* Raf. 1832). *Lantana depressa* Small, var. *floridana* (Moldenke) R. W. Sanders, Syst. Bot. 12: 55. 1987. Type: Florida, Miami-Dade Co., beach opposite Miami, Nov 1904, *Small 2101* (holotype, NY00137589).

The new name *Lantana sandersii* is proposed at the species rank for this taxon, honoring Roger W. Sanders (1950–2018) who intensively studied the taxa of *Lantana* sect. *Lantana*. The epithet *floridana* is already occupied by a different taxon at the species rank, *L. ×floridana* Raf.

Lantana sandersii (Figs. 12B and 13B) is known from peninsular Florida to southern South Carolina, mainly of coastal habitats but occasionally occurring inland in open, sandy habitats. *Lantana sandersii* is ranked as critically imperiled in South Florida by IRC (Gann et al. 2020). Major threats include introgression with the non-native *L. strigocamara* and habitat loss. Another concern is the possibility that eradication efforts aimed at *L. strigocamara* could easily mistakenly target native *L. sandersii*.

Lantana sandersii is here considered to comprise two varieties, var. *sandersii* (= *L. depressa* var. *floridana*) and var. *sanibelensis*, which are only subtly distinguishable. Populations from the Big Cypress region are here tentatively referred to var. *sandersii*; previously these populations have been called var. *sanibelensis* (Sanders 1987) but their stems are not densely spreading hirsute, rather pubescent to glabrate. Historic populations from central Florida are here referred to var. *sandersii* (Sanders 1987), but one specimen from Osceola Co. had hirsute stems more like var. *sanibelensis*. The variety *sandersii* was also historically known from the southernmost extent of scrub on the east coast (Small 1924: 89) in the Little River area of Miami-Dade Co. (*Demaree 10191* and *Sanders 1656*), but very little of this habitat remains. This area also supports the southernmost population of the scrub species *Sabal etonia* Swingle ex Nash (*Cook s.n.*, US and *Zona 67*, FLAS) and had been home to the southernmost and now locally extirpated population of *Ceratiola ericoides* Michx. (*Eaton 510*, GH and *Safford 17*, US).

Lantana sandersii was once considered endemic to Florida (Sanders 2006, 2012) but specimens from coastal Georgia and South Carolina appear to be native populations of var. *sandersii* (cited below). Elliott’s (1824) account of *L. camara* (misapplied) likely refers to *L. sandersii*, describing the stem as lacking prickles, the leaf blades tapering at the base, and the corollas bright yellow or orange. His description was based on material collected by Baldwin along the St. Marys River, a portion of which forms the border between Georgia and Florida. Some of Baldwin’s other observations clearly pertain to *L. ×floridana* or *L. strigocamara* (see below under *×L. floridana*).

Representative specimens examined of *L. sandersii* var. *sandersii*. **USA. Florida. Brevard Co.:** thicket, 10 Nov 1902, *Fredholm 5574* (GH). **Collier Co.:** Kissimmee Billy, 1 Dec 1976, *Correll 47737* (NCU); N of Copeland, 6 Jul 1990, *Judd 5962* (FLAS). **Glades Co.:** Fort Center, 10 Nov 2012, *Franck 3189* (USF [mixed collection with *L. ×floridana*?]). **Hendry Co.:** west of Snake Road, 3 Jun 1989, *Hendrickson s.n.* (FLAS); Green Glades West, 29 Jan 2021, *Franck 5147* (USF). **Highlands Co.:** Brighton, 27 Aug 1948, *West s.n.* (PAC [faint stem prickles, introgressed with *L. strigocamara*?]). **Martin Co.:** Jupiter Island, 27 Jul 1956, *Cooley et al. 4836* (GH). **Miami-Dade Co.:** Miami, Jun 1877, *Garber s.n.* (GH); Bull Key, opposite Lemon

City, 6 Nov 1903, *Small & Carter 618* (NY, mixed collection - upper left *L. ×floridana* and middle and right *L. sandersii* [possibly introgressant with *L. ×floridana*]); S of NE 10 Ave. and 215 Street, 6 Mar 1984, *Sanders 1656* (FTG); Little River, 1 Feb 1933, *Demaree 10191* (US); Key Biscayne, 2 Dec 1968, *Gillis 7265* (FTG). Osceola Co.: Kissimmee, Idora Park, 14 Apr 1938, *Singletary s.n.* (DUKE [faint stem prickles, introgressed with *L. strigocamara*?]). Palm Beach Co.: Boca Raton, 5 Oct 1977, *Nauman 229* (FTG). Polk Co.: 12 Apr 1894, *Ohlinger s.n.* (GA, VSC). Volusia Co.: New Smyrna Beach, 20 Sep 1982, *Sanders 1542* (FTG). **Georgia.** Camden Co.: Little Cumberland Island, 18 Oct 1972, *Sharpe 11* (GA). **South Carolina.** Beaufort Co.: by US highway 21 in Beaufort, 11 Oct 1956, *Bell 5243* (NCU).

Lantana sandersii* var. *sanibelensis (R.W. Sanders) A.R. Franck & Gann, comb. nov. *Lantana depressa* Small var. *sanibelensis* R.W. Sanders, Syst. Bot. 12: 55. 1987. Type: Florida, Lee Co., Sanibel Island, [ca. 26.462, -82.155], 11 May 1954, *Cooley 2674* (holotype, GH00094772; isotypes, USF13791, USF13792).

Lantana sandersii var. *sanibelensis* (Figs. 12D and 13C) is endemic to western peninsular Florida, on barrier islands from Pinellas Co. south to Lee Co. The moderately to densely hirsute stems with rather long trichomes characterize this variety, and according to Sanders (1987), the variety also has slightly smaller corollas than *L. sandersii* var. *sandersii*, which is otherwise very similar. Purely endemic lineages of *L. sandersii* var. *sanibelensis* are threatened by hybridization and admixture with *L. strigocamara*. *Lantana sandersii* var. *sanibelensis* is ranked as critically imperiled in South Florida by IRC (Gann et al. 2020).

