

FINDING *BOLTONIA DIFFUSA* (ASTERACEAE: ASTEREA)

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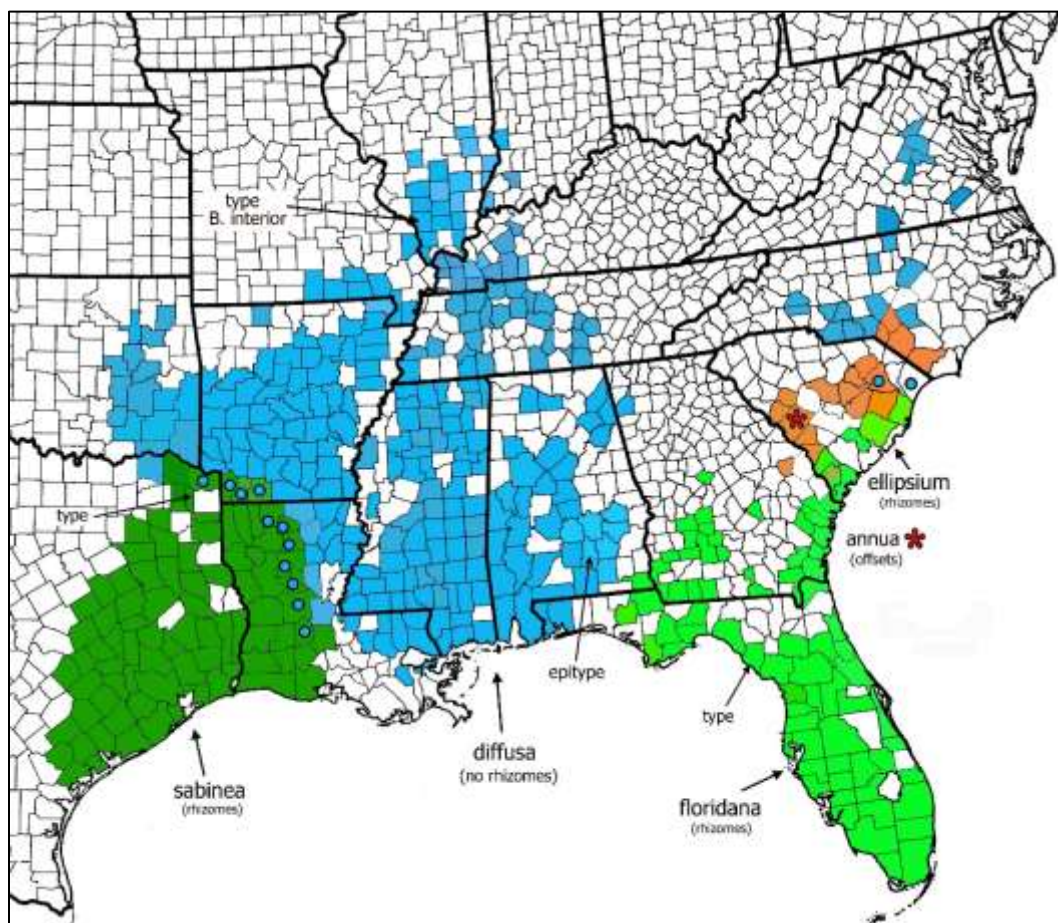
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ABSTRACT

Boltonia diffusa, as previously construed, is interpreted here as three separate species: *B. diffusa* sensu stricto (including var. *interior*), ***Boltonia sabinea* Nesom, sp. nov.**, and ***Boltonia floridana* Nesom, sp. nov.** *Boltonia sabinea* and *B. floridana* are rhizomatous, *B. diffusa* sensu stricto not. *Boltonia diffusa* is adventive on the Atlantic seaboard.

Boltonia diffusa Elliott has been seen as a wide-ranging species the south-central USA (e.g., Karaman-Castro & Urbatsch 2006; Map 1) recognized by a paniculate to subcorymboid inflorescence of small heads on long, multibracteate peduncles. The taxonomic approach here in dividing *B. diffusa* sensu lato into separate species is based on mapping that shows morphologically distinct subentities to be allopatric (from parapatric to disjunctly separate).



Map 1. Distribution of *Boltonia diffusa* sensu stricto and segregate species. *Boltonia diffusa* is adventive on the Atlantic seaboard (South Carolina, North Carolina, Virginia). *Boltonia diffusa* is closely parapatric with *B. sabinea*, less closely with *B. floridana*. *Boltonia ellipsium*, *B. annua*, and *B. angustifolia* (described in a separate manuscript) have an aspect similar to *B. diffusa*.

Geographic, morphological, and ecological criteria support the treatment of *Boltonia diffusa*, *B. sabinea*, and *B. floridana* as species. Differences in habitat seem to be subtle or non-existent and geographic barriers are not evident among these three entities. Involucral size, phyllary morphology, and achene morphology are useful in distinctions but are variable. The most diagnostic feature of difference is the production of rhizomes, which apparently is evolutionarily labile within the genus but constant (present or not) within a species. In any case, rhizome production presumably is associated with a suite of biological features different from those in a non-rhizomatous plant.

A chromosome number of $2n=18$ has been reported for *Boltonia diffusa* sensu stricto, *B. sabinea*, and *B. floridana* (summary in Nesom 2026).

Apart from rhizome production, subtlety of morphological difference among these geographic entities accounts for their lack of previous recognition, but a plant in this group with fully represented features (base, inflorescence, involucre, fruits) usually can be identified without knowledge of its geography.

