A REVISION OF THE GENUS BORRICHIA ADANS. (COMPOSITAE)¹

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ABSTRACT

Borrichia Adans. (Compositae: Heliantheae) is a small North American genus of two well-collected species and their hybrid and one species known only from the type collection. Borrichia frutescens (L.) DC. grows in saline habitats along the Atlantic and Gulf coasts from Virginia to the Yucatán. Borrichia arborescens (L.) DC. occurs along the coasts of the northern West Indies and tropical Florida where it hybridizes with B. frutescens. The hybrids were first described as a species $B. \times cubana$ Britton & Blake (pro sp.). Borrichia peruviana DC. is known from the vegetative type collection. Borrichia demissa DC. has been excluded from the genus.

Tribe Heliantheae) the "Sea Ox-eye Daisy" was that of de Candolle (1836: 488–489). Since then several species have been described and the entire field of modern biosystematics developed. I have reviewed the chromosomal biology of the genus (Semple, 1978), and a detailed study of Floridian populations of B. × cubana Britton & Blake (pro sp.) has been made (Semple & Semple, 1978). The number of estimated species has been reported recently as seven by Willis (1966: 148) and Long & Lakela (1971: 833–834) and five by Gleason (1952: 339) and Correll & Johnston (1970: 1644–1645). This paper reviews the pertinent literature on the taxonomy of the genus and provides species descriptions and a key to the revised genus.

NOMENCLATURAL HISTORY

Linnaeus (1753: 903) first described the type species as Buphthalmum frutescens L. from New World collections from Virginia and Jamaica and associated the species with the Old World taxon Buphthalmum salicifolium L. (designated type of Buphthalmum). Later, Linnaeus (1759: 1227) split B. frutescens into two species, with the Jamaican collection included in B. arborescens L. De Candolle (1836) recognized the significant differences between the Old World species, members of the Tribe Inuleae, and the New World species, and he placed the latter in Borrichia, a name proposed by Adanson (1763: 130) to honor the seventeenth century Danish botanist Ole Borch. Adanson did not list any species in his genus, however. De Candolle (1836) remedied this and in addition to the two Linnaean species which he transferred to Borrichia, B. frutescens and B. arborescens, he included three more species: B. peruviana DC., B. argentea DC. and B. demissa DC. De Candolle listed synonyms for the five

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species, as well. Of the three additional species only one, *B. peruviana*, is treated as distinct in this revision. The type collection is unfortunately vegetative only and little can be said about the taxon. The second species has been placed in synonymy under *B. arborescens* in this revision, while the third species *B. demissa* has been excluded from *Borrichia* based on fruit morphology.

Small (1903: 1262–1263) described another species, *B. glabrata* Small, from *Curtiss 1412* collected in tropical south Florida. In the 1915 edition of the *Flora of the Southeastern United States*, however, Small placed *B. glabrata* in synonymy under *B. arborescens*, having studied the species from locations other than the Florida keys.

The last species to be described was *B. cubana* Britton and Blake (Britton, 1920) based on a Cuban collection, *León 7244*. No further collections of this species were correctly identified except for those of Ekman from the same location several years later. My research has discovered ten more collections of this species made in the Florida Keys during the last 75 years by several botanists, including Small. Several extensive populations of the taxon were also located during June of 1975.

The status of each taxon was investigated through field work, chemical and cytological studies, experimental greenhouse studies when possible, and examination of herbarium specimens from the following herbaria: BUS, F, FAU, FLAS, FSU, GH, IJ, MO, MSC, SMU, TEX, TUFTS, US, USF, and WAT. The curators of these institutions are thanked for their cooperation.

Systematic Treatment

Borrichia Adans., Fam. Pl. 2: 130. 1763. Based on Dillenius Etham. tab. 83, fig. 43 = B. arborescens; fig. 44 = B. frutescens.

Diomedea Cass., Bull. Sci. Soc. Philom. Paris 1817: 70. 1817. TYPE: D. bidentata Cass. = Borrichia frutescens (L.) DC.

Soboliferous or fruticose perennials to 1.5 m tall; roots fibrous, at times adventitious; stems woody, decumbent to erect, branching, the sap sticky resinous. Leaves opposite, heteroblastic; primary stem leaves petioled to nearly sessile, occasionally serrate-dentate; secondary branch leaves progressively more linearoblanceolate, entire and reduced in size, 2-10 cm (rarely more) long, glabrous to pubescent, firm, coriaceous or succulent, mucronate, the teeth often spinulose. Inflorescence terminal solitary heads or a few heads clustered on short lateral branches. Heads globose to turbinate; phyllaries in 2-3 series, the outer ones larger and decussate, ovate with a spinulose tip or merely acute-cuspidate, 10-45; receptacle slightly convex, the paleas partially enclosing fruit, resembling the inner involucral bracts; ray florets pistillate, yellow, the strap ovate, the apex notched; disc florets perfect, yellow, tubular, the anthers black with orange connective glands, the style bifurcate, terete, the style branches papillate. Fruits (cypselas) of the periphery laterally compressed, appearing 3-angled, traversely depressed obtrullate in cross-section, those of the center 4-angled, tapering at base, rhombic in cross-section, gray to black, glabrous, faintly finely reticulate; pappus a 3-4-angled united crown, straw colored, occasionally deciduous on older fruits after release from head. Chromosome number: x = 14, n = 14.