Representative specimens examined. **USA. Florida.** Lee Co.: Wulfert, Sanibel Island, 10 Jan 1970, *Brumbach 7039* (FTG); *ibid.*, 3 Feb 1969, *Brumbach 6609* (FTG); *ibid.*, 24 Mar 1973, *Brumbach 8283* (US); Punta Rossa, Jul-Aug 1900, *Hitchcock 268* (GH); North Captiva Island, 7 May 1978, *Morrill & Harvey 61* (USF); Cayo Costa Island, 8 Apr 1991, *Young & Herwitz 534* (USF); Mound Key, 10 May 1991, *Close et al. MK0008* (USF). Pinellas Co.: Hog Island [Caladesi and Honeymoon Islands], 18 Apr 1900, *Tracy 6773* (GH); Mullet Key, 23 Jun 1976, *Thorne 48448* (USF). Sarasota Co.: Long Beach [Longboat Key], 19 Sep 1952, *Duncan et al. 14093* (GA).

Lantana strigocamara R.W. Sanders, Sida 22: 392. 2006. Type: Florida, Miami-Dade Co., Montgomery Foundation, 23 Sep 1981, *Sanders 1450* (holotype, FTG118878).

The non-native *L. strigocamara* has been naturalized throughout Florida, primarily in anthropogenically disturbed areas, but it is also categorized as an invasive species (FLEPPC 2019) for its ability to colonize relatively undisturbed habitats. It is thought to be derived from crosses of several taxa, probably including some combination of *L. nivea*, *L. scabrida*, *L. splendens*, *L. camara*, and/or *L. hirsuta* (Sanders 2012). The corollas of *L. strigocamara* are typically multicolored in each inflorescence (Fig. 13F–G).

Representative specimens examined. **USA. Florida.** Hillsborough Co.: Tampa Bay, May 1876, *Garber s.n.* (BRU). Lee Co.: Fort Myers, 12 Apr 1930, *Moldenke 947* (US). Miami-Dade Co.: Costello [Castellow] Hammock, 26 Jun 1966, *Long et al. 1883* (USF). Monroe Co.: Stock Island, Key West Botanical Garden, dense woods, 28 Aug 1954, *Killip 44384* (US); Lostman's Ranger Station, 27 Feb 1996, *Reimus 901* (FNPS).

Lantana ×floridana Raf., Atl. J. 148. 1832. Neotype (designated here): Florida, Volusia Co., New Smyrna Beach, lax shrub ca. 1 m tall, flowers opening yellow becoming orange then purplish, 2n=33, 20 Sep 1982, *Sanders 1540* (FTG120180).

=*Lantana bartramii* Baldwin ex Darl., Reliq. Baldwin 192–193, 247. 1843. Lectotype (designated here): “1482 *Lantana* Hardy native” (lectotype, PH00035034; probable isolectotype, PH00008820).

Lantana ×*floridana* was described by Rafinesque as having corollas “yellow, orange, red, crimson or scarlet on [the] same shrub” and that the leaves were “ovate lanceolate”. In the introduction to the article, Rafinesque stated “Having seen in gardens and herbals several rare or new sp. of Florida, I will here describe some of them.” Sanders (2006) implied *L. ×floridana* was based on a plant from the upper Atlantic coast of Florida, though Rafinesque does not give any specific locality information. Sanders (2006) could not locate a type specimen, and it sounds as though Rafinesque merely described the taxon based on cultivated plants he saw, without a herbarium specimen. Sanders (2006: 392) concluded that *L. ×floridana* is a hybrid betwixt *L. depressa* var. *floridana* (*L. sandersii*) and *L. strigocamara* (Sanders 2012: 438). In order to further stabilize nomenclature in the already convoluted taxonomy of *Lantana*, it is helpful to typify *L. ×floridana* in agreement with the usage given by Sanders (2006, 2012) (although it is conceivable Rafinesque instead had described a plant of *L. strigocamara*). No original material is known and here a neotype is designated for *L. ×floridana* from an area where Baldwin had also botanized. For convenience, the name *Lantana ×floridana* is here applied to hybrids of *L. strigocamara* and either variety of *L. sandersii*. Putative hybrids between *L. strigocamara* and each of the two varieties of *L. sandersii* seem morphologically indistinguishable (although Sanders 1987 purported that the angle between the midrib and blade margin was useful).

It seems plausible that Rafinesque had seen garden material produced from Baldwin’s collections of *L. bartramii*. The name *L. bartramii* was published posthumously from Baldwin’s letters through Darlington (1843). William Baldwin collected in northeastern Florida in 1816–1817, going at least as far south as New Smyrna (Darling 1843: 227). In December 1816, he found a *Lantana* around Lake George (Darlington 1843: 186, 195), the same area where Bartram (1792: 101–102) had reported it with “crimson, scarlet, orange and golden yellow” corollas in the 1770s. Baldwin further said the plant “abounds along the sea coast of Florida” (Darlington 1843: 192, 247), but these observations along the “sea coast” may partly pertain to *L. sandersii* var. *sandersii*. Baldwin mentioned his intent to send a specimen to Lambert and described its corollas as “bright yellow to crimson and purple [...] on the same plant at the same time” (Darlington 1843: 191–193). In Aug 1817, Baldwin wrote of his intent to send material to Bartram (Darlington 1843: 239) and in Aug 1818 he stated that this *Lantana* was now in flower at Bartram’s Garden, in the care of Robert Carr (Darlington 1843: 277). In 1828, a “Large flowered” plant by the name of “*Lantana bartramia*” was listed for sale from the Bartram Garden (Carr 1828).

Two specimens of original material of *L. bartramii* appear to be extant at PH, one of which was from the Lambert herbarium. Both specimens appear to have the same general morphology and development, and they are possibly duplicates. Sanders (2006) stated PH00035034 had “elements of” *L. sandersii* and concluded *L. bartramii* was synonymous with *L. ×floridana* (Sanders 2012).

