

**BOLTONIA GLASTIFOLIA, B. CUNEIFOLIA, B. ANGUSTIFOLIA, AND B. DELMARIA
(ASTERACEAE: ASTEREAE),
SPECIES OF THE ATLANTIC COAST**

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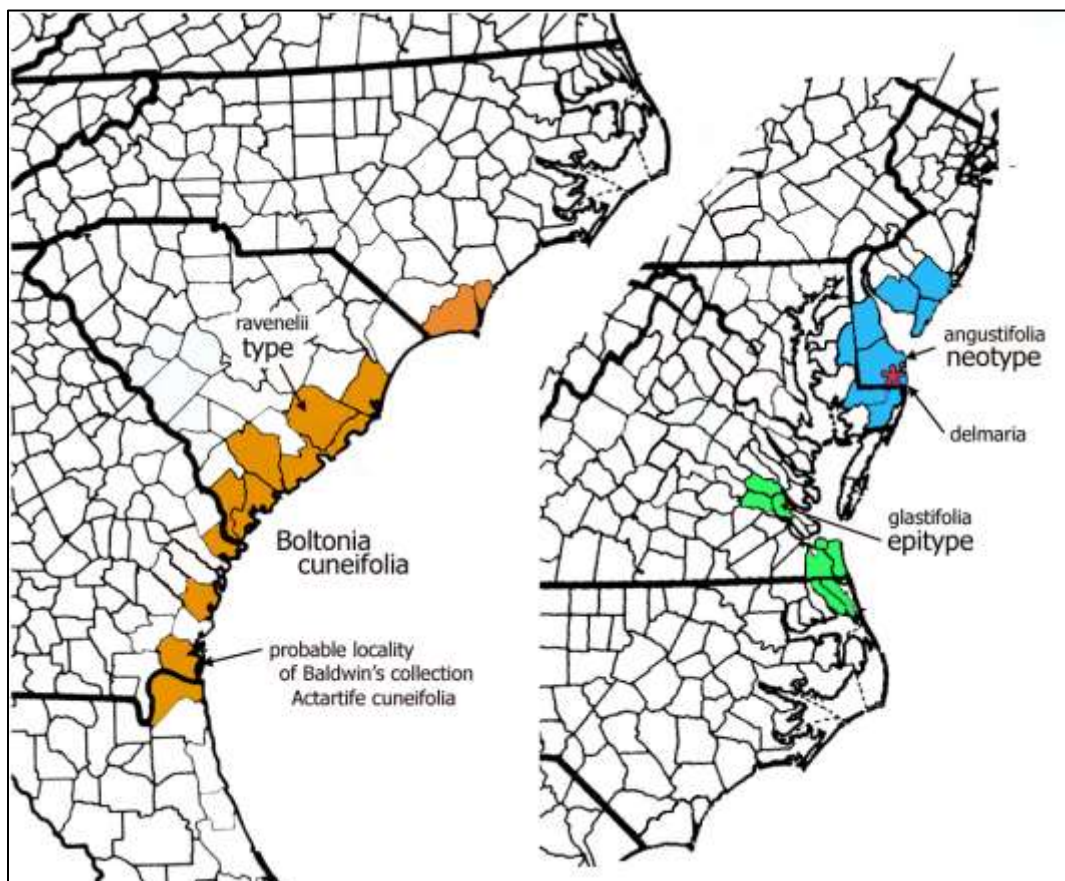
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ABSTRACT

Boltonia in bogs and swales of New Jersey, Delaware, Maryland is identified as ***Boltonia angustifolia*** (Raf.) Nesom, **comb. nov.** (neotypified here). ***Boltonia delmaria*** Nesom, **sp. nov.**, is from a small area of southeastern Delaware and occurs around the edges of woodland ponds. Plants of tidal marshes in southeastern Virginia and immediately adjacent North Carolina are identified as *B. glastifolia* (Hill) L'Hérit., epitypified (by Townsend) with a Virginia collection. Tidal marsh plants from southeastern North Carolina to southern Georgia are identified as ***Boltonia cuneifolia*** (Raf.) Nesom, **comb. nov.**, neotypified here with a William Baldwin collection.

Boltonia along and near the Atlantic coast, from New Jersey to southern Georgia, has often been identified as *B. glastifolia* — Townsend (2013) provided an epitype from southeastern Virginia for the name (otherwise typified only by an illustrated plant of unknown provenance). The present study, however, indicates that these coastal and near-coastal plants occur in geographic segments perhaps not comprising a monophyletic lineage.



Map 1. Distribution of *Boltonia glastifolia*, *B. cuneifolia*, *B. angustifolia*, and *B. delmaria*.

The New Jersey-Delaware-Maryland plants grow in bogs and swales of inland localities and were named by Rafinesque (1840) in his new genus *Actartife*. Those of the two southern segments consistently occur in tidal marshes. The middle system (*B. glastifolia* sensu stricto) is primarily in southeastern Virginia and immediately adjacent North Carolina. The southern system, from southeastern North Carolina through Georgia, carries the name *B. ravenelii* Fernald & Griscom (Fernald 1940) as well as an earlier one from Rafinesque (1840) in *Actartife*, the latter used here by neotypification as the correct name.

- 1. BOLTONIA ANGUSTIFOLIA** (Raf.) Nesom, **comb. nov.** *Actartife angustifolia* Raf., Autik. Bot. 21. 1840. **TYPE:** Not located (and see Moore 2022). **Protologue:** ... "caule dichot, corymboso angulato, fol. sessilib. longo linearib. acutis margine scabro integro, pedunculis squamosis, sq. subulatis --- Delaware, mistaken for *B. glastifolia* by Nuttall, not even of same Genus and leaves not serrate. Stem bipedal, leaves 1 or 2 inches long, flowers small, habit quite similar to *Erigeron philadelphicum*."

NEOTYPE (designated here): **Delaware.** Ellendale, 1/4 mi E of the village, moist swale along the railroad, 23 Sep 1938, R.R. Tatnall 4051 (DOV). Figure 4.

The plant alluded to by Rafinesque in 1840 and the series of historical collections (1867, 1877, 1891, 1893, 1902, 1908, 1925, 1940, mostly from around Ellendale, as cited here) show that Ellendale was often visited by botanists (e.g., Williamson 1909; Tucker & Dill 1989), surely because of the interesting array of species occurring there, and it seems probable that Rafinesque's plant came from there.

In connection with comments on *Rhexia aristosa*, Clancy (1993, p. 83) noted that four sites south of Ellendale in Sussex Co. — (a) ditches in a sandy, open pine plantation, (b) a clear-cut, (c) the edge of an excavated pond, and (d) a ditch — in 1991-1992 included an assemblage of *Amphicarpum purshii*, *Boltonia asteroides*, *Eleocharis robbinsii*, *Fuirena pumila*, *F. squarrosa*, *Hypericum adpressum*, *H. denticulatum*, *Lobelia canbyi*, *Rhynchospora fusca*, *R. gracilentia*, *R. torreyana*, and *Scleria reticularis*. The recent Ellendale collection of *Boltonia* (McAvoy 7240 in 2013) indicates that it persists there. Maryland collections are more recent (1982, 1983, 2001, 2011).