Lectotype species: Borrichia frutescens (L.) DC.

As delimited in this revision, *Borrichia* includes shrubs with opposite leaves and yellow-flowered, essentially solitary, radiate heads. The diagnostic character is the achene pappus, which is straw colored and forms a 3–4-angled united crown on the black 3–4-angled achene. The leaves of the plant are used as a medicinal tea in the Bahamas (Eldridge, 1975).

KEY TO THE TAXA OF BORRICHIA IN NORTH AMERICA AND THE WEST INDIES

- aa. Involucral bracts prominently spine tipped; leaves of primary branches serrate or dentate, villous-sericeous (rarely coriaceous and glabrous).

NOT INCLUDED IN KEY: 4. B. peruviana, known only from the vegetative type collection. See text.

1. Borrichia frutescens (L.) DC., Prodr. 5: 488. 1836.

Buphthalmum frutescens L., Sp. Pl. 903. 1753. TYPE: Virginia (?BM, not seen).

B. incanum Mill., Gard. Dict., ed. 8. 1768. TYPE: Bahamas (not seen).

Diomedia bidentata Cass., Dict. Sci. Nat. 13: 283. 1819. Based on Buphthalmum frutescens L.

Borrichia frutescens (L.). DC. var. angustifolia DC., Prodr. 5: 489. 1836. TYPE: Mexico,
Tampico, Berlandier 126 (G, seen on microfiche).

Soboliferous perennials, forming dense clones, overwintering by rhizomes, fruticose perennials in areas without killing frosts. Leaves heteroblastic villoussericeous; primary branch leaves petiolate, obovate to elliptic, the apex acute or mucronate, the margins basally serrate-dentate spinulose (rarely along most of margin), the blade attenuate, the petiole with one or more pairs of large spinulose teeth near the base; secondary branch leaves becoming progressively more sessile, entire, oblanceolate-linear, the apex acute or mucronate. Heads solitary, terminal and on lateral branches near the shoot apex, globose; peduncles 2-6 cm long; phyllaries in 3-4 unequal series, 20-40, the outer shorter, 2-4 mm long, the apex obovate with a woody recurved spine, the inner similar with the spines spreading to erect, 3-6 mm, sericeous except for the spines; receptacle slightly convex, the chaff folded, oblanceolate, 4-6 mm long, with a long orange yellow, woody spine 1.5–3 mm long, becoming thickened with age; ray florets pistillate, fertile, yellow, 15–30; disc florets perfect, fertile, yellow, 20–75. Fruits (cypselas) black at maturity, 3-4 angled, the peripheral ones traversely depressed obtrullate in cross-section, the inner rhombic in cross-section, 2.5-4(-5) mm long; pappus a 4-angled united crown, straw colored. Heads disintegrating after one or more seasons, globose, the outer phyllaries fully reflexed due to the thickening of the phyllaries, chaff, and fruit. Chromosome number: n = 14 (rarely 3x).

DISTRIBUTION AND HABITAT

Borrichia frutescens is a common member of the salt marsh community and brackish backwaters along the Gulf and Atlantic coasts from Virginia to the west coast of the Yucatán Peninsula in Mexico. The species occurs inland along the Rio Grande Valley in Texas and as far as the State of Coahuila in northern Mexico. It is present along the coasts of the Bermuda Islands, but normally is absent from the West Indies. The species was collected once on Grand Bahama Island, Allen 29 (GH), annotated by Britton & Millsaugh as B. aborescens (probably because the plant is neotonous), and was collected near Havana, Cuba, Ekman 13,292 (F, CH, NY, US). The duplicates range from typical B. frutescens to more B. cubana-like and may represent part of a hybrid swarm. These collections by Eckman were originally identified as B. cubana and are from the type location of that taxon. Both the Cuban and Bahamian collections are probably only chance introductions. Figure 1 (dots) illustrates the distribution of the species based on herbarium collections.