An early specimen of this hybrid group was collected from the western coast in Manatee Co., Florida in Jun 1845 (*Rugel 129*, FLAS, US). It has sparsely prickly stems and leaf blades somewhat more broadly ovate than *L. sandersii*. A collection (*Moldenke 797*) from Key West may be this hybrid, which alternatively was figured by Sanders (2012) to be a hybrid of *L. strigocamara* and *L. depressa* s.str. No taxa of *Lantana* sect. *Lantana* are known to be native to the Florida Keys, which makes the Key West specimen peculiar. Some hybrids were identified in the Cape Sable region of Monroe Co. and in Hillsborough Co., yet no “pure” *L. sandersii* was located or identified in these areas (Sanders 1987). Possibly, admixture has completely removed purely endemic lineages in these areas, or maybe they remain undetected, or perhaps admixed propagules could be dispersing into these areas.

An early specimen collected by Simpson in 1891 was stated to be from “Point Losmans” which is an area along the north side of Key McLaughlin which now uses the descriptor “Lostman’s”. In earlier

maps up until at least 1911, the area was referred by the term “Lawson” probably referring to the surgeon general Thomas Lawson. So, it seems over time, the descriptor Lawson changed to Losman or Lossman which then became Lostman.

Representative specimens examined. **USA. Florida.** Indian River, 1874, *Palmer s.n.* (US). Brevard Co.: south of Cocoa Beach, 9 Aug 1929, *O'Neill s.n.* (US). Broward Co.: Dania Beach, 31 Apr 1977, *Biernacki s.n.* (FTG). Citrus Co.: near Hells Gate, mouth of Homosassa River, 3 Jul 1936, *Correll 5805* (GH). Collier Co.: south port of Naples, 18 Sep 1952, *Duncan et al. 14087* (GA); Fakahatchee Strand State Park, 25 Sep 2000, *Owen FS0342* (USF). Duval Co.: vicinity of Jacksonville, 1877, *Curtiss s.n.* (US). Hardee Co.: 10 mi. W of Bowling Green, 24 Jul 1977, *Kuczynski s.n.* (USF). Highlands Co.: Sebring, 20 May 1925, *Palmer 27448* (A). Hillsborough Co.: Long Key, 6 Aug 1894, *Lewton s.n.* (NY); Tampa, 24 Mar 1923, *Churchill s.n.* (GH). Lake Co.: Eustis, 1-15 Jun 1894, *Nash 943* (A, GH, US); E of Eustis, 7 May 1918, *Small 8666* (NY). Lee Co.: Mound Key, Estero Bay, 20 Apr 1964, *Lakela et al. 27034* (USF); Mound Key, Estero Bay, 11 Aug 1973, *Todd 11* (FLAS, USF); Eastern Sanibel, 5 Oct 1976, *Brumbach 9058* (USF). Manatee Co.: Jun 1845 *Rugel 129* (FLAS, US); Anna Maria Key, 7 Jun 1918, *Barrett 5* (US). Martin Co.: Jupiter Island, 2 Apr 1970, *Dunn 16607* (USF). Monroe Co.: Northwest Cape, 6 Sep 1979, *Avery & Russell 2146* (FNPS); *ibid.*, 16 Apr 1996, *Seavey & Seavey 1181*; *ibid.*, 30 Jun 1996, *Seavey & Seavey 1163*; *ibid.*, *Seavey & Seavey 1162*; Point Losmans [Lostmans] Key, May 1891, *Simpson 198* (US); Key West, dry sandy soil, shrubs low, spreading, ca. 4 ft. tall, flowers varying from pink to lavender, 19 Mar 1930, *Moldenke 797* (DUKE, NY). Palm Beach Co.: Ocean Drive, N of Juno Beach, 30 Sep 1962, *Lakela 25425* (USF). Pasco Co.: Anclote Key, 21 May 1918, *Howell 940* (US). Sarasota Co.: Keys, Sarasota, 1876, *Garber s.n.* (US); Anna Maria Key, 12 Apr 1917, *Cuthbert 1527* (FLAS). St. Johns Co.: Anastasia Island, 21 May 1897, *Barnhardt 2241* (NY). Volusia Co.: Turtle Mound, ca. 6 mi. SSE of New Smyrna Beach along the coast, 20 May 1981, *Hansen & Robinson 8250* (USF).

Lantana* × *strigodepressa A.R. Franck, hybr. nov. Type: Florida, Miami-Dade Co., SW 120th Ave and Bailes Road, Goulds, 25.554°, -80.385°, 13 May 2020, *Franck & Alexander 4814* (holotype, FTG; isotype, USF).

Description: Shrub, to 1 m tall, stems spreading to ascending. Stem with minute prickles, moderately pilose on young parts, hairs to 1 mm long. Leaf blades ovate, scabrous on both surfaces, 1.3–1.7 times longer than wide, 1.6–4 cm long, 2.2 cm wide. Corolla limb 5–6 mm wide, the tube 6–8 mm long. Fruit 4 mm wide.

The name *L. ×strigodepressa* is introduced for hybrids between *L. strigocamara* and *L. depressa* s. str. (Figs. 12C and 13E). This naming device is similar to the construction of the species epithet *strigocamara* which alluded to elements of the strigose and camara groups of *Lantana*.

Representative specimens examined. **USA. Florida.** Miami-Dade Co.: Old Cutler Road, just N of junction with 173 St., 8 Dec 1981, *Sanders & Popenoe 1469* (FTG); SE corner of Krome Ave. and Bauer Dr., 26 Sep 1995, *Bradley 272* (FTG); Tamiami Pineland Preserve, 31 Aug 1995, *Bradley 145* (FTG); Red Road and SW 114th Terrace, 12 Mar 1964, *Weinfeld 35* (USF); Buena Vista, 27 Dec 1929, *Moldenke 307a* (NY); near Snapper Creek Hammock, 19 Jun 1915, *Small & Mosier 6367* (NY); SW 67 St. and SW 75 Ct., 9 Mar 1975, *Hill 2537* (FTG).