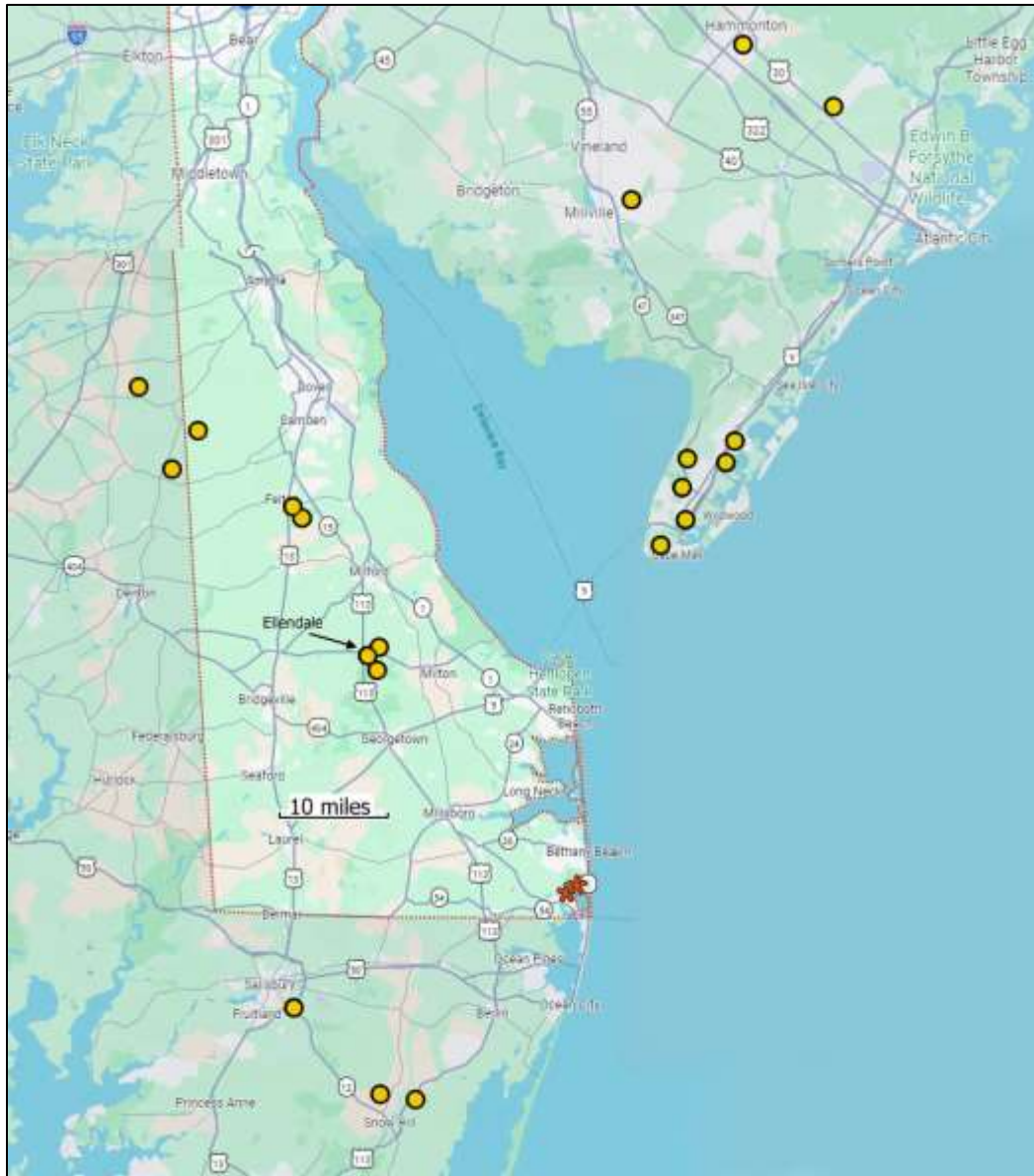
Rafinesque's *Florula Delawarica* was never published and the manuscript, which he had given to Benjamin Barton, has not been located (Tucker & Dill 1989) — it apparently was based on a walking trip by Rafinesque through Delaware in 1804. He returned to Italy in 1805, taking with him "nearly 10,000 herbarium specimens from Delaware, the District of Columbia, Maryland, Pennsylvania, and Virginia" (fide Tucker & Dill). A herbarium survey by Moore (2022) did not encounter a collection identified as *Actartife*.

Rafinesque (1840) described two species in his new genus *Actartife* — from his descriptions and comments, it is clear that these belong in *Boltonia* L'Hérit. Merrill (1949) noted that each of those names was a synonym of "*Boltonia asteroides*." The second species, *A. cuneifolia*, is the same as Fernald's intended concept of *Boltonia ravenelii*.

Herbaceous perennials, fibrous-rooted, glabrous, rhizomatous, not producing leaves during flowering. **Stems** 50–100 cm, erect, 1 from the base, not fistulose. **Leaves:** basal absent at flowering; lower and midcauline oblong-linear, 4–10 cm long, 2–5 mm wide, relatively even-sized up to the inflorescence, then becoming smaller and bracteate. **Inflorescence** paniculate to subcorymboid or heads solitary on ascending peduncles 2–5 cm long, peduncles mostly with 2–5 small or minute bracts. **Receptacle** low-conic. **Involucres** 4.5–5 mm wide (pressed); phyllaries oblong-lanceolate, in 3–4 series of subequal to unequal length, inner 2.5–3 mm long, midzone linear-oblong, dark-resinous (oil tubes), extending fully to the phyllary apex, apex lance-acute, outer often grading into distal peduncular bracts. **Ray flowers** 18–30, corollas 6–8 mm long, white rarely to bluish. **Disc corollas** 1.8–2.2 mm long. **Achenes** obovate, rarely with a third nerve and wing, 1.5–2 mm long, broadly white-winged, awns 0.8–1 mm long. Figures 1-17.

Flowering August-September. Moist swales along roads and railroads, bogs, Carolina bay wetland, ditches, wet pastures, powerline ROWs, mostly sandy sites.

Boltonia angustifolia is similar in most respects to *B. ellipsium* (Nesom 2026), and they have similar habitats, but the leaves of the latter usually are narrowly elliptic (vs. oblong-linear in *B. angustifolia*, whence Rafinesque's apt epithet) and range to a greater width. It is plausible that they are evolutionary sisters.



Map 2. Distribution of *Boltonia angustifolia*. Delaware is outlined in red. *Boltonia delmaria* (asterisks) is described here from the Assawoman Wildlife Area of Sussex Co., Delaware. Tatnall (1946) noted the occurrence of *Boltonia* in Talbot Co., Maryland — that record probably was based on Earle 3114 (PH), which is *Erigeron annuus*.

Additional collections. Delaware. Kent Co.: Felton, Aug 1867, *Canby s.n.* (NY, PH); Felton, bogs, 25 Sep 1873, *Commons s.n.* (PH); 1 mi SE of Marydel, E side of Hwy 208, 0.4 mi N of Hwy 206, weedy ditch between two ponds, standing water, common, 10 Sep 1986, *Seyfried & Burbage CEP86-403* (DOV). Sussex Co.: Ellendale, along ditches, Aug 1891, *Canby s.n.* (DOV); Ellendale, upland meadows, 16 Sep