MORPHOLOGICAL VARIATION

The species varies greatly in size of the heads and the degree of leaf serration-dentation. Field observations indicate that the variation in head size is in part due to environmental factors. The time of year when the head is produced and the general vigor of the plant affect head size. Various degrees of leaf serration-dentation occur throughout the range, although extreme forms are more common in southern Texas. Typically the blade margins are serrate along the basal third to half, while some specimens have some leaves with most of the blade serrate: Flamingo, Florida, Godfrey et al. 63379 (FSU); Nuevo Laredo, Nuevo León, Mexico, Frey & Frey 2337 (GH). While isolated individuals may appear to warrant taxonomic status, such extremes merely represent the ends of continuous variation of several characters in a single phenotype.

On some specimens the outer two involucral bracts may be large (1–2 cm) and appear more leaflike due to the lack of the long woody spine. The extreme forms of this variation are again merely the end of a continuum and do not warrant taxonomic recognition.

Field studies revealed that some plants may rarely produce leaves that are glabrate in part or entirely. This may represent some environmentally induced return to the seedling leaf form. Experimentally grown plants were found to produce several pairs of juvenile leaves that were glabrate and without serratedentate margins before producing more typical leaves. In this condition the seedlings may be confused with *B. arborescens*, although the involucral bracts that are produced by such unusually early flowering plants are typical. Figure 2 illustrates the branching pattern, leaves, involucre and phyllaries, and a disc fruit of *B. frutescens*.

BERMUDA. Castle Harbor, Admiral's Cove, Brown & Britton 968 (NY). Long Bird Is., Marble 762 (NY). St. David's Is., Red Bay, Brown & Britton 1063 (NY). Walsingham, Brown & Britton 281(F, GH, NY, US); Collins 305 (F, NY, US); Rankin s.n. (NY); Marsh 1636 (F, GH, SMU, TEX).

MEXICO. CAMPECHE: S of Lerma, Sauer 2429 (F). YUCATÁN: Progresso, Gaumer 1161

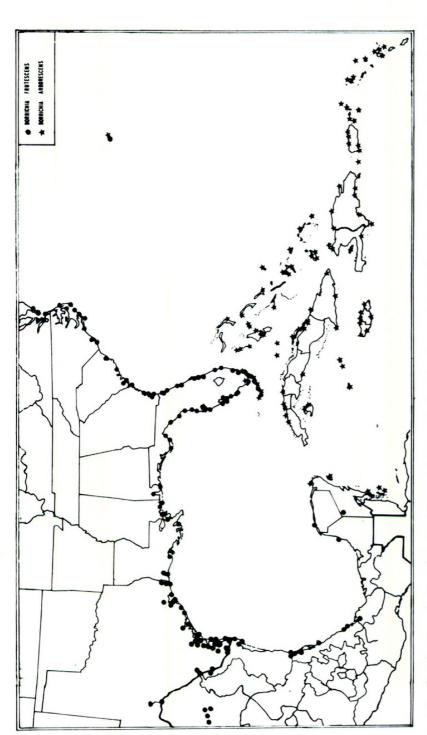


FIGURE 1. The distribution of *Borrichia frutescens* (dots) and *B. arborescens* (stars) based on herbarium collections. *Borrichia* × cubana (not shown) occurs in the Florida keys and was collected in 1917 and 1921 at the type locality west of Havana, Cuba.

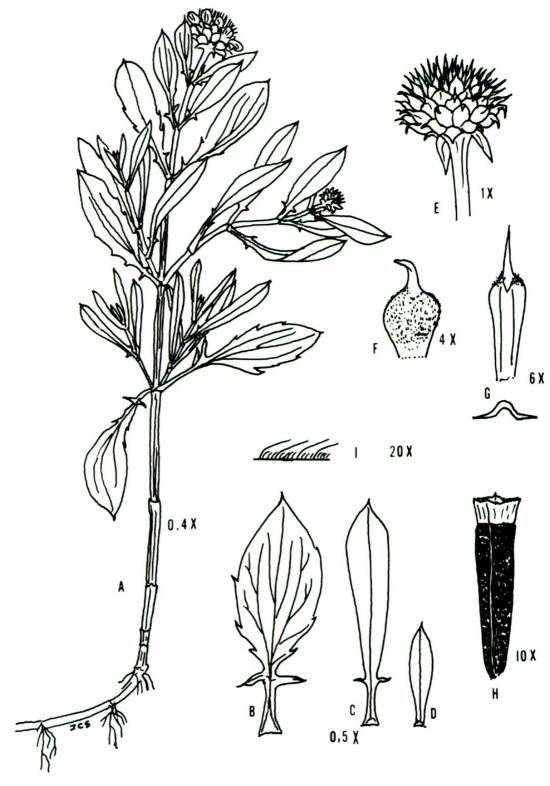


FIGURE 2. Borrichia frutescens (L.) DC.—A. Shoot from rhizome.—B-D. Primary stem leaf, branch leaf, higher level branch leaf, respectively (pubescence not indicated; all at same scale).—E. Fruiting head.—F. Phyllary of middle series.—G. Receptacle chaff.—H. Mature fruit of central disc floret.—I. Leaf surface pubescence diagram. (Based on many collections.)