ACKNOWLEDGEMENTS

We are sincerely grateful to numerous herbaria staff and colleagues, including B (Robert Vogt), BM (Mark Carine), C (Olof Ryding), DR (Frank Müller), DWC (Ronald McColl, Sharon Began), FLAS (Marc Frank, Lucas Majure, Kent Perkins), FTG (Brett Jestrow, James Lange, Beth Milne, Jennifer Possley), G (Laurence Loze, Fred Stauffer), M (Andreas Fleischmann, Siegfried Springer, Hans-Joachim

Esser), MA (Esther García Guillén, Eva García Ibáñez), NY (Barbara Thiers), P (Cécile Aupic, Florian Jabbour), PH (Jordan Teisher), USF (Keith Bornhorst, Bruce Hansen, Shawn Landry, Leenil Noel, Diane TeStrake). Thanks also to Roger Hammer, Rosalind Rowe, Karen Rogers, Jay Horn, and the TREC personnel (Zachary Brym and Cliff Martin), as well as to Miami-Dade Co. staff for support and access to parks (Jane Dozier, Dallas Hazelton, Eric King, Tiffany Melvin, Molly Messer, Tonya Nimark, Sonya Thompson, Vanessa Trujillo, and Alície Warren), and for permits and support in North Key Largo (Trudy Ferraro, Paul Rice, and Scott Tedford). Thanks to George Wilder (SWF), Richard Wunderlin (USF), and Keith Bradley for their improvements to the manuscript.

LITERATURE CITED

- Acevedo-Rodríguez, P. and M. T. Strong. 2012. Catalogue of Seed Plants of the West Indies. Smithsonian Contributions to Botany 98: 1–1192.
- Adams, C. D. 1972. Flowering Plants of Jamaica. University of the West Indies, Mona, Jamaica.
- Albritton, J. W. 2009. A 1700-year history of fire and vegetation in pine rocklands of National Key Deer Refuge, Big Pine Key, Florida: charcoal and pollen evidence from Key Deer Pond. M.S. thesis, University of Tennessee, Knoxville, Tennessee.
- Bartram, W. 1792. Travels through North and South Carolina, Georgia, East and West Florida, the Cherokee Country, the extensive territories of the Muscogulges or Creek Confederacy, and the Country of the Chactaws. James & Johnson, Philadelphia.
- Bolter, K. P. 2014. Perceived risk versus actual risk to sea-level rise: a case study in Broward County, Florida. Ph.D. dissertation, Florida Atlantic University, Boca Raton, Florida.
- Boniface, B. G. 1971. A Historical Geography of Spanish Florida, circa 1700. M.A. thesis, University of Georgia, Athens.
- Borgen, L. 1980. Chromosome numbers of Macaronesian flowering plants III. Botanica Macaronesica 7: 67–76.
- Broun, M. 1936. Some impressions of the “Land of Ferns,” and a Florida fern garden. American Fern Journal 26: 55–59.
- Browne, P. 1756. The Civil and Natural History of Jamaica. T. Osborne and J. Shipton, London.
- Cannon, P., T. Wilmers, and K. Lyons. 2010. Discovery of the imperiled Miami blue butterfly (*Cyclargus thomasi bethunebakeri*) on islands in the Florida Keys National Wildlife Refuges, Monroe County. Southeastern Naturalist 9: 847–853.
- Carlo, T. A. and J. M. Morales. 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. Ecology 97: 1819–1831.
- Carr, R. 1828. Periodical catalogue of fruit and ornamental trees and shrubs, green house plants, &c. cultivated and for sale at Bartram’s Botanic Garden, Kingsessing. Russell and Martien, Philadelphia.
- Carson, R. L. 1956. Miami: 1896 to 1900. Tequesta 16: 3–13.
- Corbett, T. G. 1974. Migration to a Spanish imperial frontier in the seventeenth and eighteenth centuries: St. Augustine. Hispanic American Historical Review 54: 414–430.
- Corrêa, A. M. and E. R. Forni-Martins. 2004. Chromosomal studies of species of Rubiaceae (AL de Jussieu) from the Brazilian cerrado. Caryologia 57: 250–258.
- Correll, D. S. and H. B. Correll. 1982. Flora of the Bahama Archipelago. A.R. Gantner Verlag KG, Vaduz, Liechtenstein.
- Czarnecki II, D. M., A. J. Hershberger, C. D. Robacker, D. G. Clark, and Z. Deng. 2014. Ploidy levels and pollen stainability of *Lantana camara* cultivars and breeding lines. HortScience 49: 1271–1276.
- Dahlgren, B. E. 1940. Travels of Ruiz, Pavón, and Dombey in Peru and Chile (1777–1788) by Hipólito Ruiz. Field Museum of Natural History, Botanical Series, vol. 21.
- Darlington, W. 1843. Reliquiae Baldwiniae. Kimber and Sharpless, Philadelphia.
- Deng, Y.-F. 2016. Two proposals to amend the Code concerning type designation. Taxon 65: 646–647.
- Dillon, L. S. 1956. Wisconsin climate and life zones in North America. Science 123: 167–176.