1891, *Canby s.n.* (US); Ellendale, ditches, 16 Sep 1891, *Canby s.n.* (NY); Ellendale, bogs, 16 Aug 1877, *Commons s.n.* (GH, NY); Ellendale, bogs, 21 Sep 1892, *Commons s.n.* (DOV, PH); Ellendale, bogs, 26 Aug 1897, *Commons s.n.* (PH); just E of Ellendale, S side of Hwy 16, common along edge of ditches on acid-peaty soil, 19 Sep 2013, *McAvoy 7240* (DOV); Ellendale, 14 Sep 1902, *Norton s.n.* (MARY); E of Ellendale, moist, open sandy depression, 5 Sep 1925, *Pennell 12872* (PH); 3 mi SE of Ellendale, roadside ditch, 8 Aug 1939, *Tatnall 4314* (DOV, GH); Ellendale, damp soil, 29 Aug 1908, *Williamson s.n.* (PH-3). **Maryland.** Caroline Co.: Jackson Lane Cleaved Glade, 39.060936 N, 75.752474 W, Delmarva Bay, 20 Aug 1982, *Boone s.n.* (TAWES). Queen Anne's Co.: E side of Teats Branch Rd and 0.3 mi N the intersection with Busic Church Road, 39.149636 N, 75.819849 W, abundant along edge of road immediately adjacent to mailbox and in wet pasture/Carolina bay wetland kept in early succession by landowner by mowing and horse pasturing, with *Eryngium aquaticum*, *Coreopsis rosea*, *Lycopus americanus*, 16 Aug 2011, *Knapp 3329* (TAWES). Wicomico Co.: 5 mi SE of Salisbury, Johnson Road, wooded roadside, 3 Aug 1940, *Tatnall 4619* (DOV). Worcester Co.: 4 mi NNW of Snowhill, small roadside swale at bend in Forrest Rd, 0.6 mi NW of Voting House Rd, 3 Sep 1983, *Hirst 605* (DOV); [N of Snowhill, between Forest Lane Rd and Disharoon Rd], Colbourne, from Indiantown take Hwy 354 NE to the intersection of Forest Lane Rd, take Forest Lane Rd NW for about 1.3 miles to a logging road on the left, follow this logging road to the powerline, 38.228649 N, 75.415289 W, plants on SE under wet open powerline right-of-way, huge population, 22 Aug 2001, *Knapp 29-01* (TAWES). **New Jersey.** Atlantic Co.: Hammonton, edge of stream, 4 Sep 1917, *Gershoy 702* (PH); Egg Harbor City, moist soil, 14 Aug 1912, Hamm 1369 (PH). Cape May Co. (representative): Bennett, 1 mi W of church, bog, clay bottom, 7 Sep 1934, *Chrysler s.n.* (PH); Cold Spring, clay bottom bog, 30 Aug 1917, *Gershoy s.n.* (GH); Cape May Court House, salt marsh, 13 Aug 1912, Hamm 1313 (PH); vicinity of the bogs W of the railroads near Bennett, 13 Aug 1911, *Pretz 3791* (PH); just W of Cold Spring-Villas Rd, bog, common, 23 Jun 1939, *Schmid, Jr. s.n.* (PH); Green Creek, 15 Aug 1909, *Stone 11963* (PH); 1 mi W of Bennett, bog, 4 Sep 1910, *Stone 5512* (GH); 2 mi W of Bennett, 11 Sep 1910, *Stone 13612* (PH); Bennett, bog, 4 Sep 1920, *Stone s.n.* (GH); Bennett, bog, 8 Aug 1925, *Stone s.n.* (PH); 1 mi W of Reading RR Station, 4 Sep 1907, *Van Pelt s.n.* (PH); Green Creek, near E end lane to Bay, N of Creek, 15 Aug 1909, *Van Pelt s.n.* (PH). Cumberland Co.: Ca. 1 mi N of Leamings Mill along Mays Landing Road, dumped sand, 15 Sep 1935, *Long 47570* (PH-2).

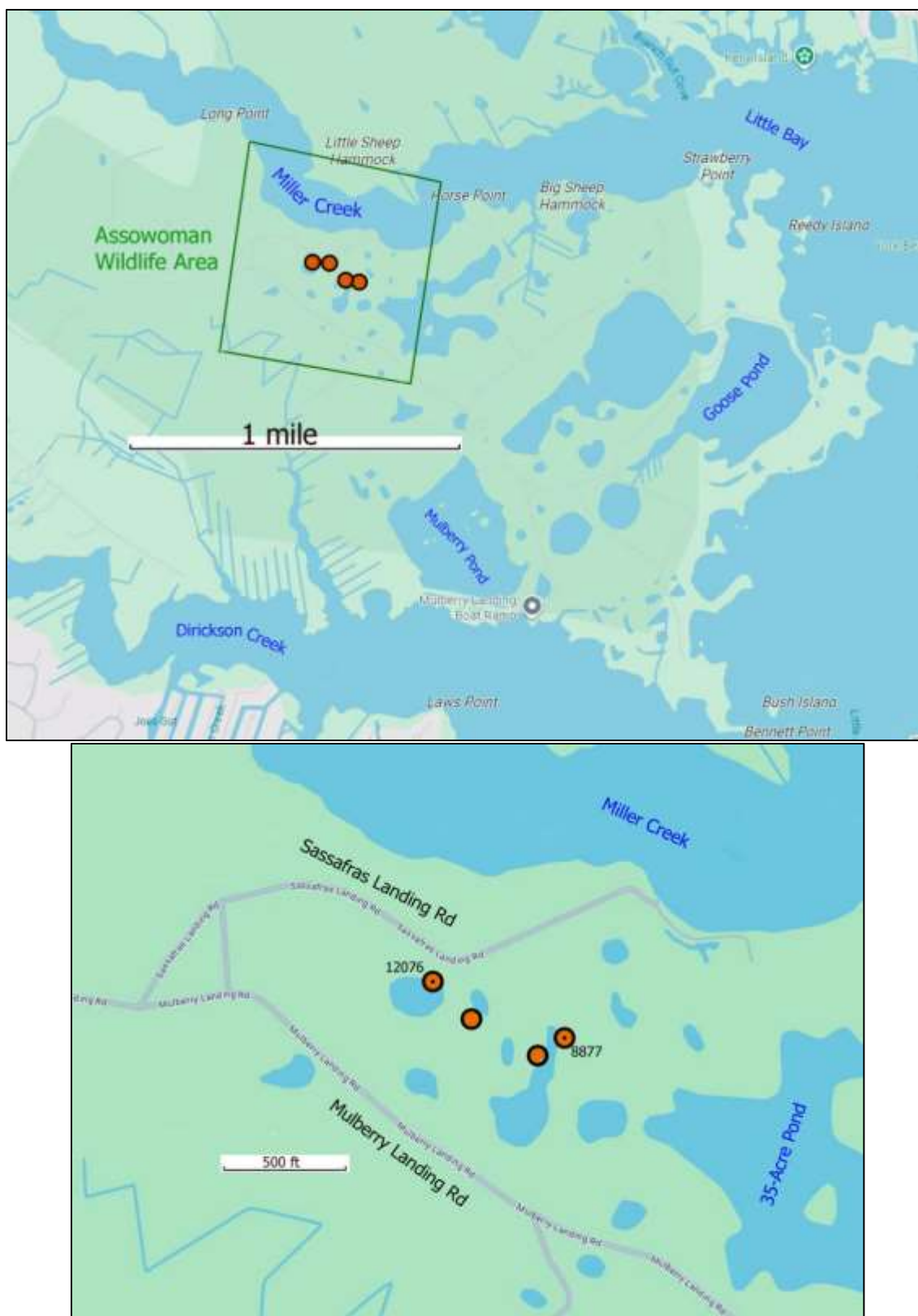
2. BOLTONIA DELMARIA Nesom, **sp. nov.** **TYPE: Delaware.** Sussex Co.: 2 mi ESE of Bayard, Assawoman Wildlife Area, 38.4986 N, 75.0878 W, sunny wet edge of shallow, natural pond in wet-mesic deciduous forest, frequent, 29 Sep 2007, *R.F.C. Naczi 12076* (holotype: NY; isotypes: PH, VDB).

Distinct from *Boltonia angustifolia* in its wider leaves, corymboid inflorescence with foliaceous bracts reaching the lower nodes, peduncles with fewer bracts, and longer phyllaries.