1. Rhizomes absent; rays 28-35; phyllaries in 3-4(-5) series of unequal length, midline distinctly broadening distally; achenes 1.3-1.5 mm long ***Boltonia diffusa***
1. Rhizomes present; rays 14-28; phyllaries in 2-3 series of equal to subequal length, midline not broadening distally; achenes 1.6-2 mm long ***Boltonia sabinea***
1. Rhizomes absent; peduncles with 5-8 bracts; phyllaries in 3-4(-5) series of unequal length, midline distinctly broadening distally; rays 28-35, consistently white; achenes 1.3-1.5 mm long ***Boltonia diffusa***
1. Rhizomes present; peduncles mostly with 1-3(-5) bracts; phyllaries in 2-3 series of equal to subequal length, midline not broadening distally; rays 18-25, white to blue or lavender; achenes 0.5-0.8 mm long ***Boltonia floridana***

1. **BOLTONIA DIFFUSA** Elliott, Sketch Bot. S. Carolina 2: 400. 1823. **TYPE:** Protologue: "Grows in damp rich soils between the Chatahouchie and Alabama," noted by Fernald (1940) to be "somewhere between southwestern Georgia and northwestern Florida and western Alabama." Specimen with no collection information (possible holotype: CHARL-Elliott Herbarium). Map 2 shows the area between the Alabama and Chattahoochee rivers (which is in Alabama) — an epitype is designated and the locality marked on the map.

EPITYPE (designated here): **Alabama**. Crenshaw Co.: 20.2 mi E of Georgiana by Hwy 106, Patsulga [Patsaliga] Creek [31.5956 N, 86.4042 W], recently logged bottoms of creek, moister sandy disturbed areas along small branch, 26 Sep 1999, R. Kral 88968 (USCH; isoeotypes: NLU, VDB).

Boltonia interior (Fernald & Griscom) G.N. Jones in Jones & Fuller, Vasc. Pl. Illinois, 478. 1955. *Boltonia diffusa* var. *interior* Fernald & Griscom, Rhodora 42: 490. 1940. **TYPE:** **Illinois**. [Jackson Co.]: De Soto, Aug 1862, G. Vasey s.n. (holotype: GH 02215292). Figure 5.

Fernald's concept (1940) of typical *Boltonia diffusa* was of rhizomatous plants ("from subterranean rhizomes and stolons") — his concept of var. *interior* contrasted especially in its lack (usually) of rhizomes ("plerumque estolonifera"). Thus his var. *interior* is equivalent to what is here considered typical *B. diffusa* and the significance of rhizome production is clarified here with the recognition of *B. sabinea* and *B. floridana*.

Among the paratypes of var. *interior*, as identified here:

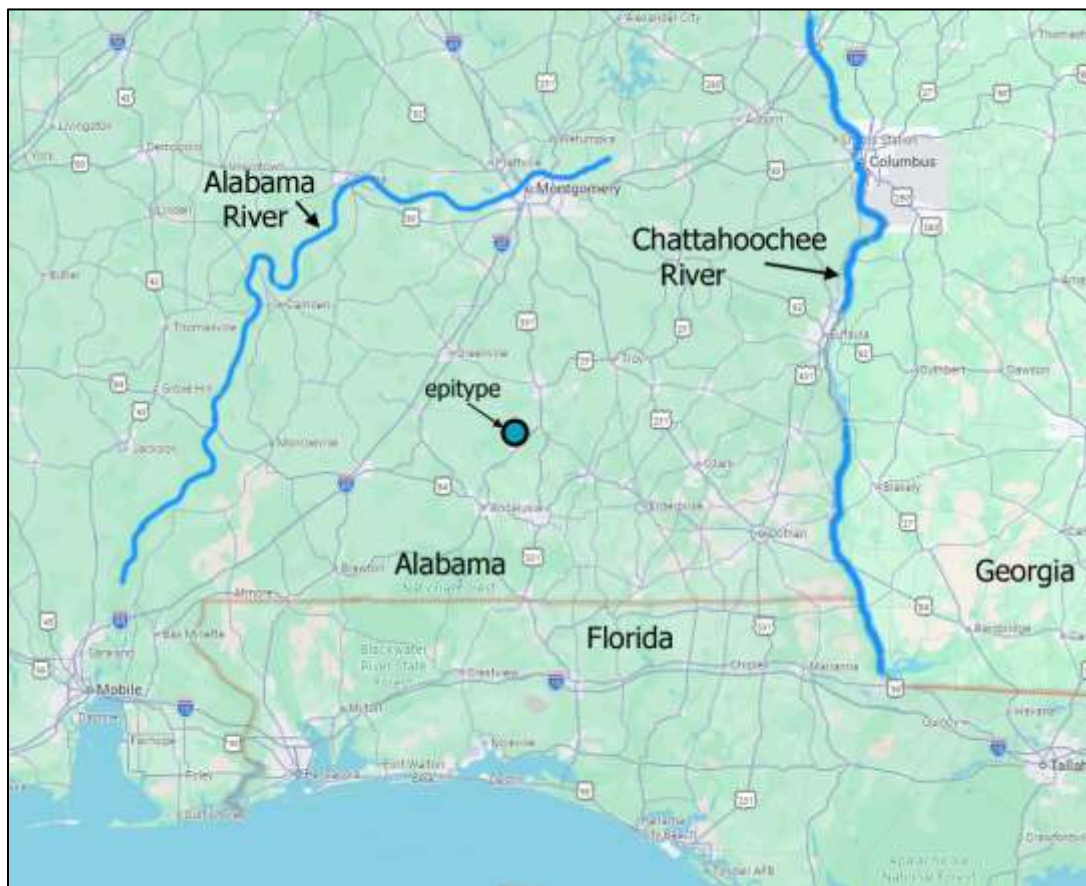
B. diffusa — *Donnell Smith* s.n. (GH; Mississippi); *Tracy & Lloyd* 485 (GH; Mississippi); *Demaree* 8786 (GH, NY; Arkansas); *Demaree* 10858 (BUT, GH, NY, SD; Arkansas); *Smith & Hodgdon* 4078 (GH; Kentucky); *Svenson* 4257 (GH; Tennessee).