(F, MO, US); Lundell 7951 (F, GH, NY, TEX, US). COAHUILA: W of Hermanas, Turner 6350 (TEX). Cuatro Ciénegas, Marsh 2033 (F, GH, TEX). QUINTANA ROO: Lake Chichan-kanab, Gaumer 2209 (F, GH, MO, US). SAN LUIS POTOSÍ: Haciende de Angosturo, Pringle 3757 (F, GH, MO, US). TAMAULIPAS: S of Matamoros, Wooten 29 (US). Tampico, Palmer 100 (F, GH, MO, NY, US). VERACRUZ: Barra de Tuxpan, Sauer & Gade 2985 (F). 4 km S of state line, Newling & Gómez-Pompa 388 (GH). 8 km before Tampico. Chiang 73 (F, GH).

United States. Alabama: Mobile, Dauphine Is., Mohr s.n. (US). Florida: Brevard Co., Titusville, Nash 2289 (F, GH, MO, NY, US). Broward Co., Hollywood, Demaree 18714 (FLAS). Collier Co., Marco, Hitchcock s.n. (F); Standley 12793 (US). Citrus Co., Pirates Cove, Genelle & Fleming 1272 (USF). Dade Co., Coconut Grove, Young 50 (US). Elliot's Key, Small & Nash s.n. (NY). Homestead, Godfrey 58125 (USF). Miami, Garber s.n. (GH, NY); Small 5456 (GH, NY, US); Small & Carter 1214 (F, NY). Duval Co., Shell Is., Curtiss 1413 (F, MO, US). Franklin, NE of Alligator Pt., Kral 2798 (FLAS, GH, NY, USF). Hernando Co., Pine Is. causeway, Kral 7015 (FLAS, GH, USF). Hillsborough Co., Mullet Key, Long 1264 (USF). NW Tampa, Lakela 25012 (GH). Indian River Co., Vera Beach, Demaree 41973 (SMU). Lee Co., Punta Rassa, Hitchcock 136 (F, GH, MO, NY, US). Standley 265 (F, GH, MO, US). Monroe Co., Big Pine Key, Killip 41804 (F, US); Traverse 715 (GH, SMU, TEX). Flamingo, Traverse 624 (SMU, TEX). Pasco Co., Port Richey Bay, Lakela & Patman 9983 (FLAS, GH, USF). Wakulla Co., Panacea Shores, Henderson 63-1241 (TEX). GEORGIA: Glynn Co., Brunswick, Small s.n. (F, NY). St. Simon's Is., Cronquist 5351 (GH, MO, NY, SMU). McIntoch Co., Sapelo Is., Duncan 20162 (GH, SMU, TEX, UC). LOUISIANA: Cameron Pa., Cameron, Tracy 8664 (F, GH, MO, NY, US). MISSISSIPPI: Harrison Co., Biloxi, Ship Is., Demaree 31909 (F, TEX), 35023 (USF). Jackson Co., Horn Is. Wildlife Refuge, Valentine s.n. (FLAS, SMU). NORTH CAROLINA: Carteret Co., Beaufort, Godfrey 6492 (US); leClair 5863 (NY); Channell & Rock s.n. (GH). Hyde Co., Ocracoke Is., Kearney 2285 (US). south CAROLINA: Charleston Co., McClellanville, Godfrey & Tryon 251 (F, GH, MO, NY, US). Horry Co., Lillte R. Bindge, Bell 7711 (USF). TEXAS: Calhoun Co., Port. Alto, Drushel s.n. (MO). Cameron Co., Boca Chica, Webster & Wilbur 3042 (SMU). Galveston Co., E of Alvin, n = 14₁₁ Raven & Gregory 19413 (TEX). Karnes Co., S of Kenedy, Johnson 960 (SMU). Kenedy Co., El Toro Is., Tharp 49128 (US). Nueces Co., Corpus Christi, Heller 1786 (GH, MO, NY, SMU, US). San Patricio Co., Aransas Pass, Schulz 834 (US). Sinton, Wolcott & Barkley 16-413 (GH, NY, TEX). Webb Co., E of Laredo, Gutierrez 88 (SMU, TEX). Banks of the Pecos, Wright 1407 (GH, MO, NY, US). VIRGINIA: Accomac Co., Chincoteague Is., Eiten 936 (NY). Anne Northland (20) (CH). Co., Lynnhaven Inlet, Randolph 429 (GH).

WEST INDIES. BAHAMAS: Grand Bahama Is., Allen 29 (CH).

2. Borrichia arborescens (L.) DC., Prodr. 5: 489. 1836.

Buphthalmum arborescens L., Syst. Nat., ed. 10. 1227. 1759. Based on Plumier, Pl. Amer. tab. 106, fig. 2. 1756.