Herbaceous perennials, fibrous-rooted, glabrous, rhizomatous, not producing leaves during flowering. **Stems** 40–100 cm, erect, 1 from the base, not fistulose. **Leaves**: basal absent at flowering; lower and midcauline oblong-linear, 5–10 cm long, 4–9 mm wide, relatively even-sized up to the inflorescence. **Inflorescence** corymboid, heads solitary or usually on peduncles mostly 1–4 cm long, peduncles mostly with 0–2 small bracts. **Receptacle** low-conic. **Involucres** 5–6 mm wide (pressed); phyllaries oblong-lanceolate, in 3–4 series of subequal to unequal length, inner 3–4 mm long, midzone linear-oblong, dark-resinous (oil tubes), extending fully to the phyllary apex, apex lance-acute, outer often grading into distal peduncular bracts. **Ray flowers** 26–32, corollas 9–10 mm long, white to pink or lilac. **Disc corollas** 2 mm long. **Achenes** obovate, 1.5–2 mm long, narrowly winged, awns 1–1.2 mm long. Figures 18-23.

Flowering August-September. Banks and shallow water at pond edges.

Additional collections. Delaware. Sussex Co., Assawoman Wildlife Area: 2 mi E of Bayard, just off Sassafra Landing Road and S of Miller Creek, small woodland pond, 23 Aug 1984, *Hirst 604* (DOV); coastal plain pond, abundant, 22 Sep 2001, *McAvoy 5306* (DOV); 2.3 mi ESE of Bayard, 38.497778 N, 75.086111 W, lightly shaded, shallow water at edge of natural pond, infrequent, 22 Sep 2001, *Naczi 8877* (DOV).



Map 3. Distribution of *Boltonia delmaria*. Assowoman Wildlife Area, Sussex Co., Delaware. Undotted symbols are *Hirst 604* and *McAvoy 5306*, which unambiguously occur in this immediate area but for which precise coordinates were not given.

Geography and habitat (and rhizomes) of these plants are similar to *Boltonia angustifolia*, but the corymboid inflorescence with little-reduced foliar bracts, fewer peduncular bracts, and larger heads give them a distinct aspect.

3. BOLTONIA GLASTIFOLIA (Hill) L'Hérit., *Sertum Anglicum*, 16. 1788. *Matricaria glastifolia* Hill, Hort. Kew ed. 1: 19, fig. 3. 1768. *Boltonia asteroides* var. *glastifolia* (Hill) Fernald, *Rhodora* 42: 486. 1940. Protologue: "Caulis tripedalis ramosus, subdichotomus; geniculis paululum intumescens. Folia lanceolata, sessilia, integerrima. Corollae radii purpurascens. Perennis. Ex America boreali. Augusto florens." **HOLOTYPE**: Hortus Kewensis (Hill) ed. 1, p. 19, fig. 3. 1768. Figure 24.

When L'Héritier made the combination, he described the proximal leaves as serrate, in contrast to the Hill's description and illustration of entire-margined leaves.

EPITYPE (Townsend 2013): **Virginia**. James City Co.: Fresh tidal marsh of Chickahominy River, below Barrat's Bridge (or Ferry), 19 Sep 1939, *M.L. Fernald and B. Long 11466* (NY; isopitypes: GH-2, PH, US). Figure 25.

Herbaceous perennials, glabrous, fibrous-rooted, rhizomatous, without basal offsets. **Stems** 60–120 cm, often thickened at the base but not fistulose, 1 from the base. **Leaves**: basal and lower cauline deciduous by flowering, cauline mostly narrowly elliptic to elliptic-oblong, 4–11 cm long, 4–12(–20) mm wide, largest at midstem then quickly reduced to linear bracts. **Inflorescence** usually paniculate, peduncles 2–5(–8) cm long, with 1–3 minute bracts. **Receptacles** low-conic. **Involucre** 5–6 mm wide (pressed); phyllaries narrowly oblong, in 2–3(–4) series of subequal length, inner 2.5–3 mm long, dark midregion narrowly oblong and distinctly elliptic to oblong in the distal half, sometimes discontinuous (like beads), margins broad and prominent scarious, apex acute to acute-acuminate, not apiculate. **Ray flowers** 26–38, corollas 6–8 mm long, white to lilac or blue. **Disc corollas** 1.6–1.8 mm long. **Achenes** depressed elliptic to broadly obovate-elliptic to obovate with truncate apex, 2–2.5 mm long, 1.2–1.8 mm wide, ray achenes sometimes 3-winged, awns 0.8–0.1 mm long, corona barely evident as a few fimbria. Figures 24–32.

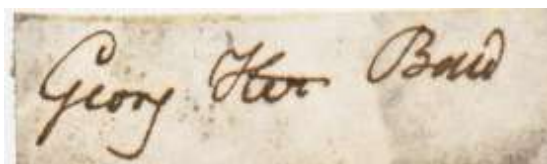
Flowering September–October. Tidal marsh along rivers and creeks.

Additional collections. North Carolina. Camden Co.: E of Elizabeth City, E side of Pasquotank River on Hwy 158, marsh, 26 Sep 1967, *Radford 11532* (APSC, BALT-2, BRY, KE, MEM, MUR, NCU, PEMB, USAM, WWC). **Currituck Co.**: Point Harbor, sandy shore of Currituck Sound, 5 Oct 1950, *Godfrey 51009* (DUKE, NCSC). **Virginia. Charles City Co.**: Near Cypress Bank Landing, fresh tidal margins of Chickahominy River, 9 Sep 1941, *Fernald & Long 13813* (BUT, GA, GH, PH-2, TENN); N of Holdcroft, Graves Landing, fresh tidal shore of Chickahominy River, 10 Sep 1941, *Fernald & Long 13816* (GH, PH); Wilcox Neck, sandy and muddy tidal shore of Chickahominy River, 13 Sep 1941, *Fernald & Long 13817* (BUT, PAC, PH, RSA); Chickahominy Shores, tidal marsh, 11 Oct 1969, *Harvill 23097* (FARM). **Chesapeake City**: 2.3 mi ENE of Northwest, Northwest River Park, along a small gut 0.1 mi NE of the confluence of the Northwest River and Indian Creek, oligohaline wind tide marsh, occasional, 17 Oct 1995, *Fleming 11529* (GMUF). **James City Co.**: Ca. 5 mi W of Toano, tidal marsh of Chickahominy River, 13 Aug 1939, *Menzel 311* (GH); ca. 5 mi W of Toano, edge of tidal marsh of Chickahominy River, 27 Aug 1939, *Menzel 316* (GH, WILLI-2); ca. 5 mi W of Toano, tidal marsh of Chickahominy River, 24 Sep 1939, *Menzel 370* (WILLI). **New Kent Co.**: W of Walker, fresh tidal marsh by Lacey Creek, 9 Sep 1941, *Fernald & Long 13814* (PH); Walker, fresh tidal marsh by Chickahominy River, 10 Sep 1944, *Fernald & Long 13815* (BUT, GH, PH). **Norfolk Co.**: Near Northwest, fresh reed-marsh and swale along Northwest River, 11 Oct 1941, *Fernald & Long 14048* (BUT, GA, PH, GH, TENN); Northwest, 6 Sep 1893, *Heller 1248* (DOV, PH-2, RSA-2, VPI). **Virginia Beach City**: Pungo Ferry, brackish marsh, 22 Sep 1933, *Fernald & Griscom 2914* (GH); 2.3 mi SW of Creeds, along SE side of Milldam Creek, 0.25 mi NW of its confluence with the North Landing River, frequent in low, oligohaline wind-tide marsh, 11 Sep 1995, *Fleming 11264* (WILLI); 1.8 mi. NW of Creeds, 0.3 mi. NW of the Pungo Ferry Road bridge, island of the North Landing River, locally common along the river channel edge in low, oligohaline wind-tide marsh, 18 Oct 1995,

Fleming 11543 (FARM, GMUF, LYN, VPI, WILLI); marshy swale just W of Pungo Ferry, 5 Oct 1973, *Harvill 30252* (FARM, WILLI); 2.5 mi SE of Blackwater and 2.25 mi SW of Creeds, S shore of Milldam Creek 1/4 mi above its confluence with North Landing River, 11 Oct 1984, *Wieboldt 5391* (CM, VPI, WILLI).