B. sabinea — *Heller* 4229 (GH, NEB, NY; Miller Co., Arkansas). Clearly rhizomatous.

B. latisquama — *Stevens* 2094 (GH, OKL, OKLA; Washington Co., Oklahoma).

Herbaceous perennials, glabrous, fibrous-rooted, without rhizomes, sometimes with sessile basal offsets. **Stems** 60–120 cm, not fistulose. **Leaves**: basal and lower cauline deciduous by flowering, cauline mostly narrowly elliptic-oblongate, 4–11 cm long, 4–15 mm wide, gradually smaller up to the heads, then bracteate. **Inflorescence** corymboid to subcorymboid, subcorymboid-paniculate, or paniculate, heads essentially solitary or usually on peduncles (1–)2–5(–8) cm long, with 5–8 minute bracts. **Receptacles** low-conic. **Involucres** 3.5–5 mm wide (pressed); phyllaries narrowly oblong, in 3-4(–5) series of unequal length, inner 2–2.5 mm long, outermost grading into subtending bracts, dark midregion widening distally, base and margins whitish, apex acute to acute-acuminate, not apiculate. **Ray flowers** 28–35, 5–6 mm long, **Disc corollas** 1.5 mm long. **Achenes** 1.3–1.5 mm long, ray achenes sometimes 3-nerved and 3-winged, shoulders rimmed by oil tubes, awns 1.3–1.5 mm long, usually absent on ray achenes. **Chromosome number**, $2n=18$.

Flowering August–October. Prairies, fields, edges of pine and oak-hickory woods, clearcut woods, roadsides, power line ROWs, flood plains, seasonally wet depressions, ditches, creek banks, spoil banks.



Map 2. *Boltonia diffusa* sensu stricto — epitype locality (Crenshaw Co. Alabama), between the Alabama and Chattahoochee rivers.

***Boltonia diffusa* adventive on the Atlantic seaboard.** **North Carolina.** Alamance Co.: Cane Creek Mountains Natural Area, along abandoned road between Longleaf Loop Trail and base of mountain, open sunny area, 26 Sep 2021, *McCormick s.n.* (NCU). Cabarrus Co.: [near Stanfield], W side of Mt. Pleasant Road (State Rd 1006), ca. 0.75 m S of Joyner Road (State Rd 1105), moist low area, 29 Sep 1998, *Soule & Gaffney s.n.* (UNCC). Catawba Co.: Kale Road, 100 meters N of Long Bay Parkway, in the power line right-of-way beside the road, with *Silphium compositum*, *Liatris graminifolia*, *Liatris squarrosa*,