Diomedea indentata Cass., Bull. Sci. Soc. Philom. Paris. 1817: 70. 1817.

D. glabrata H.B.K., Nov. Gen. Sp. Pl. 4: 213. 1820. TYPE: Cuba (not seen). Cites Buphthal-mum arborescens L.

D. argentea H.B.K., Nov. Gen. Sp. Pl. 4: 213. 1820. TYPE: Cuba (not seen). Cites Buphthal-mum Peruvianum Lam. and B. lineare Willd. Sensu D.C. pro parte ex syn. B. peruviana and B. lineare.

Buphthalmum canum L'Her. ex Dun. in DC., Prodr. 5: 489. 1836, pro syn.

B. argentea (H.B.K.) DC., Prodr. 5: 489. 1836.

Borrichia glabrata Small, Fl. S.E. U.S. 1263. 1903. TYPE: Florida, Curtiss 1412 (NY, holotype; F, GH, MO, NY, isotypes).

Fruticose perennials to 1.5 m tall, decumbent to ascending, forming clones by rooting or drooping stems and by rhizomes. Leaves succulent, opposite, oblanceolate-oblinear, very shortly petioled, the blade attenuate; juvenile leaves of seedlings glabrous, apically serrate; adult leaves entire, mucronate, 5–10(–15) cm long, becoming reduced in size on higher order branches. Heads solitary, ovate; peduncles 0.5–5 cm long; phyllaries 10–16, the outer in pairs, succulent, ovate-elliptic, obtuse or acute, glabrate or sericeous, 6–9 mm long, the inner

oblance olate acute to rounded, glabrous, 6–9 mm long; receptacle slightly convex, the chaff similar to the inner phyllaries, oblance olate-linear, acute to rounded apically; ray florets pistillate, fertile, yellow, 7–15; disc florets perfect, fertile, yellow, 20–50. *Fruits* (cypsela) black at maturity, 4-angled, traversely depressed obtrullate to rhombic in cross-section, 3.5–5 mm long, pappus a 4-angled united crown, straw colored; heads hemispheric at maturity, dark brown with the apices of the phyllaries and chaff often disintegrating, whole heads disintegrating after one or more seasons. Chromosome number: $n=14_{\rm II}$ (possibly an euploid with 2n=26–30).

DISTRIBUTION AND HABITAT

Borrichia arborescens is common along the rocky coasts and sandy marshes and beaches of the Florida Keys, Bermuda, the West Indies from Jamaica and Guadeloupe northward, and the barrier islands of Belize and the east coast of the Yucatán Peninsula. The species's northern extension in the United States is Miami, Florida. Figure 1 (stars) shows the distribution of Borrichia arborescens based on herbarium collections. In frequently collected areas some symbols have been left out for clarity.

MORPHOLOGICAL VARIATION

Two forms typically occur throughout the range: sericeous individuals with obovate-oblanceolate to oblanceolate leaves and glabrate individuals with similar or more linear leaves. The shape of the leaf varies considerably, even on the same plant in some cases. In the Florida Keys the glabrous form is the only one present, while elsewhere both forms may occur. Field work in the Bahamas indicates that the pubescent form may be an ecotype more adapted to the rocky limestone coasts, while the glabrous form is more common in the mangrove swamp areas and brackish lagoons. This is not absolute though and both forms may occur in most habitats.

Small (1903) segregated the extremely large glabrate-leaved individuals as B. glabrata, but later reconsidered and treated the form merely as a variety. In the Bahamas many plants were found to possess both glabrate and pubescent leaves. Borrichia argentea was the name applied to the other end of the continuum; plants with small, obovate, pubescent leaves. Near George Town, Great Exuma, Bahamas, individuals were found with leaves of the glabrata-type and leaves of the argentea-type. The existence of such populations indicates the existence of a single variable species. I (Semple, 1970) found the same situation for Conocarpus erectus L. and noted the existence of the intermediate forms in Borrichia arborescens. Plants with both glabrous and pubescent leaves have been collected throughout most of the range of the species and such intermediates probably exist everywhere both pure forms do. On Jamaica the pubescent form is dominant and the glabrous form is nearly absent. Some small islands appear to have only one form. This may be due to chance introduction of just the one form, but environmental factors favoring one form may exist. The genetics of the conditions have not yet been studied. One plant grown from seed was observed to cycle between glabrate leaves produced in late winter and spring and pubescent leaves produced in the summer and fall. These observations