Boltonia glastifolia is rhizomatous, has largest leaves at midstem abruptly reduced in size to linear bract, a paniculate inflorescence, broad achenes with narrow but thick wings, and hyaline phyllary margins much like *B. latisquama* and *B. recognita*. Its tidal marsh habitat is consistent.

- 4. BOLTONIA CUNEIFOLIA** (Raf.) Nesom, **comb. nov.** *Actartife cuneifolia* Raf., Autikon 20. 1840. Protologue: "... caule erecto paucifl. sulcato, fol. sessilib, cuneatis mucronatis, margine integro scabro, infimis subspatulatis, pedunc. subnudis---Florida, found by Bald, deemed *B. asteroides*, which differs by leaves oblong amplex. dentate, lower pinnatifid. Stem pedal nearly simple, leaves uncial, flowers like *Erigeron*, perianthe imbricate subulate as in all *Boltonias*." **NEOTYPE** (designated here): "Georg Fløx Bald," no other information but see notes below (PH). Figure 35.



The Baldwin specimen has a possibly original annotation as *Boltonia glastifolia*, but Rafinesque didn't say who "deemed" it *B. asteroides*, or perhaps, if he was indeed looking at the PH specimen, perhaps he understood *B. glastifolia* to be part of *B. asteroides*. In any case, this is the only collection of *Boltonia* by Baldwin known to me, and it thus it seems clear enough that Rafinesque was referring to this species. Duplicates of his specimen might be found at P or elsewhere (Stuckey 1971). Before Baldwin's collection was acquired by Elias Durand and then situated at PH, it was briefly in the possession of Rafinesque.

William Baldwin was active as a collector in southeastern Georgia and adjacent Florida around 1812-1816, especially in the area of the St. Marys River, which forms the state border between Camden Co., Georgia, and Nassau Co., Florida. The probable location is mapped (Map 1) as Camden Co., Georgia.

Boltonia ravenelii Fernald & Griscom, *Rhodora* 42: 488. 1940. **TYPE: South Carolina.** [Berkeley Co.]: Santee Canal, rich swamps, Oct [1846], *H.W. Ravenel s.n.* (holotype: GH 105837; probable isotypes: BR, GH-2215088, USCH-HWR-0000661). Figures 41, 42. The USCH label has "S.C. Oct rich swamps near Biggin bridge rare!"

Herbaceous perennials, glabrous, fibrous-rooted, rhizomatous, without basal offsets. **Stems** 80–200 cm, 1 from the base, often thickened at the base but not fistulose. **Leaves**: basal and lower cauline deciduous by flowering, cauline mostly elliptic-lanceolate to elliptic-oblongate, evenly spaced, reaching the inflorescence as foliar bracts, 6–9 cm long, 10–25 mm wide. **Inflorescence** corymboid to subcorymboid, peduncles 2–5(–8) cm long, with 1–3 linear bracts. **Receptacles** low-conic. **Involucre**s 3.5–5 mm wide (pressed); phyllaries narrowly oblong, in 2–3 series of subequal length, inner 1.8–2 mm long, dark midregion narrowly oblongate and broadened in the distal half, margins not scarious, apex acute to acute-acuminate, not apiculate. **Ray florets** 25–30, corollas 7–8 mm long, white, turning pale lavender or pink. **Disc corollas** 1.6–1.8 mm long. **Achenes** 1.5–2.5 mm long, 1.1–1.5 mm wide, obovate or obovate-triangular to broadly ovate-elliptic, ray achenes sometimes with a short 3rd wing, awns 0.8–1.2 mm long. **Chromosome number**, $2n = 18$ (*Anderson 8902*, Jasper Co., South Carolina). Figures 33-47.

Flowering (June, July-) August-October. Freshwater tidal marsh and marsh edges, swamp edges, river edges, fresh water marsh, bottomland forest, swampy ditches and woods.