- Elliott, S. 1824. A Sketch of the Botany of South-Carolina and Georgia, vol. 2. J.R. Schenck, Charleston.
- Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida peninsula. *Ornithological Monographs* 50: 1–113.
- FLEPPC (Florida Exotic Pest Plant Council). 2019. 2019 List of Invasive Plant Species. Florida Exotic Pest Plant Council. Internet: www.fleppc.org
- Florentín, J. E., A. A. C. Fader, R. M. Salas, S. Janssens, S. Dessein, and E. L. Cabral. 2017. Morphological and molecular data confirm the transfer of homostylous species in the typically distylous genus *Galianthe* (Rubiaceae), and the description of the new species *Galianthe vasquezii* from Peru and Colombia. *PeerJ* 5: e4012.
- FNAI (Florida Natural Areas Inventory). 2010. Guide to the Natural Communities of Florida. FNAI, Tallahassee, Florida.
- Freid, E., J. Francisco-Ortega, and B. Jestrow. 2014. Endemic seed plants in the Bahamian archipelago. *The Botanical Review* 80: 204–230.
- Gann, G.D., K.A. Bradley, and S.W. Woodmansee. 2002. Rare Plants of South Florida: Their History, Conservation, and Restoration. Institute for Regional Conservation. Miami, Florida.
- Gann G. D., C. G. Stocking, and collaborators. 2001–2020. Floristic Inventory of South Florida Database Online. The Institute for Regional Conservation. Delray Beach, Florida. <https://www.regionalconservation.org/ircs/database/Database.asp>. Accessed 7 Sep 2020.
- GBIF (Global Biodiversity Information Facility). 2020a. *Spermacoce verticillata* L. <https://www.gbif.org/species/2918574>. Accessed 10 Aug 2020.
- GBIF (Global Biodiversity Information Facility). 2020b. *Melanthera nivea* (L.) Small. <https://www.gbif.org/species/2918574>. Accessed 3 Sep 2020.
- Gifford, M. J. 2008. Everything is ballast: an examination of ballast related practices and ballast stones from the Emanuel Point shipwrecks. M.A. thesis, University of West Florida, Pensacola.
- Gleason, P. J. and P. Stone. 1994. Age, origin, and landscape evolution of the Everglades peatland. *in* Everglades: the ecosystem and its restoration. S. M. Davis and J. C. Ogden (eds.). St. Lucie Press, Boca Raton, Florida.
- Gooding, E. G. B., A. R. Loveless, and G. R. Proctor. 1965. Flora of Barbados. Her Majesty's Stationery Office, London.
- Graenicher, S. 1930. Bee-fauna and vegetation of the Miami region of Florida. *Annals of the Entomological Society of America* 23: 153–174.
- Hammer, R. L. 1997. Have we lost the young palm orchid? *The Palmetto*, Spring 1997: 8–9.
- Hanan, E. J., M. S. Ross, P. L. Ruiz, and J. P. Sah. 2010. Multi-scaled grassland-woody plant dynamics in the heterogeneous marl prairies of the southern Everglades. *Ecosystems* 13: 1256–1274.
- Harley, G. L., H. D. Grissino-Mayer, and S. P. Horn. 2012. Fire history and forest structure of an endangered subtropical ecosystem in the Florida Keys, USA. *International Journal of Wildland Fire* 22: 394–404.
- Herndon, A. 1987. The re-instatement of *Borreria terminalis* Small (Rubiaceae). *Sida* 12: 79–89.
- Howard, R.A. 1989. Flora of the Lesser Antilles, vol. 6. President and Fellows of Harvard College, Jamaica Plain, Massachusetts.
- Huffman, J. M. 2006. Historical fire regimes in southeastern pine savannas. Ph.D. dissertation, Louisiana State University, Baton Rouge, Louisiana.
- Kartesz, J. T. and K. N. Gandhi. 1992. A new combination in *Spermacoce* (Rubiaceae) and lectotypification of *Borreria terminalis*. *Brittonia* 44: 370–371.
- Keith, D. H. 2006. The Molasses Reef Wreck. *in* Underwater Cultural Heritage at Risk: Managing Natural and Human Impacts. R. Grenier, D. Nutley and I. Cochran (eds.). Heritage at Risk 82–84.
- Knapp, W. M., A. Frances, R. Noss, R. F. C. Naczi, A. Weakley, G. D. Gann, B. G. Baldwin, J. Miller, P. McIntyre, B. D. Mishler, G. Moore, R. G. Olmstead, A. Strong, K. Kennedy, B. Heidel, and D. Gluesenkamp. 2020. Vascular plant extinction in the continental United States and Canada. *Conservation Biology* 35: 360–368.