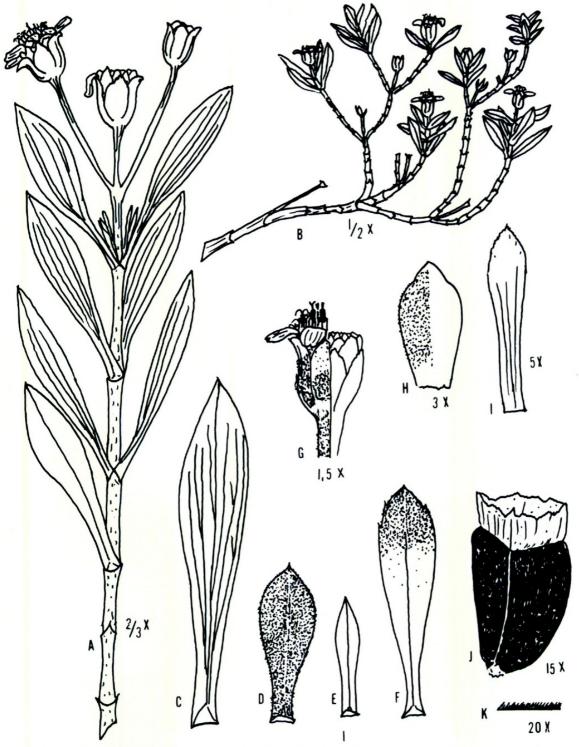


FIGURE 3. Borrichia arborescens (L.) DC.—A. Terminal portion of a young shoot.

—B. Branch from an older procumbent plant.—C-F. Variation in leaf morphology (all the same scale).—C. Glabrous leaf of the glabrata-form.—D. Pubescent leaf of the argentea-form.

—E. Glabrous leaf from an upper branch (pubescent leaves look similar).—F. Juvenile leaf of a plant that later produced pubescent leaves.—G. Head illustrated in flowering condition on the left side and fruiting condition on the right side.—H. Phyllary (one side illustrates location of pubescence when present).—I. Receptacle chaff.—J. Fruit of peripheral floret (central floret fruit similar to Fig. 2H).—K. Leaf surface diagram illustrating nature of pubescence when present on leaves.

were made while the plant was in a greenhouse in Canada, so conditions may be too different from the wild habitat for the observations to be of great significance. The observations do indicate that the nature of the indument can be changed by modification of the environment. Figure 3 illustrates the morphological characteristics of *B. arborescens*.

Belize Glover's Reef, Long Cay, Fosberg & Sachet 53804 (GH, MO). Ambergris Cay on Barrier Reef, Stoddart 445 (UH), 446 (IJ, US). Stamn Creek, Shipp 575 (F, GH, MO, NY).

BERMUDA. Gibbit Is., Collins 304 (F, GH, NY, US), 397 (GH). Hungry Bay, Bailey et al. s.n. (GH). Long Bud Is., Brown 707 (GH, US, NY), 709 (GH, NY). Smith's Parish, Flatts Inlet, Moore 2851 (F, GH, NY). Warwick, Manuel 104 (GH); Robinson 170, 171, 172 (all GH).

MEXICO. QUINTANA ROO: Tancah, Steere 2529 (US). Holbox Is., Gaumer s.n. (US). Cozumel Is., Gaumer 89 (NY).

UNITED STATES. FLORIDA: Dade Co., Coral Gables, King's Bay Country Club, Morton (BUS). Elliott's Key, Caesar's Rock, Britton 370 (F, NY). Small & Nash s.n. (NY). Key Largo, Newport, Eaton 429 (TEX). Traverse 662 (GH, SMU, TEX). Miami, Small & Wilson 1894 (NY). Sands Key, Rodham s.n. (GH). Monroe Co., Bahia Honda, Simpson 365 (F, US). Big Pine Key, Killip 41688 (F); Killip & Swallen 49303 (US); Seibert 1267 (GH, MO). Everglades Natl. Park, Graighead s.n. (GH). Grassy Key, Stern 1482 (GH, US). Key West, Lakela 27823 (GH); Hitchcock s.n. (F). Little Torch Key, D'Arcy 3046 (FLAS). Lower Matecumbe Key, O'Neill 7613 (GH, NY, US); Weber s.n. (FLAS). Marquesas Keys, Lansing 2157 (F, NY). Ragged Keys, Small & Carter 3120 (NY). Torch Key, Curtiss 5436 (GH, MO, NY, US).