Additional collections. Florida. Nassau Co.: 1/4 mi SW of Little St. Marys River bridge, ca. 3.2 mi NE of Hwy 301 (and Hillard), bordering Rte 115A, dry sandy loam (severe drought this season) at edge of small *Nyssa-Hypericum* swamp, 3 Jun 2000, *Anderson 19312* (USCH); ca. 4.1 air mi NE of Boulogne, St. Marys Conservation Area NE part, along St. Marys River between Flat Landing and Elbow Landing, inundated edge of river at base of NE-facing slope, 18 Oct 1991, *Orzell & Bridges 18531* (FTG, USF); ca. 10 mi NW of Yulee, White Oak Plantation bordering on the St. Marys River, at the terminus of Brick Yard Road just at the end of Sandy Bluff Road near the river, along river edge, 23 Oct 1997, *Wilbur 69500* (DUKE); ca. 10 mi NW of Yulee, White Oak Plantation bordering on the St. Marys River, ca. 1/10 mi from the East Gate Guard House on Wingate Landing Road starting just beyond gate and running west, very close to the wooden bridge over the Little St. Marys River, roadside bank bordering swampy ditch and woods, common, 24 Oct 1997, *Wilbur 69632* (DUKE). **Georgia.** Camden Co.: Ca. 6 air mi S of Kingston, along edge of St. Marys River beside Hwy 17 bridge, open sun of wet sandy loam, 5 Oct 1985, *Anderson 8906* (FSU-2, GA-2); ca. 6 air mi S of Kingston, along edge of St. Marys River in shade of Hwy 17 bridge (see 8906 for sun-form), 5 Oct 1985, *Anderson 8907* (FSU-3, GA). Chatham Co.: Ca. 1.5 air mi NE of Port Wentworth, along Middle River on Onslow Island just S of Hwy 17, frequent with *Aster subulatus* and *Aster tenuifolius* in mud, 5 Oct 1985, *Anderson 8905* (FSU, GA, LSU); Port Wentworth, along E bank of the Savannah River ca. 2 mi upstream from Hwy 17, freshwater tidal marsh, locally abundant with *Zizania aquatica* and *Amaranthus cannabinus*, 22 Sep 1985, *Aulbach-Smith 3800* (FSU); Argyle Island, marsh along Back River, 17 Sep 1958, *Mellinger s.n.* (NCU); Argyle Island, edge of marsh, S side of Hwy 17, 17 Sep 1958, *Mellinger s.n.* (GA, GAS, NCU); Argyle Island, edge of *Peltandra* marsh, 17 Sep 1958, *Mellinger 855* (GAS); along old Hwy 17, by Happy Hunting Club woods, 13 Oct 1960, *Mellinger 1834* (GAS); Onslow Island, mud, *Peltandra* marsh, 20 Oct 1958, *Mellinger 844* (GAS); Savannah-Ogeechee Canal Nature Center/Ogeechee River Nature Preserve, 681 Fort Argyle Road (Hwy 204), margin of Ogeechee River, mud flats bordering tidal floodplain forest, scattered but common, 25 Aug 2012, *Zomlefer 2844* (GA). McIntosh Co.: 7 mi N of Darien along Hwy 17, wet roadside, 20 Oct 1987, *Angerman s.n.* (GA, USCH, VSC); few miles W of Darien, edge of creek, 5 Oct 1940, *Eyles 7622* (GEO, GH, NCSC); Champney Island, Altamaha WMA, along edge of the South Altamaha River, just N of the Hwy 95 bridge, disturbed habitat, 1 Aug 1997, *Govus 864* (GA); Butler Island, Darien: Altamaha Waterfowl Mgmt Area, river bank, to 7 feet tall, common, 17 Sep 1961, *Harmer 1349* (GA); just below Darien, edge of nearly fresh marshes of Altamaha River, 17 Sep 1903, *Harper 2003* (GH, NEB, US); Butler Island, Darien, Altamaha Waterfowl Mgmt Area, edge of marsh, 12 Sep 1958, *Scharnagel 48* (GA). **North Carolina.** Brunswick Co.: Mallory Creek, ca. 7.6 mi S of Hwy 17 off Hwy 133, 6 Sep 1963, *Bradley 1611* (GMUF); near Town Creek, 8 mi S on Hwy 133 from its jct with Hwy 17, 14 Sep 1963, *McCrary 1241* (NCU); beside Sand Castle Lane close to Hwy 904, E of Waccamaw River, few plants, 2 Oct 1993, *Sorrie & LeBlond 7738* (NCU). New Hanover Co.: Wilmington, along bank of Northeast Cape Fear River, near bridge of Hwy 74-76-421, 10 Oct 1966, *Bradley 3580* (CM, COLO, DSC, FLAS, GAS-2, GH, IND, NCU, SIU, TENN, USCH); 421 Sand Ridge Natural Area, along shore of Fishing Creek E of Hwy 421, freshwater tidal marsh, 12 Jul 2002, *LeBlond 5647* (NCU); Hwy 17 on W bank of Cape Fear River opposite Wilmington, roadside, 26 Sep 1965, *McCrary 1910* (NCU). **South Carolina.** Beaufort Co.: 0.2 mi NE of Neue River on Hwy 170, swamp, 11 Oct 1956, *Bell 5289* (NCU); 2.1 mi E of Yemassee, 1.1 mi SE of Hwy 21, Hollings ACE Basin Natl Wildlife Refuge, Upper Combahee Unit, S side of Combahee River, 11 Aug 2017, *Bradley 7455* (USCH-2); Sugar Hill Boat Landing, off River Road near Big Estate community, 2 Oct 2005, *Payne 3910* (CLEMS). Berkeley Co.: 3 mi NE of Pineville, along Santee River, 11 Sep 1939, *Godfrey 8155* (GH, MO-3); Jamestown, Chargeurs Wool, wool-washing facility, low woods on the bank of the Santee River at the terminus of service road that follows pipes to the river, 24 Aug 2004, *Lee 435* (USCH); N side of Lake Moultrie and S of Pineville, Sandy Beach Waterfowl Mgmt Area, boggy, peaty ground of open impoundment, 6 Sep 1991, *Nelson 11326* (USCH); N of Jamestown, S side of Santee River, immediately W of boat landing on W edge of Hwy 17A, shady woods at edge of rapidly flowing freshet within bottomland forest, 6 Sep 2006, *Nelson 26200* (NCU, USCH); Jamestown, parking lot on boat landing, S side of Santee River on W side of Hwy 17, 28 Sep 2012, *Nelson 31550* (USCH); 4 air mi S of Cordesville post office, edge of marsh overlooking upper arm of old rice field on W side of Cooper River (E branch) just NW of caretaker's home, uncommon, 25 Oct 2023, *Nelson 45258* (USCH); where Rock Branch on Santee Branch drains into Four Hole Swamp, marl forest above limestone, 12 Oct 2001, *Pittman 10120107*

(USCH); Dutart Creek and Santee River, Francis Marion Natl Forest, marl outcrop near mouth of creek, 3 Oct 2000, *Pittman 10030045* (USCH); French Quarter Creek, tidal freshwater marsh, many plants 4-5 feet tall, 22 Sep 1994, *Porcher 2388* (CLEMS); Dean Hall Plantation, west branch of Cooper River, abandoned rice fields, fresh water marsh, 2 Oct 1982, *Porcher 205B* (CLEMS). Charleston Co.: Near Osborne, abundant in swale, 21 Oct 1950, *Godfrey 40935* (DUKE, FSU, GH, NCSC). Colleton Co.: 1.77 mi S of Ritter, within channel of Ashepoo River just E of Hwy 303, 11 Sep 2010, *Nelson 28733* (GH, NCU, USCH) and *Nelson 28740* (GH, NCU). Dorchester Co.: 0.1 mi N of Colleton Co. line on Hwy 15, marsh of Edisto River, 2 Oct 1967, *Radford 11562* (APSC, BALT, BOON, BRY, CLEMS, ECUH, ERSK, FUGR, KE, MEM, MUR, NCSC, NCU, NLU, PEMB, UNCC, USAM, WWC). Georgetown Co.: Near Georgetown, Baruch Plantation, fresh water marshes, 27 Aug 1967, *Barry 246* (USCH); S of Murrell's Inlet off Hwy 17, old canals at Brookgreen Gardens, common in shallow marshes, 2 Oct 1993, *Mellichamp s.n.* (UNCC); Georgetown, end of "Pole Yard" boat landing on E(S) side of Hwy 17 at N Santee River, edge of tidal marsh, 13 Aug 1993, *Nelson 15052* (USCH); Georgetown, Sandy Island, edge of Thoroughfare Creek, ca. 1 river mile upstream from confluence of Marion Creek, waters edge and within remnant of tidal swamp, 20 Sep 1997, *Nelson 18698* (USCH); Georgetown, between Litchfield and Murrells Inlet, E edge of rice field/marsh below overlook, below visitor's center and education center, 30 Sep 2000, *Nelson 21621* (USCH); just W of Murrells Inlet off US 17, along S side of Brookgreen Creek at N edge of old rice field, edge of creek on edge of roadbed, 30 Sep 2000, *Nelson 21646* (USCH); just S of Thoroughfare Creek and ca. 0.52 air mi due E from Pee Dee River opposite Guendalos Plantation, freshwater tributary of Guendalose Creek, regularly flooded with tide, fairly robust herbs in a clump, rooted on top of stump, 13 Oct 2006, *Nelson 26285* (USCH); jct of Thoroughfare Creek and Long Creek near Pee Dee River, freshwater marsh, 27 Sep 1983, *Pinson 765* (CCUH); Georgetown, Prince George Tract, E edge of Waccamaw River near N edge of property, damp ground in old rice field marsh, 14 Oct 1996, *Seckinger 609* (USCH); 3 mi NE of Yauhannah, Pee Dee River, swamp forest, 20 Oct 1957, *Radford 31403* (NCU). Jasper Co.: 6.9 mi S of Ridgeland on Hwy 17, 29 Jun 1956, *Ahles 15801* (NY); 0.35 mi N of Hwy 17 in Savannah Natl Wildlife Refuge (basically at state line), Little Back River, muddy shores with *Zizania* and *Amaranthus australis*, 5 Oct 1985, *Anderson 8902*, voucher for chromosome count of n=9 II (BRY, FSU-2, LSU, USCH); ca. 5 mi SW of Hardeeville, marshy margin of Union Creek, abundant, 28 Sept 1983, *Aulbach-Smith 2857* (NLU); W Hardeeville, Boat Landing Road, 0.5 mi S of Hwy 321, 5 mi W of Hwy 17, 24 Sep 1984, *Mawhinney s.n.* (USF).