Helianthus microcephalus, *Angelica venenosa*, *Crotalaria sagittalis*, *Cassia nictitans*, 8 Aug 2010, Holdsclaw 269 (NCU). Lincoln Co.: Campground Road, 0.5 km E of Pine Ridge Drive, across the road from Bethel United Methodist Church, power line right-of-way, with *Rubus argutus*, *Erianthus contortus*, *Solidago nemoralis*, *Solidago arguta*, *Cassia fasciculata*, *Aster dumosus*, *Lespedeza procumbens*, 24 Aug 2010, Holdsclaw 296 (NCU). Moore Co.: Whispering Pines, Weymouth Woods Sandhills Nature Preserve, 8 Oct 1972, Carter 266 (WEWO); 3 mi WNW of Whispering Pines on Hwy 22, damp pasture, 16 Sep 1973, Carter 929 (WEWO); Little River upstream of Ray's Bridge Road, disturbed floodplain of blackwater stream, abundant in old clearing beside small road, with *Quercus nigra*, *Pinus taeda*, *Liquidambar styraciflua*, *Rubus arguta*, *Symphyotrichum dumosum*, 21 Aug 2007, Sorrie 12003 (NCU-2, US); S of Cool Springs Road, powerline at floodplain of McLendons Creek, occasionally cut swath through broad floodplain of brownwater creek, common, 13 Oct 2018, Sorrie 13679 (NCU); Person Co.: Ca. 8 mi NE of Roxboro, Mayo Reservoir at boat access ramp at the terminus of Hwy 1515 on the E side of the reservoir, woods and cut-over opening, 9 Oct 1994, Wilbur 63029 (DUKE). Richmond Co.: E side of Pee Dee River, N of Hwy 74 boat launch parking lot, disturbed clearing of powerline near river, rare, with *Acalypha rhomboidea*, *Sida spinosa*, *Eupatorium serotinum*, *Carex typhina*, *Carex corrugata*, saplings of oaks, hickories, hackberry, boxelder, green ash, 19 Aug 1999, Sorrie 10279 (NCU-2). Stanly Co.: 0.4 mi NNE of Palestine, roadside ditch on woodland border, 24 Sep 1956, Ahles 19986 (GA, GH, NCU). Union Co.: Indian Trail-Fairview Road, midway between Hwy 1514 and 1526, roadside powerline, dry to wet, scattered, with *Solidago rugosa* var. *celtidifolia*, *Rudbeckia fulgida*, *Symphyotrichum dumosum*, 17 Aug 2010, Sorrie 12653 (NCU). Wake Co.: between Raleigh and Garner, roadside banks and ditches, very abundant in an old field, 7 Sep 1950, Godfrey 50504 (BRY, DUKE, GH, IND, NCSC, PAC, US-2); Hwy 1172 (Old Smithfield Rd) 0.35 mi W of Hwy 55 (Feltonville), roadside grassland, perhaps remnant of previous fire-maintained grassland, now bordered by shortleaf and loblolly pine/oak forest, 11 Oct 1996, McMillan 1963 (NCSM). **South Carolina.** Beaufort Co.: Near Big Estate community, Sugar Hill Boat Landing, off of River Road, with *Eupatorium serotinum*, *Apios americana*, *Verbena scabra*, *Persicaria arifolia*, *Murdannia keisak*, *Leersia virginica*, *Bidens laevis*, *Aeschynomene indica*, 2 Oct 2005, Payne 3910 (CLEMS). Berkeley Co.: N side of Lake Moultrie and S of Pineville, Sandy Beach Waterfowl Management Area, occasional on boggy peaty ground of open impoundment, 6 Sep 1991, Nelson 11326 (USCH); Dean Hall Plantation, west branch of Cooper River, abandoned rice fields/fresh water marsh, 2 Oct 1982, Porcher 2056 (CLEMS). Dorchester Co.: 0.1 mi N of Colleton Co. line on Hwy 15, marsh of Edisto River, 2 Oct 1967, Bozeman 11562 (ASPC, BALT, BOON, BRY, CLEMS, ECUH, ERSK, FUGR, KE, MEM, MUR, NCSC, NCU, NLU, PEMB, UNCC, USAM, WWC). Florence Co.: 2 mi SW of Effinham, roadside at jct of Hwy 147 and LRSP Road, 26 Sep 1985, Swails 85/379 (FMUH). Georgetown Co.: Brookgreen Gardens, 30 Sep 2000, Nelson 21646 (LSU-4, USCH). 3.5 mi SSE of Outland [on SC Hwy 261, Hemingway Hwy/Choppee Rd], near SC Hwy 513 [Pleasant Hill Drive], fresh-water marsh, 23 Aug 1957, Radford 28622 (FSU, NCU, USF, see comments below). Hampton Co.: Lake Warren State Park, low margin, 14 Oct 1988, Batson s.n. (USCH). Jasper Co.: Jasper State Park, wet ditch bank, 15 Oct 1988, Batson s.n. (USCH). Horry Co.: Waccamaw River Heritage Preserve, just W of East Bear Grass Rd, ca. 2.4 km S of Chestnut Crossroads, recently cleared mitigation/restoration site, with dense *Kelloggloa verrucosa*, *Scirpus cyperinus*, 29 Aug 2019, Bradley 10172 (USCH). **Virginia.** Cumberland Co.: Ca. 5 mi N of Farmville, Small colony on roadside adjacent to clearcut along Hwy 45, 16 Sep 2005, Fleming 15333 (VPI). Fluvanna Co.: Careysbrook, Hwy 15 between Rte 615 and Fluvanna Middle School, damp, weedy and scrubby swale along abandoned C&O railroad R-O-W, 310 ft, common, 12 Sep 1993, Fleming 8618 (GMUF, LYN, VPI) and 19 Sep 1993, Fleming 8687 (FARM, GMUF, WILLI); 1.8 mi SSE of Kents Store, Hwy 604, 1.2 mi NE of Hwy 610, damp swale in pipeline clearing, just S of Hwy 604, 390 ft, ca. 6 large clumps, local, 19 Sep 1995, Fleming 11345 (GMUF, WILLI); Carysbrook, W side of Rte 615, 0.3 mi N of jct with Hwy 15, scores of plants along open fencerow, 300 ft, with *Sorghastrum nutans*, *Andropogon*, *Solidago*, 10 Oct 1993, Stevens 23982 (FARM, VPI). Goochland Co.: 2.0 mi NW of Shannon Hill, in NW corner of county, just E of jct Hwy 250 and Hwy 653, 37.901887 N, 78.063669 W, powerline ROW, 290 ft, 27 Sep 2021, Fleming 18902 (GMUF, VPI) and 30 Aug 2021, Fleming 18792 (GMUF, VPI). Halifax Co.: 3.5 mi NE of South Boston, JH Kerr-Wolf Trap WMA, colony in weedy clearing along WMA road, W of the Banister River, 7 Aug 1997, Fleming 13708 (GMUF). Louisa Co.: 1.6 mi S of Quail, E side of Rte 683, at sharp bend 0.3 mi S of Fork Creek, seasonally wet depression in cutover woods, 450 ft, colony of ca. two dozen plants, local, 21

Sep 1996, *Fleming 12532* (GMUF, VPI, WILLI); 1.25 mi WNW of Mineral, Louisa County Public School property, powerline ROW, SW of its intersection with Hwy 33 and W and SW of the Louisa Co. school complex, 38.014029 N, 77.931668 W, damp to dry habitats in ROW, 400 ft, abundant, thousands of plants here, certainly one of the largest populations of this species known in Virginia, 19 Sep 2021, *Fleming 18870* (GMUF). Orange Co.: Jct of Hwy 691 and the powerline, roadside, 26 Sep 1999, *Williams 190* (GMUF). Sussex Co.: 4.5 mi W of Wakefield, N of Hwy 604, ca. 1.0 mi NE of jct with Hwy 606, Nature Conservancy Piney Grove Preserve, 36.97021739 -77.0771638, locally common in dry area of an open, savanna-like pine woodland managed by prescribed fire, 24 Sep 2019, *Fleming 17443* (GMUF, WILLI).