- Knorr, P. O. 2006. The case for high-order, Pleistocene sea-level fluctuations in southwest Florida. M.S. thesis, University of South Florida, Tampa, Florida.
- Kocis, D. L. 2012. Reconstruction of fire history in the National Key Deer Refuge, Monroe County, Florida, U.S.A.: the Palmetto Pond macroscopic charcoal record. M.S. thesis, University of Tennessee, Knoxville, Tennessee.
- Laessle, A. M. 1944. A study of quail food habits in peninsular Florida. *Proceedings of the Florida Academy of Sciences* 7: 155–171.
- Lance, R. 2004. *Woody Plants of the Southeastern United States: A Winter Guide*. University of Georgia Press, Athens.
- Lewis, W. H. 1962. Chromosome numbers in North American Rubiaceae. *Brittonia* 14: 285–290.
- Lewis, W. H., Y. Suda, and R. L. Oliver. 1967. Chromosome numbers of Phanerogams. 2. *Annals of the Missouri Botanical Garden* 54: 178–181.
- Lockwood, J. L., M. S. Ross, and J. P. Sah. 2003. Smoke on the water: the interplay of fire and water flow on Everglades restoration. *Frontiers in Ecology and the Environment* 1: 462–468.
- Liogier, A. H. 1962. *Flora de Cuba*. Vol 5. Rubiales — Valerianales — Cucurbitales — Campanulales — Asterales. Editorial Universitaria, Universidad de Puerto Rico, Rio Piedras, Puerto Rico.
- Liogier, A. H. 1985. *Descriptive flora of Puerto Rico and adjacent islands*, vol. 5. Editorial de la Universidad de Puerto Rico.
- Liogier, A. H. 1995. *La Flora de la Española VII*. Universidad Central del Este, San Pedro de Macorís, Dominican Republic.
- Long, R. W. 1970. Additions and nomenclatural changes in the flora of southern Florida — I. *Rhodora* 72: 17–46.
- Long, R. W. and O. Lakela. 1971. *A Flora of Tropical Florida*. University of Miami Press, Coral Gables.
- Lorence, D. H. 2012. *Chiococca*. in Rubiaceae a Verbenaceae. *Flora Mesoamericana*. G. Davidse, M. Sousa Sánchez, S. Knapp & F. Chiang Cabrera (eds.). Missouri Botanical Garden, St. Louis.
- Marx, H. E., N. O'Leary, Y. W. Yuan, P. Lu-Irving, D. C. Tank, M. E. Múlgura, and R. G. Olmstead. 2010. A molecular phylogeny and classification of Verbenaceae. *American Journal of Botany* 97: 1647–1663.
- Maschinski, J., E. Sirkin, and J. Fant. 2010. Using genetic and morphological analysis to distinguish endangered taxa from their hybrids with the cultivated exotic pest plant *Lantana strigocamara* (syn: *Lantana camara*). *Conservation Genetics* 11: 1607–1621.
- Miguel, L. and E. L. Cabral. 2013. *Borreria krapocarmeniana*, a new cryptic species recovered through taxonomic analyses of *Borreria scabiosoides* and *Borreria linoides* (Spermacoceae, Rubiaceae). *Systematic Botany* 38: 769–781.
- Morgan, G. S. 2002. Late Rancholabrean mammals from southernmost Florida, and the Neotropical influence in Florida Pleistocene faunas. *Smithsonian Contributions to Paleobiology* 93: 15–38.
- Moore, S. M. and A. B. Rendle. 1936. *Flora of Jamaica*, vol. 7. British Museum, London.
- NatureServe. 2020. NatureServe Explore. NatureServe, Arlington, Virginia. <https://explorer.natureserve.org/>. Accessed 4 Sep 2020.
- Nuttall, T. 1822. A catalogue of a collection of plants made in East-Florida, during the months of October and November, 1821. By A. Ware, Esq. *American Journal of Science and Arts* 5: 286–304.
- Olmsted, I., W. B. Robertson, Jr., J. Johnson, and O. L. Bass, Jr. 1983. The vegetation of Long Pine Key, Everglades National Park. Report SFRC-83/05, South Florida Research Center, Homestead, Florida.
- Parks, J. C. 1973. A revision of North American and Caribbean *Melanthera* (Compositae). *Rhodora* 75: 169–210.
- Parks, J. C. 2006. *Melanthera*. in *Flora of North America, north of Mexico (FNA)*. FNA Editorial Committee (eds.). New York and Oxford.
- Paudyal, S. K., P. G. Delprete, S. Neupane, and T. J. Motley. 2018. Molecular phylogenetic analysis and generic delimitations in tribe Chiococceae (Cinchonoideae, Rubiaceae). *Botanical Journal of the Linnean Society* 187: 365–396.

- Petuch, E. J. 1987. The Florida Everglades: A Buried Pseudoatoll? *Journal of Coastal Research* 3: 189–200.
- Porter, D. M. 1980. The vascular plants of Joseph Dalton Hooker's An Enumeration of the plants of the Galapagos Archipelago; with descriptions of those of which are new. *Botanical Journal of the Linnean Society* 81: 79–134.
- Proctor, G. R. 1984. Flora of the Cayman Islands. *Kew Bulletin Additional Series* 11: 1–834.
- Richards, J. H. and P. C. Olivas. 2020. A common-mesocosm experiment recreates sawgrass (*Cladium jamaicense*) phenotypes from Everglades marl prairies and peat marshes. *American Journal of Botany* 107: 56–65.
- Robbins, A. M. J., C. M. Eckelmann, and M. Quinones. 2008. Forest fires in the insular Caribbean. *Ambio* 37: 528–534.
- Robinson, B. L. 1899. Revision of the North American species of *Tephrosia*. *Botanical Gazette* 28: 193–202.
- Rogers, G. K. 2005. The genera of Rubiaceae in the southeastern United States, part II. Subfamily Rubioideae, and subfamily Cinchonoideae revisited (*Chiococca*, *Erithalis*, and *Guettarda*). *Harvard Papers in Botany* 10: 1–45.
- Saha, A. K., S. Saha, J. Sadle, J. Jiang, M. S. Ross, R. M. Price, L. S. L. O. Sternberg, and K. S. Wendelberger. 2011. Sea level rise and South Florida coastal forests. *Climatic Change* 107: 81–108.
- Salvato, M. H. and H. L. Salvato. 2008. Notes on the feeding ecology of *Strymon acis bartrami* and *Anaea troglodyta floridalis*. *Florida Scientist* 71: 323–329.
- Sanders, R. W. 1987. Identity of *Lantana depressa* and *L. ovatifolia* (Verbenaceae) of Florida and the Bahamas. *Systematic Botany* 12: 44–60.
- Sanders, R. W. 2001. The genera of Verbenaceae in the southeastern United States. *Harvard Papers in Botany* 5: 303–358.
- Sanders, R. W. 2006. Taxonomy of *Lantana* sect. *Lantana* (Verbenaceae): I. Correct application of *Lantana camara* and associated names. *Sida* 22: 381–421.
- Sanders, R. W. 2012. Taxonomy of *Lantana* sect. *Lantana* (Verbenaceae): II. Taxonomic revision. *Journal of the Botanical Research Institute of Texas* 6: 403–441.
- Sargent, C. S. (ed.). 1889. Portions of the journal of André Michaux, botanist, written during his travels in the United States and Canada, 1785 to 1796. *Proceedings of the American Philosophical Society* 26: 1–145.
- Shaw, C. 1975. The pine and hammock forestlands of Dade County. Florida Division of Forestry.
- Small, J. K. 1905. Additions to the flora of subtropical Florida. *Bulletin of the New York Botanical Garden* 3: 419–440.
- Small, J. K. 1913. *Flora of the Southeastern United States*, 2nd ed. New York.
- Small, J. K. 1918. Botanical exploration in Florida in 1917. *Journal of the New York Botanical Garden* 19: 279–290.
- Small, J. K. 1924. The land where spring meets autumn. A record of exploration in Florida in December, 1921. *Journal of the New York Botanical Garden* 25: 53–94.
- Small, J. K. 1933. *Manual of the Southeastern Flora*. New York.
- Sobrado, S. V. and E. L. Cabral. 2015. Intraspecific variation of insertion/length of stamens in homostylous flowers of a new species and three other species of *Borreria*: An unusual case in Rubiaceae. *Phytotaxa* 206: 53–73.
- Spies, J. J. and H. du Plessis. 1987. Sterile *Lantana camara*: fact or theory. *South African Journal of Plant and Soil* 4: 171–174.
- Standley, P. C. 1934. Rubiales, Rubiaceae, part 4. *North American Flora* 32: 229–300.
- Steinbauer, M. J., R. Otto, A. Naranjo-Cigala, C. Beierkuhnlein, and J. M. Fernández-Palacios. 2012. Increase of island endemism with altitude–speciation processes on oceanic islands. *Ecography* 35: 23–32.