Boltonia cuneifolia might be seen as a southward continuation of *B. glastifolia* along the Atlantic Coast, but the hiatus in distribution (ca. 200 miles of coastline) in North Carolina exists despite intensive exploration, especially by the botanists led by A.E. Radford collecting for the Flora of the Carolinas project. *Boltonia cuneifolia* and *B. glastifolia* may prove to be sisters, but the inflorescence (corymboid vs. paniculate) and distribution of cauline leaves (continuing into the inflorescence vs. reduced to linear bracts) give them a different aspect, and *B. cuneifolia* has smaller involucre and phyllaries lack the scarious margins characteristic of *B. glastifolia*.

Around St. Marys River in Nassau Co., Florida, collections have been made of tall, large-leaved plants identified here as *Boltonia floridana* (rhizomatous, but with a paniculate inflorescence of heads on long, multibracteate peduncles) with the aspect of *B. cuneifolia* (*Wilbur 68606, 68235, 68768, 68782* — DUKE) — it's easy to speculate that these may be genetically influenced by *B. cuneifolia*.

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Thanks to the staff at NCU and PH for help during recent study there.

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Figure 1. *Boltonia angustifolia*. Cape May Co., New Jersey. Chrysler s.n. (CHRB).



Figure 2. *Boltonia angustifolia*. Cape May Co., New Jersey. Gershoy 701 (GH).



Figure 3. *Boltonia angustifolia*. Cape May Co., New Jersey. Stone s.n. (NY).

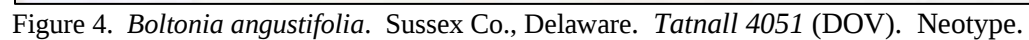


Figure 4. *Boltonia angustifolia*. Sussex Co., Delaware. Tatnall 4051 (DOV). Neotype.



Figure 5. *Boltonia angustifolia*. Sussex Co., Delaware. Commons s.n. (PH).

Figure 6. *Boltonia angustifolia*. Kent Co., Delaware. Canby s.n. (PH).

Figure 7. *Boltonia angustifolia*. Sussex Co., Delaware. Williamson s.n. (PH).

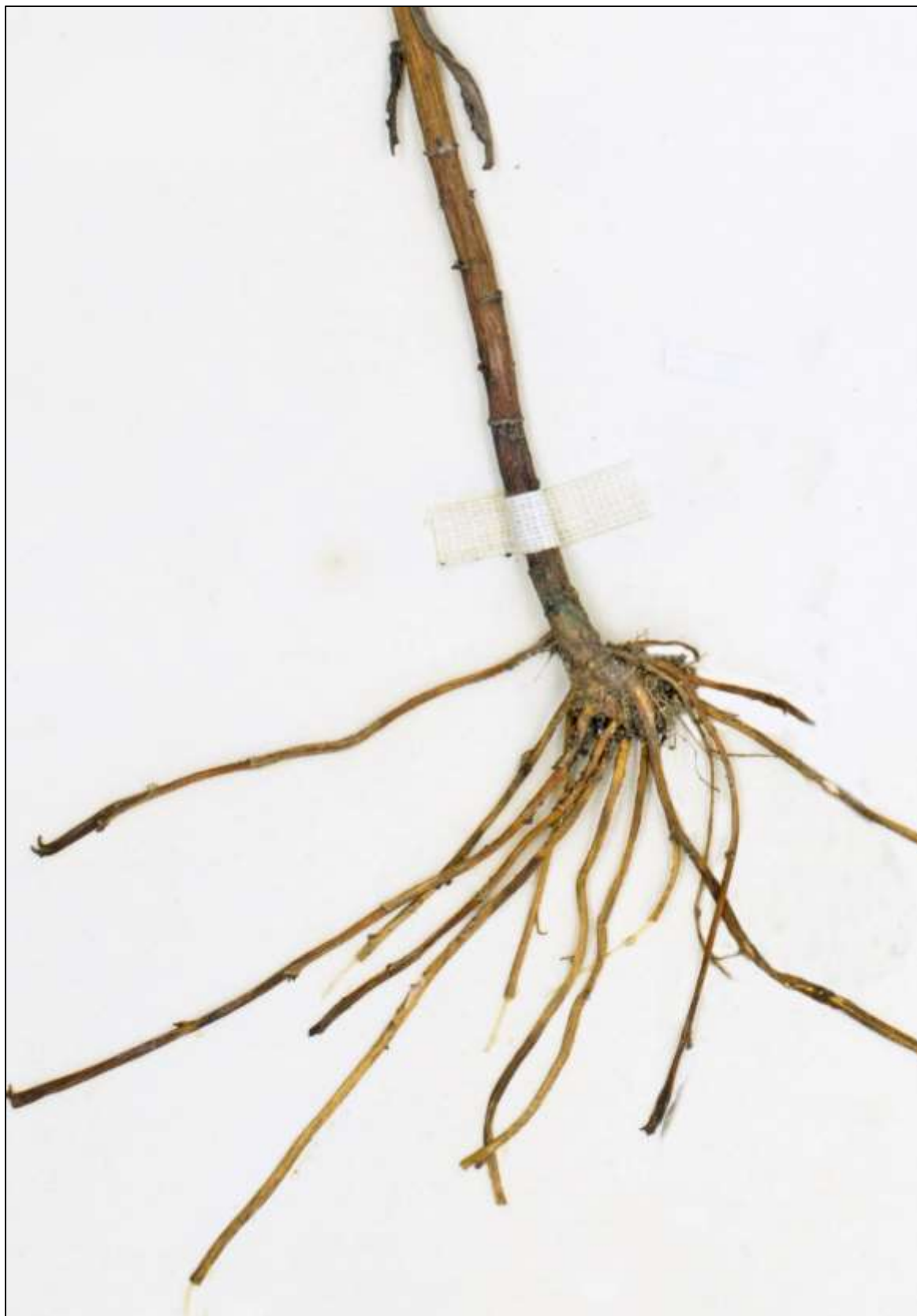


Figure 8. *Boltonia angustifolia*. Sussex Co., Delaware. Detail from Figure 7.



Figure 9. *Boltonia angustifolia*. Sussex Co., Delaware. Canby s.n. (NY).



Figure 10. *Boltonia angustifolia*. Sussex Co., Delaware. Commons s.n. (NY).

Nesom: *Boltonia glastifolia*, *B. cuneata*, *B. angustifolia*, *B. delmaria*



Figure 11. *Boltonia angustifolia*. Kent Co., Delaware. Seyfried & Burbage CEP86-403 (DOV).

Nesom: *Boltonia glastifolia*, *B. cuneata*, *B. angustifolia*, *B. delmaria*



Figure 12. *Boltonia angustifolia*. Sussex Co., Delaware. Williamson s.n. (PH).

Figure 13. *Boltonia angustifolia*. Kent Co., Delaware. Commons s.n. (PH).