Plants of *Radford 28622* (FSU, NCU, USF) from Georgetown Co., South Carolina, are unusual, although identified here as *Boltonia diffusa* (Figs. 6, 7). The non-rhizomatous base and paniculate inflorescence with multibracteate peduncles are like *B. diffusa*, but the heads are smaller (inner phyllaries 1.8–2.2 mm long vs. 2–2.5 mm), achenes longer (1.8–2 mm long vs. 1.3–1.5 mm), and pappus of disc florets mostly just a crown, the outer florets also with awns. Three plants are represented — the FSU specimen was found by Anderson (1987) to have 7% pollen fertility, and mature achenes of the NCU specimen are sterile (normal size but unfilled) (pers. observ.).

A collection from eastern Alabama has small heads like *Boltonia diffusa*, ebracteate peduncles like *B. apalachicolensis*, and long rhizomes — Oktibbeha Co.: 5 mi W of Starksville, infrequent, 1 Aug 1956, *Ray 7347* (NCU); rhizomes are not apparent on *Ray 7347* (USF). *Folk 335* (MISSA) from Oktibbeha Co. is *B. apalachicolensis*, as correctly identified by the collector. Other collections from Oktibbeha Co. (via SERNEC) are *B. diffusa*.

2. BOLTONIA SABINEA Nesom, **sp. nov.** **TYPE: Texas.** Morris Co.: Daingerfield State Park, low moist grounds, 6 Sep 1947, *E. Whitehouse 19158* (holotype: SMU; isotypes: NY, US).

Similar to *Boltonia diffusa* in inflorescence of small heads on long, multibracteate peduncles and short-awned achenes; different in its rhizomatous habit, phyllaries in equal to subequal series, the dark midline not broadened distally, fewer ray florets, and longer achenes.

Herbaceous perennials, glabrous, fibrous-rooted, rhizomatous. **Stems** 60–150 cm, not (or rarely) fistulose. **Leaves**: basal and lower cauline (or often all leaves) deciduous by flowering, cauline mostly narrowly oblong-elliptic to oblong-lanceolate, mostly 4–8 cm long, 4–10(–15) mm wide, bracteate in the inflorescence. **Inflorescence** corymboid to subcorymboid, subcorymboid-paniculate, or paniculate, heads essentially solitary or usually on peduncles (0.5–)1.5–5 cm long, with 2–8 minute bracts. **Receptacles** low-conic. **Involucres** 3–4.5 mm wide (pressed); phyllaries narrowly oblong, in 2–3 series of equal to subequal length, inner 2–2.5 mm long, dark midregion narrowly oblong to oblanceolate and even in width, margins prominent whitish, apex acute to acute-acuminate, not apiculate, outer grading into peduncle bracts. **Ray flowers** 14–28, 3.5–6 mm long, **Disc corollas** 2 mm long. **Achenes** 1.6–2 mm long, sometimes 3-nerved and 3-winged, shoulder and apex rimmed by an oil tube, awns ca. 1 mm long, absent on ray achenes. **Chromosome number**, $2n=18$.

Flowering (July-) August–October (-November). Floodplains and terraces, around bogs, ponds, and borrow pits, roadsides, ditches, sandy ravines, coastal prairie, pine flatwoods, post oak woods and savannas, pine-oak woods, black clay, sandy clay, sandy loam, clay loam.

Boltonia sabinea is variable in inflorescence structure and has a wide tolerance in habitat, but there are no morphological discontinuities within the range mapped here and its distribution is similar to other West Gulf Coastal Plain endemics (Sorrie & Weakley 2001).

Distinctions between *Boltonia sabinea* and *B. diffusa* are subtle, and where they appear to be closely parapatric in Louisiana and Arkansas (Map 1), unequivocal identifications should rely on the presence/absence of rhizomes.

Wet habitats of other *Boltonia* along the coast of Louisiana (Vermilion and Cameron cos.) and adjacent southeastern Texas (Chambers Co.) seem unusual for *B. sabinea*. Two collections from wet prairie in Cameron Parish have an aspect like *Boltonia diffusa* — with abundant distal cauline leaves and a corymboid to subcorymboid inflorescence of few heads on ebracteate peduncles — but they are rhizomatous (the root sometimes cylindric-obconic (carrot-shaped) and densely fibrous-rooted) and the heads are larger and the rays atypically long compared to typical *B. sabinea*. They perhaps are phenotypic responses to the habitat but need further study.

Cameron Parish.: Cameron Prairie Wildlife Refuge, wet prairie west of the refuge headquarters [ca. 29.98 N, 93.10 W], 21 Oct 1999, *Hunter 11* (LSU); ca. 12 mi W of Hackberry, via private roads, 29.996593 N, 93.557674 W, historically grazed wet coastal prairie, burned 30 Jan 2015, common in wet inter-mound flat with *Spartina patens*, *Paspalum urvillei*, *Tridens strictus*, *Andropogon glomeratus*, *Iva annua*, *Acmella oppositifolia*, *Symphyotrichum divaricatum*, *Bidens*, 12 Oct 2015, *Reid 9553* (LSU).