- Steyermark, J. A. 1971. Rubiáceas nuevas de los Andes y Cordillera de la Costa de Venezuela. *Acta Botánica Venezuelica* 6: 99–196.
- Steyermark, J.A. 1972. *Borreria* (Rubiaceae). in *The botany of the Guayana Highland, Part IX*. B. Maguire and collaborators (eds.). *Memoirs of the New York Botanical Garden* 23: 805–832.
- Sundberg, S. D. and D. J. Bogler. 2006. *Baccharis*. in *Flora of North America: North of Mexico*, vol. 20: Asteraceae. *Flora of North America Editorial Committee*. Oxford University Press, Oxford and New York; p. 23–34.
- Taylor, C. M., J. A. Steyermark, P. G. Delprete, A. Vincentini, R. Cortés, D. C. Zappi, C. H. Persson, C. B. Costa & E. Anunciação. 2004. Rubiaceae. in *Flora of the Venezuelan Guayana*. J. A. Steyermark, P. E. Berry, and B. K. Holst (eds.). *Missouri Botanical Garden Press*, St. Louis.
- Taylor, D. L. 1981. Fire history and fire records for Everglades National Park, 1948–1979. Report T-619, South Florida Research Center, Homestead, Florida.
- Taylor, W. K. and E. M. Norman. 2004. André Michaux Visits Spanish East Florida, Spring 1788. *Castanea, Occasional Papers in Eastern Botany* 2: 119–129.
- Thiers, B. 2020. *Index Herbariorum*. William and Lynda Steere Herbarium, New York Botanical Garden. (<http://sweetgum.nybg.org/science/ih/>).
- Tweed, T. A. 1995. An emerging Protestant establishment: religious affiliation and public power on the urban frontier in Miami, 1896–1904. *Church History* 64: 412–437.
- Tursi, R. M., P. T. Hughes, and E. A. Hoffman. 2012. Taxonomy versus phylogeny: evolutionary history of marsh rabbits without hopping to conclusions. *Diversity and Distributions* 19: 120–133.
- Urban, I. 1898. *Bibliographia Indiae occidentalis botanica*. *Symbolae Antillanae* 1: 3–192.
- Urban, I. 1920–1921. *Flora domingensis*. *Symbolae Antillanae* 8: 1–860.
- URS Corporation Southern. 2007. Miami-Dade County Environmentally Endangered Lands Program Management Plan. Part II: Management of Specific Habitat Types. Chapter 1: The Pine Rockland Habitat. With support of The Institute for Regional Conservation and Muller and Associates, Inc.
- U.S. Census Bureau. 1994. *Geographic Areas Reference Manual (GARM)*. Bureau of the Census, Economics and Statistics Administration, U.S. Department of Commerce.
- U.S. Census Bureau. 2010. State area measurements and internal point coordinates. (<https://www.census.gov/geographies/reference-files/2010/geo/state-area.html>, 25 April 2020).
- U.S. Census Bureau. 2020. QuickFacts. Florida. (<https://www.census.gov/quickfacts/fact/table/FL/PST045219>, 15 Oct 2020).
- USDA (United States Department of Agriculture). 2019. 2017 Census of Agriculture. Florida. State and County Data. Volume 1. Geographic Area Series Part 9. AC-17-A-9. USDA, Washington, D.C.
- Weakley, A. S., R. J. LeBlond, B. A. Sorrie, C. T. Witsell, L. D. Estes, K. Gandhi, K. G. Mathews, and A. Ebihara. 2011. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. *Journal of the Botanical Research Institute of Texas* 5: 437–455.
- Wiersema, J. H., P. G. Delprete, J. H. Kirkbride, and A. R. Franck. 2017. A new weed in Florida, *Spermacoce latifolia*, and the distinction between *S. alata* and *S. latifolia* (Spermacoceae, Rubiaceae). *Castanea* 82: 114–131.
- Willard, D. A. and C.W. Holmes. 1997. Pollen and geochronological data from South Florida: Taylor Creek Site 2. Open-file Report 97-35, U.S. Geological Survey.
- Willard, D. A. and C. E. Bernhardt. 2011. Impacts of past climate and sea level change on Everglades wetlands: placing a century of anthropogenic change into a late-Holocene context. *Climate Change* 107: 59–80.
- Willard, D. A., C. E. Bernhardt, C. W. Holmes, B. Landacre, and M. Marot. 2006. Response of Everglades tree islands to environmental change. *Ecological Monographs* 76: 565–583.
- Williams, R. O. and E. E. Cheesman. 1928. *Flora of Trinidad and Tobago*. Rubiales. Government Printer, Port-of-Spain.
- Wunderlin, R. P. 1979. Notes on *Spermacoce* and *Mitracarpus* (Rubiaceae) in southeastern United States. *Phytologia* 41: 313–316.