WEST INDIES. BAHAMAS: Abaco, Sandy Pt., Proctor 30548 (IJ). Acklin's Is., Brace 4397 (F, NY). Andros Is., Golden Cay, Dawson 26895 (US). Andros Town, Dawson 26622 (US). Bimini, NIS., Howard 10018 (GH, NY, SMU, US). SIS., Port Royal, Rabbit Cay, Gillis 11313, 11314 (both IJ). Caicos, Middle Is., Burch 4293 (NY). Crooked Is., Hitchcock s.n. (MO). Eleuthera Is., the Current, Lewis 7197 (MO, NY). Great Exuma, Jewfish Light Chain, Hummingbird Cay, Nickerson & Kessler 2743 (GH). Grand Turk, East Bay, Proctor 8771 (IJ); Nash & Taylor 3886 (F, NY). Inagua, Sandy Pt., Nash & Taylor 1390 (NY); Dunbar 77 (GH). Mayaguana Is., Abraham Bay, Wilson 7525 (F, GH, NY). New Providence Is., Nassau, Wright 9, 25 (both F, GH, NY). Salt Key Bank, Anguilla, Wilson 8075 (MO, NY), 8107 (F, NY). Watlings Is., Wilson 7288 (F, GH, NY). CAYMAN ISLANDS: Grand Cayman, Armour 1239 (F); Brunt 1687, 1884 (both IJ), 268 (MO, NY); Proctor 11989 (GH). Little Cayman, Kings 40 (MO, NY). CUBA: Camaquey, Cayo Palo, Shafer 2732 (F, NY, US). Cayo Paredon Grande, Shafer 2759 (F, NY, US). Havana, Havana, Curtiss 750 (F, GH, MO, NY, US). Playa de Marianas, León 3713, 5024 (both NY). Isle of Pines, Bibijagua, Jemmings 114 (GH, NY, US). Matanzas, Britton & Shafer 44 (NY). Oriente, S of Cape Cruz, León 16349 (NY). Santiago, Clemente 5318 (NY). Pinar Del Río, Mariel, Palmer & Riley 729 (US). Santa Clara, Cienfuegos, Jack 8304 (US). Gavitán, Howard 4962 (GH, NY). Santiago, Baracoa, Pollard et al. 197 (F, GH, MO, NY, US). HAITI: Bayeux in Dept. du Nord, Eleman 2556 (GH, IJ). Mahautiere, Eyerdam 87 (F, GH, US). La Gonave Is., Bouchia Lagone, Ekman 8688 (F, NY). Tortue Is., La Valle, Leonard 11430 (GH, NY, US). Holdridge 1417 (NY, US). JAMAICA: Bluefields Bay, Harris 9975 (NY, US). Port Antonio, Maxon & Killip 282 (US); Millspaugh 985 (F); Wight 160 (F, NY). Hanover, Esher Cove, Proctor 23470 (IJ). Middlesex Co., Dry Harbour, Hunnewell 11173 (GH). St. Ann's Hall, Fosberg 42686 (US). St. Mary, Port Maria, Proctor 7531 (IJ). Oracabessa, Proctor 6648 (IJ, US). St. Thomas, Holland Bay, Bengry s.n. (FLAS, IJ, MO). Westmoreland, Homer's Cove, Proctor 33070 (IJ). LESSER ANTILLES: Anquilla, Flat Cap Pt., Proctor 17628 (IJ). Antiqua, Mamora Bay, Box 1302 (US). Barbuda, Cowan 1667 (GH, IJ, NY, US). Guadeloupe, Grande Terre, Moule, Proctor 19960 (IJ, US). Marie Galante, Anse Piton, Proctor 21096 (IJ, US). St. Croix, Ricksecker 24 (F, GH, MO, NY, US). Virgin Is., Anegada Is., D'Arcy 4806 (US). PUERTO RICO: Arecibo, Sargent 771 (US, TEX). Guanica, Velez 645 (NY). Salimas de Cabe, Urban 535 (GH, US). San Juan, Underwood & Griggs 916 (NY, US). Is. Culebra, Britton & Wheeler 239 (NY, US). Mona Is., Britton et al. 1765 (NY). Vieques Is., Shafer 2671 (NY, US). SANTO DOMINGO: Barahona, Beata Is., Howard 12422 (GH, US). Trujin, Abbott 1681 (US). Ciudad Trujillo, Allard 14386 (US). Puerta Plata, LaBoca Cliffs, Ekman 14589 (GH, US); Jiménez 4358A (US). San Pedro de Macoris, Rose et al. 4263 (NY, US). Samana Penisula, Cape Samana, Abbott 1188a (US).