3. BOLTONIA FLORIDANA Nesom, **sp. nov.** **TYPE: Florida.** Highlands Co.: Venus, abundant in shallow marshes and ditches on low pinelands and prairies, 7 Nov 1945, *L.J. Brass 15665* (holotype: FLAS; isotypes: ARCH, GH, US, USF).

Similar to *Boltonia diffusa* sensu stricto in relative openly branched inflorescence, small heads, and short awns; different in its rhizomes, more diffuse (paniculate) inflorescence, few peduncular bracts, longer inner phyllaries, fewer rays, and shorter achenes. Different from *B. ellipsium* in its shorter peduncles with fewer bracts and emerging at wide angles (divaricate), and smaller achenes (1–2 mm long vs. 2–2.5 mm).

Herbaceous perennials, fibrous-rooted, glabrous, with thin rhizomes up to 12 cm long, not producing leaves during flowering. **Stems** 50–200 cm high, 1-numerous from the base, not fistulose. **Leaves:** basal absent at flowering, cauline often all deciduous; lower and midcauline narrowly elliptic, 5–7 cm long, 4–7 mm wide, relatively even-sized up to the inflorescence, then becoming bracteate. **Inflorescence** initially paniculate but becoming corymboid as secondary heads develop distally, heads solitary or usually on divaricate to acute-ascending peduncles 2–8 cm long, peduncles mostly with 1–3(–5) minute bracts. **Receptacles** low-conic. **Involucres** 3.5–4 mm wide (pressed); phyllaries narrowly oblong-lanceolate, in 2–3 series of equal to subequal length, inner 2–2.5 mm long, with a dark, linear-oblong midzone not broadening distally, apex lance-acute, outermost grading into peduncle bracts. **Ray flowers** 18–25, corollas 6–8 mm long, white or often blue to violet. **Disc corollas** 1.5–1.8 mm long. **Achenes** obtriangular-obovate with narrow whitish margins, 1–2 mm long; awns ca. 0.5–0.8 mm long. **Chromosome number**, $2n=18$.

Flowering (August-) September–November (-December). Pine and pine-saw palmetto flatwoods, cypress domes, marshy pond and lake shores, grass-sedge bogs, ditches and swales, low roadsides and other disturbed sites, fire lanes, borrow pits.

Boltonia floridana is allopatric with (south of) *B. ellipsium* (also rhizomatous) and in a different habit, thus should not be confused. At the western tip of the Florida peninsula and adjacent Alabama, where *B. floridana* occurs in close proximity to *B. diffusa*, presence/absence of rhizomes provides an unequivocal identification.

***Boltonia floridana* in South Carolina.**

Beaufort Co.: Near Big Estate community, Sugar Hill Boat Landing, off of River Road, with *Eupatorium serotinum*, *Apios americana*, *Verbena scabra*, *Persicaria arifolia*, *Murdannia keisak*, *Leersia virginica*, *Bidens laevis*, *Aeschynomene indica*, 2 Oct 2005, *Payne 3910* (CLEMS). Berkeley Co.: N side of Lake Moultrie and S of Pineville, Sandy Beach Waterfowl Management Area, occasional on boggy peaty ground of open impoundment, 6 Sep 1991, *Nelson 11326* (USCH); Dean Hall Plantation, west branch of Cooper River, abandoned rice fields/fresh water marsh, 2 Oct 1982, *Porcher 2056* (CLEMS). Dorchester Co.: 0.1 mi N of Colleton Co. line on Hwy 15, marsh of Edisto River, 2 Oct 1967, *Bozeman 11562* (ASPC, BAL, BOON, BRY, CLEMS, ECUH, ERSK, FUGR, KE, MEM, MUR, NCSC, NCU, NLU, PEMB, UNCC, USAM, WWC). Georgetown Co.: Brookgreen Gardens, 30 Sep 2000, *Nelson 21646* (LSU-4,

USCH). Hampton Co.: Lake Warren State Park, low margin, 14 Oct 1988, *Batson s.n.* (USCH). Jasper Co.: Jasper State Park, wet ditch bank, 15 Oct 1988, *Batson s.n.* (USCH).

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Figure 1. *Boltonia diffusa*. Crenshaw Co., Alabama, Kral 88968 (USCH). Epitype.



Figure 2. *Boltonia diffusa*. Crenshaw Co., Alabama, Kral 88968 (VDB). Iso-epitype.



Figure 3. *Boltonia diffusa*. Crenshaw Co., Alabama, Kral 88968 (NLU). Iso-epitype.



Figure 4. *Boltonia recognita*. Cook Co., Illinois, Burnham s.n. (GH). Holotype of *Boltonia latisquama* var. *microcephala* (= *B. latisquama*). The aspect is similar to the type of *B. diffusa* var. *interior* (Fig. 5) but they differ in features of the involucre and fruit.



Figure 5. *Boltonia diffusa*. De Soto [Jackson Co.], Illinois, G. Vasey s.n. (GH). Holotype of *Boltonia diffusa* var. *interior*.



Figure 6. *Boltonia* aff. *diffusa*. Georgetown Co., South Carolina, Radford 28622 (USF). Sterile fruits, see text comments.



Figure 7. *Boltonia* aff. *diffusa*. Detail from Radford 28622 (see Fig. 6).