- Wunderlin, R. P. 1998. Guide to the Vascular Plants of Florida. University Press of Florida, Gainesville, Florida.
- Wunderlin, R. P. and B. F. Hansen. 2011. Guide to the Vascular Plants of Florida. University Press of Florida, Gainesville, Florida.
- Wunderlin, R. P., B. F. Hansen, and J. Beckner. 2000. Botanical exploration in Florida. *in* Flora of Florida, vol. 1. R. P. Wunderlin and B. F. Hansen (eds.). University Press of Florida, Gainesville, Florida.
- Wunderlin, R. P., B. F. Hansen, and A. R. Franck. 2018. Flora of Florida, vol. 5. University Press of Florida, Gainesville, Florida.
- Wunderlin, R. P., B. F. Hansen, A. R. Franck, and F. B. Essig. 2020. Atlas of Florida Plants (<http://florida.plantatlas.usf.edu/>). [S. M. Landry and K. N. Campbell (application development), USF Water Institute.] Institute for Systematic Botany, University of South Florida, Tampa.
- WWF (World Wildlife Fund). 2020. South Florida rocklands. Prepared by Dinerstein, E., A. Weakley, R. Noss, and K. Wolfe. <https://www.worldwildlife.org/ecoregions/nt0164>
- Young, F. N. 1968. The case of the vanishing tree snail. *The American Biology Teacher* 30: 420-425.
- Zong, C. 2015. Late Pleistocene sea levels and resulting changes in global land distributions. M.S. thesis, University of Kansas, Lawrence, Kansas.

Appendix 1. Endemic taxa of terrestrial extreme southern Florida, south of 26.25° N (undoubtedly this list is not exhaustive).

Birds (*Ammodramus maritimus mirabilis*); **crustacean** (*Procambarus milleri*); **insects** (*Anaea troglodyta floridalis*, *Ataenius superficialis*, *Belocephalus micanopy*, *B. sleighti*, *Cicindelidia floridana*, *Cyclargus thomasi bethunebakeri*, *Cycloptilum irregularis*, *Dialictus flaveriae*, *Gryllus cayensis*, *Heraclides aristodemus ponceanus*, *Orocharis diplastes*, *O. tricornis*, *Strymon acis bartrami*); **mammals** (*Odocoileus virginianus clavium*, *Neotoma floridana smallii*, *Oryzomys argentatus*, *Peromyscus gossypinus allapaticola*, *Sylvilagus palustris hefneri*); **reptiles** (*Diadophis punctatus acricus*, *Plestiodon egregius egregius*, *Tantilla oolitica*); **snails** (*Cerion incanum*, *Orthalicus floridensis*, *O. reses*); and **plants** (*Amorpha herbacea* var. *crenulata*, *Andropogon miamiensis*, *Argythamnia blodgettii* [if distinct from *A. argothamnoides*], *Asplenium ×biscaynianum*, *Borreria terminalis*, *Brickellia mosieri*, *Chamaecrista deeringiana* [probable endemic, reported elsewhere], *Chamaecrista keyensis*, *Chromolaena frustrata*, *Consolea corallicola*, *Dalea floridana*, *Didymoglossum punctatum* subsp. *floridanum*, *Digitaria pauciflora*, *Euphorbia conferta*, *Euphorbia deltoidea* [4 subsp.], *Euphorbia garberi*, *Euphorbia pinetorum*, *Euphorbia porteriana*, *Galactia pinetorum*, *Galactia smallii*, *Govenia floridana*, *Indigofera keyensis* [if distinct from *I. oxycarpa* and *I. scabra*], *Lantana depressa* (s. str.), *Lechea lakelae*, *Linum arenicola*, *Linum carteri*, *Linum smallii*, *Melanthera parvifolia*, *Opuntia abjecta*, *Opuntia ochrocentra*, *Sabal miamiensis*, *Schizachyrium rhizomatum*, *S. sericatum* [if distinct from *S. gracile*], *Sideroxylon reclinatum* subsp. *austrofloridense*, *Solidago chrysopsis*, *Stenaria nigricans* var. *floridana*, *Tectaria ×amesiana*, *Tephrosia angustissima* var. *angustissima*, *Tragia saxicola*).

Appendix 2. Vascular plant taxa endemic to South Florida and presumed extinct (Gann et al. 2002, 2020; Knapp et al. 2020).

Eriochloa michauxii var. *simpsonii*, *Govenia floridana*, *Lechea lakelae*, *Tectaria ×amesiana*, *Tephrosia angustissima* var. *angustissima*.

Appendix 3. Native vascular plant taxa probably extirpated in the wild from South Florida and not present elsewhere in Florida, but presumed extant outside of Florida (Gann et al. 2020). All taxa below were restricted to extreme southern Florida (south of 26.25° N) except two marked with an asterisk (*) were found north of 26.25° N.

Adiantum villosum, *Amaranthus crassipes* (if native), *Amyris balsamifera*, *Baccharis dioica*, *Brassia caudata*, *Bulbophyllum pachyrachis*, *Chloris elata*, *Cissampelos pareira*, *Cyperus lentiginosus* (if native), *Didymoglossum lineolatum*, *Epidendrum acunae*, *Euploca fruticosa*, *Lepanthopsis melanantha*, *Macradenia lutescens*, *Maxillaria parviflora*, *Melochia tomentosa*, *Peperomia magnoliifolia*, *Pleopeltis marginatum*, *Pteris quadriaurita**, *Rhipsalis baccifera*, *Serpocaulon triseriale*, *Spiranthes amesiana* (if distinct from *S. torta*), *Tectaria coriandrifolia*, *Tillandsia fasciculata* var. *clavispica*, *T. fasciculata* var. *fasciculata*, *Trichocentrum carthagenense*, *Tridens eragrostoides*, *Utricularia amethystina**, *Vachellia macracantha*, *Vanilla dilloniana*, *Varronia bahamensis*.