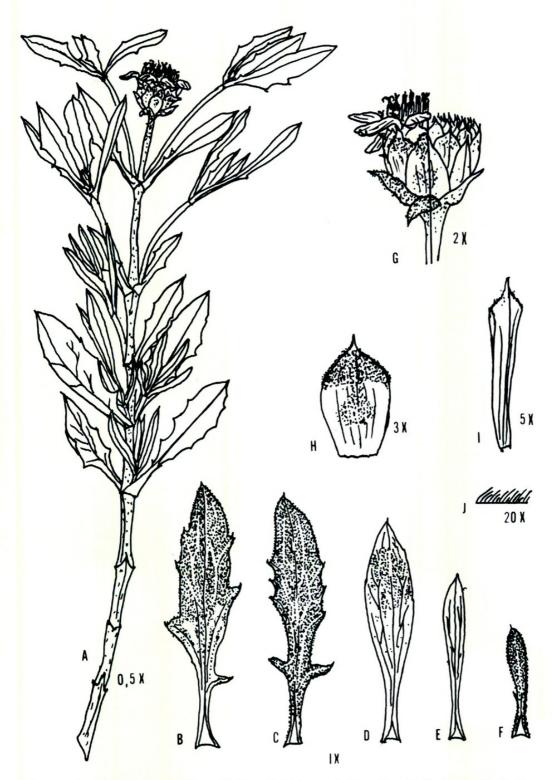


FIGURE 4. Borrichia × cubana Britton & Blake.—A. Branch.—B-F. Range in leaf morphology present on same plant.—B-C. Leaves occurring on primary and secondary stems and branches.—D. Leaf occurring on secondary and higher level branches.—E-F. Leaves occurring on higher level branches.—G. Head illustrated in flowering condition on the left side and fruiting condition on the right side.—H. Phyllary of middle series.—I. Receptacle chaff.—J. Leaf surface diagram illustrating nature of pubescence when present on leaves.

3. **Borrichia** × **cubana** Britton & Blake (pro sp.) stat. nov., Mem. Torrey Bot. Club 16: 116. 1920. TYPE: Cuba, Havana, swamp near Atares Castle, June 1917, *León 7244* (NY, annotated as the holotype by E. K. Schofield, 1973; NY, annotated as isotype by E. K. Schofield, 1973).

Fruticose perennials. Leaves opposite, heteroblastic; primary stem leaves elliptic petiolate, serrate-spinulose along the mid portion of the blade, undulate and coriaceous, more succulent with age; upper branch leaves reduced, sessile, oblanceolate-linear, glabrate to long puberulent. Heads solitary, hemispherical; phyllaries 16–25, in several subequal series, 5–8 mm long, ovate with cuspidate tips, pubescence similar to that of the leaves; chaff slightly folded, oblanceolate cuspidate, but not spinulose, equal to the bracts in length; ray florets pistillate, apparently fertile, yellow, 14–25; disc florets perfect, apparently fertile, yellow, 25–60. Fruit (cypsela) black at maturity, 4-angled, traversely depressed obtrullate to rhombic in cross-section, 3–5 mm long; head brown to black at maturity, hemispheric; phyllaries not thickening with age. Chromosome number: $n = 14_{\rm H}$; Semple (1978) described meiosis in the hybrids.

Detailed experimental and field observations that support the status change of this taxon from that of species to a hybrid between B. frutescens and B. arborescens were given by Semple & Semple (1978). In the protologue Britton noted that he thought that $B. \times cubana$ was closely related to B. frutescens. The plants are intermediate in nearly all characters between the two parental species. The bracts are large like B. arborescens and cuspidate, which is intermediate between the acute arborescens condition and the spinulose frutescens condition. The hybrids are common in the Florida Keys, the only area where the two parent species are normally sympatric. No hybrids have yet been collected from Bermuda, but they may be present since both parents occur there. There appears to be, or has been, only one population of hybrids in Cuba—namely, the type locality from which several collections were made in 1917 and 1921 (León 6870, 7244 and Ekman 13292, respectively). The latter is a mixed collection of specimens appearing to be $B. \times cubana$ and some B. frutescens and may represent a sample of a hybrid swarm. It is possible that Ekman sampled the actual parent involved in the cross, but this can not be proven.

Experimental crosses were made between B. frutescens and B. arborescens. The F_1 progeny were morphologically similar to cuttings of B. \times cubana collected in Florida. Figure 4 illustrates the intermediate morphological condition of B. \times cubana.

Cuba. наvana: Castillo de Etares, Ekman 13292a (GH, NY, MO, US); León 6870 (NY).

UNITED STATES. FLORIDA: Dade Co., Adams Key, Small & Mosier 5736 (USF). Coral Gables, King's Bay Country Club, Semple 1698 (MO, US, WAT). S of Elliott's Key, Caesar's Rock, Britton 369 (F, NY). E of Gould, Black Point, Semple 1709 (CAN, MO, WAT, US). Miami, MacArthur Causeway, Semple 1703 (MO, US). Sands Key, Semple 1700-6 (MO, US). Monroe Co., Big Pine Key, Cornman 2111 (MO); Seibert 1270 (GH, MO); Semple 1737 (MO, US, WAT). Craig Key, Semple 1755 (MO, US). Key West, Small & Small 4911 (GH, US). Long Key, Long et al. 2249 (USF). Lower Matecumbe Key, Semple 1719 (MO, US). Marquesas Group, Man Key, Lansing 2360 (F, NY). Woman Key, Lansing 2420 (F). Saddle Bunch Keys, Semple 1734 (MO, US).



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