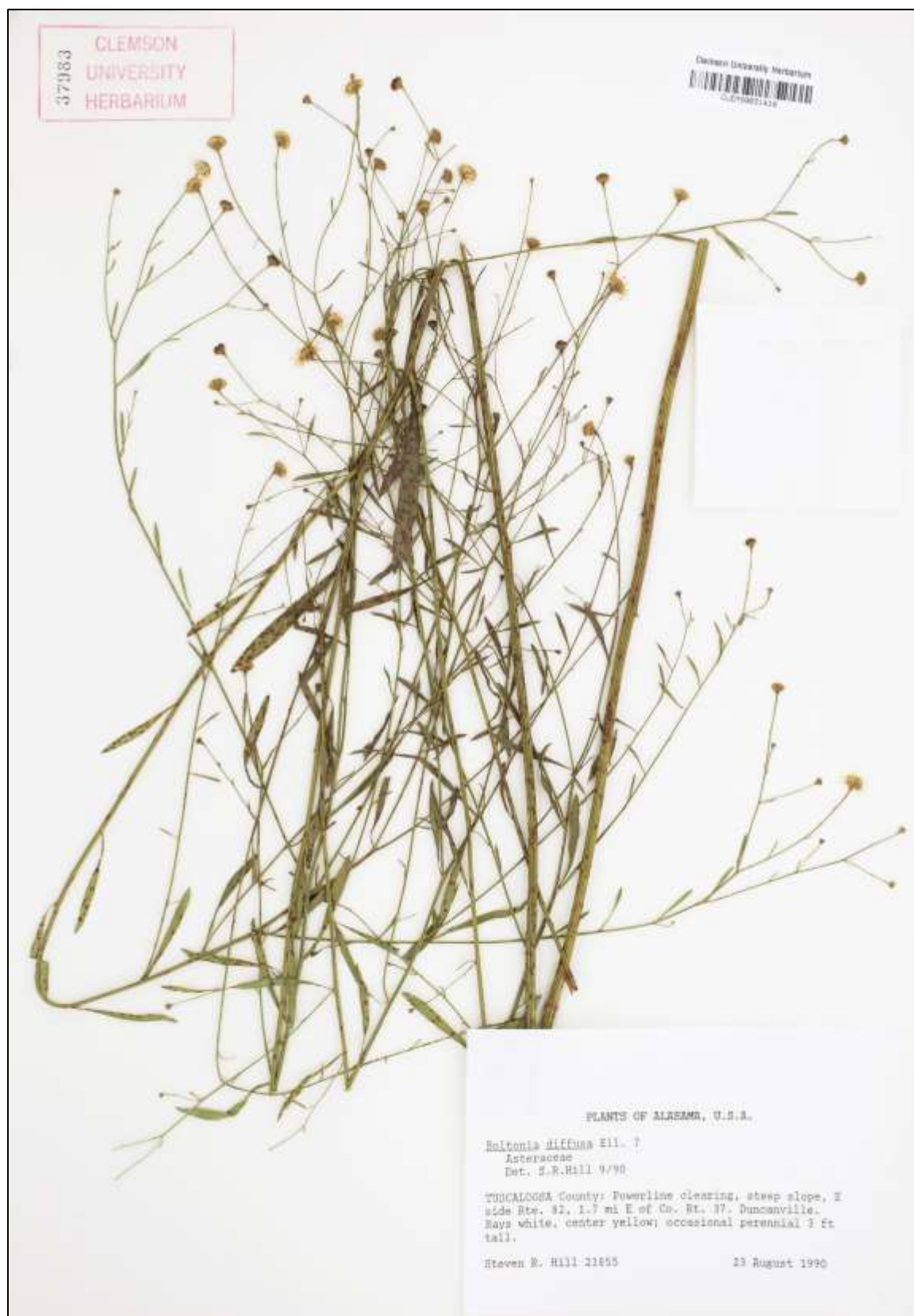


Figure 8. *Boltonia diffusa*. Tuscaloosa Co., Alabama, Hill 21855 (CLEMS).



Figure 9. *Boltonia diffusa*. Butler Co., Alabama, *Diamond 21002* (TROY).



Figure 10. *Boltonia diffusa*. Ouachita Par., Louisiana, Thomas 93766 (KANU).



Figure 11. *Boltonia diffusa*. Chicot Co., Arkansas, Demaree 67596 (WILLI).



Figure 12. *Boltonia diffusa*. Little River Co., Arkansas, Miller 522b (UARK).

Figure 13. *Boltonia diffusa*. Monroe Co., Arkansas, Soteropoulos 18-0757 (STAR).



Figure 14. *Boltonia diffusa*. Coal Co., Oklahoma, Taylor 20869 (DUR).



Figure 15. *Boltonia diffusa*. Marshall Co., Kentucky, Medley 14767 (APSC).



Figure 16. *Boltonia diffusa*. Lawrence Co., Illinois, Hill 39101 (UMVT).



Figure 17. *Boltonia diffusa*. Hinds Co., Mississippi, Temple 14011 (MISS).

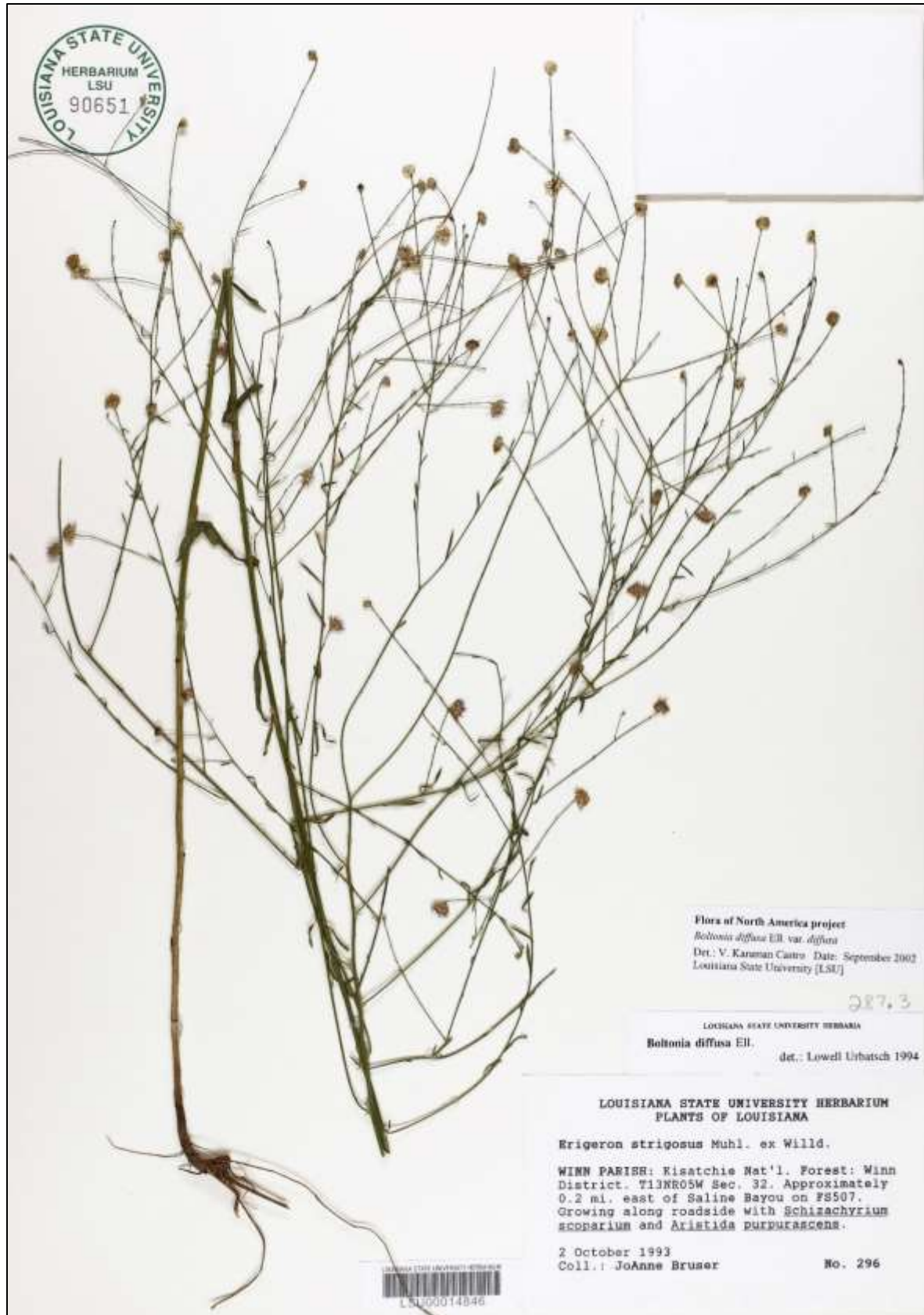


Figure 18. *Boltonia sabinea*. Winn Par., Louisiana, Bruser 296 (LSU).



Figure 19. *Boltonia sabinea*. Caddo Par., Louisiana, Raven 20385 (DS). Voucher for $2n=9$.



Figure 20. *Boltonia sabinea*. Morris Co., Texas, Whitehouse 19158 (SMU).

Figure 21. *Boltonia sabinea*. Bowie Co., Texas, Correll 24784 (LL).



Figure 22. *Boltonia sabinea*. Brazoria Co., Texas, Rosen 3106 (BRIT).



Figure 23. *Boltonia sabinea*. Brazoria Co., Texas, Rosen 3130 (BRIT).



Figure 24. *Boltonia sabinea*. Harris Co., Texas, Turner 4606 (TEX). Voucher for n=9.



Figure 25. *Boltonia sabinea*. Galveston Co., Texas, Turner 1898 (SMU).



Figure 26. *Boltonia sabinea*. Titus Co., Texas, Whitehouse17736 (SMU).



Figure 27. *Boltonia floridana*. Dixie Co., Florida, Anderson 12378 (USCH).



Figure 28. *Boltonia floridana*. Lanier Co., Georgia, Orzell 17652 (GA).



Figure 29. *Boltonia floridana*. Charlotte Co., Florida, Baltzell 7872 (FLAS).



Figure 30. *Boltonia floridana*. Highlands Co., Florida, Brass 15665 (US).



Figure 31. *Boltonia floridana*. Leon Co., Florida, Godfrey 73049 (TTRS).



Figure 32. *Boltonia floridana*. Baker Co., Georgia, Godfrey 82463 (TTRS).



Figure 33. *Boltonia floridana*. Sumter Co., Georgia, Norris 6553 (BRY).



Figure 34. *Boltonia floridana*. Jefferson Co., Florida, Godfrey 65993 (FLAS).



Figure 35. *Boltonia floridana*. Leon Co., Florida, Godfrey 52508 (DUKE).