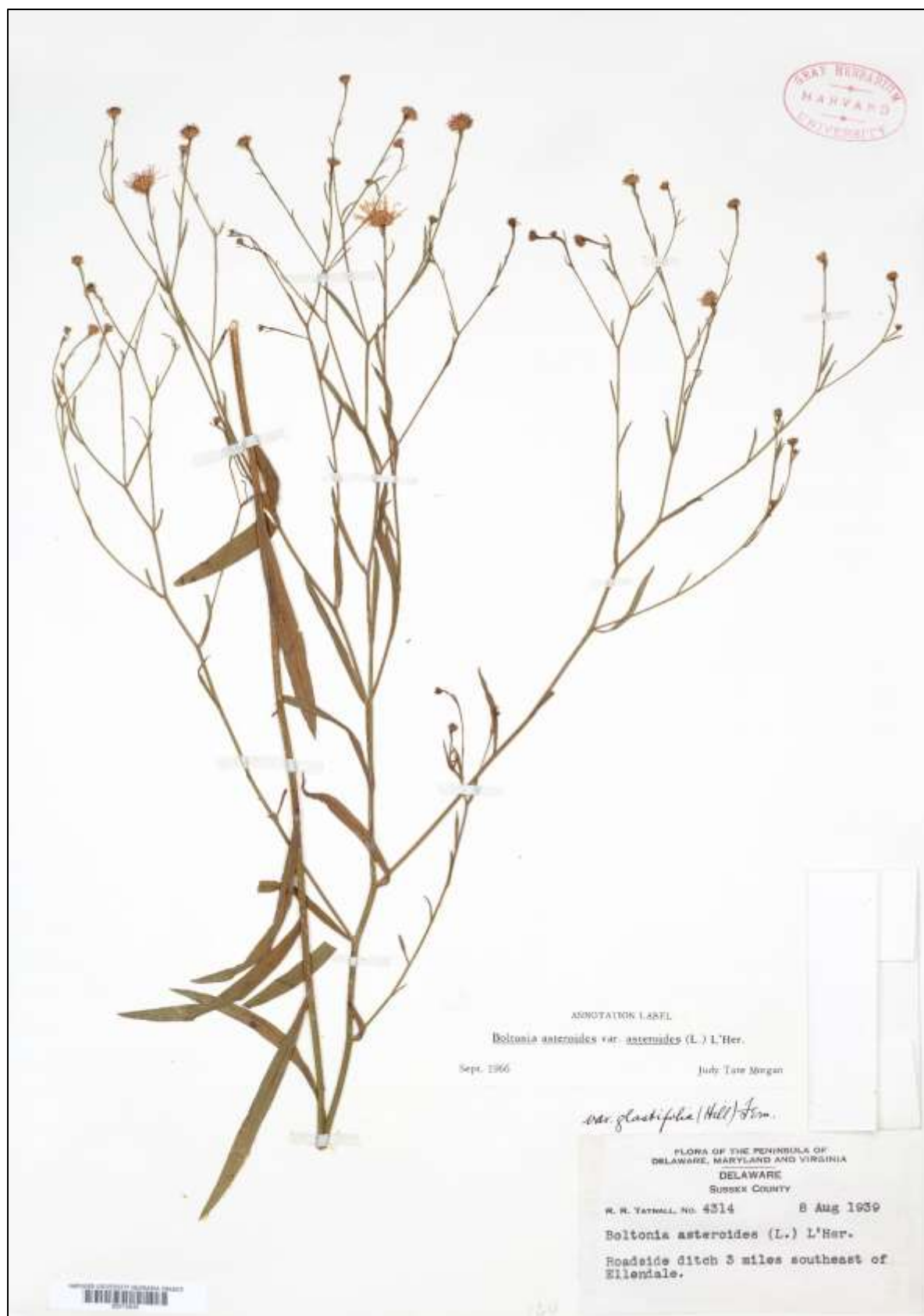
Figure 14. *Boltonia angustifolia*. Sussex Co., Delaware. Tatnall 4314 (GH).



Figure 15. *Boltonia angustifolia*. Sussex Co., Delaware. Commons s.n. (PH).



Figure 16. *Boltonia angustifolia*. Worcester Co., Maryland. Knapp 29-01 (TAWES).



Figure 17. *Boltonia angustifolia*. Queen Anne's Co., Maryland. Knapp 3329 (TAWES).



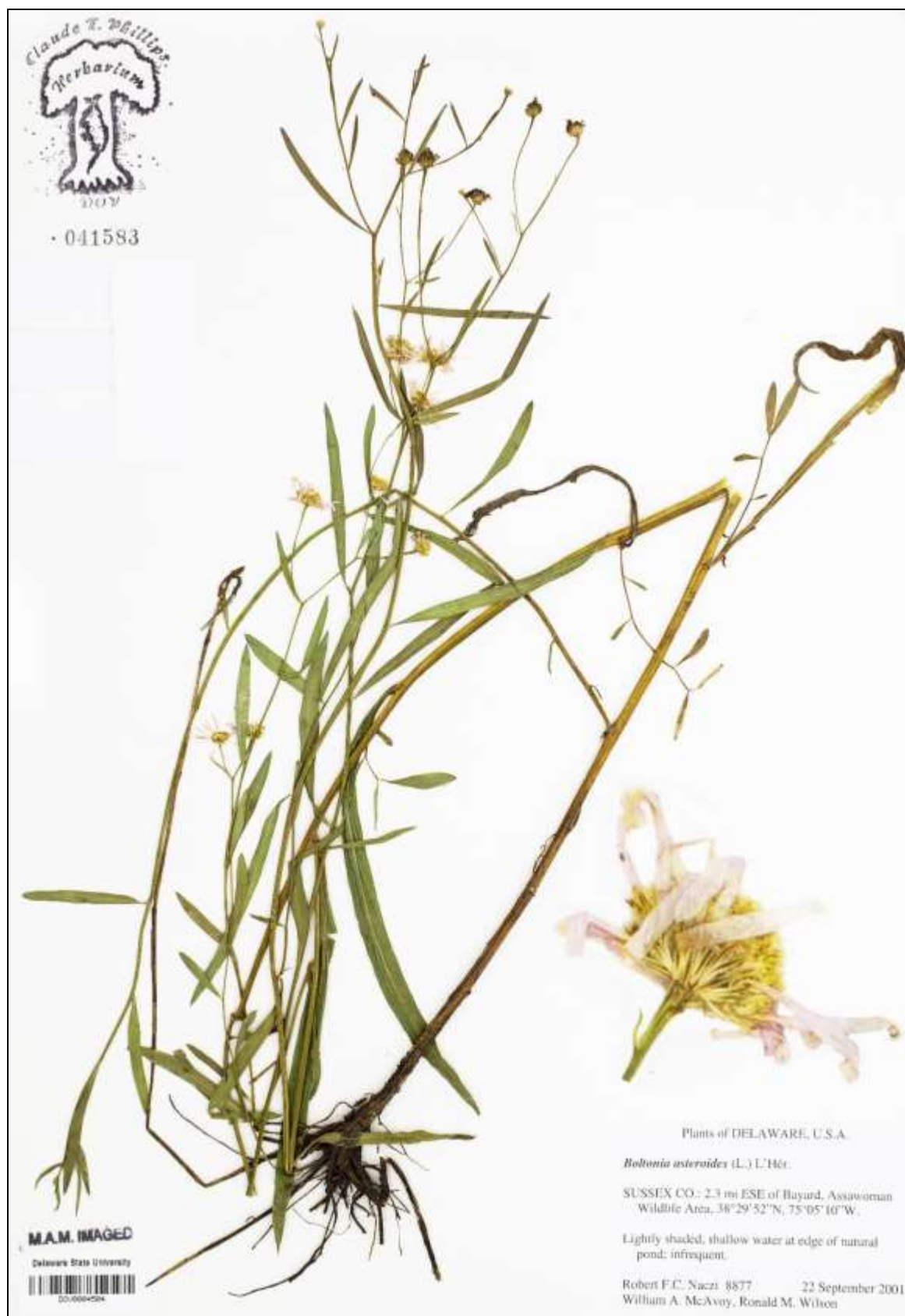
Figure 18. *Boltonia delmaria*. Sussex Co., Delaware. Naczi 12076 (NY). Holotype.



Figure 19. *Boltonia delmaria*. Sussex Co., Delaware. Naczi 12076 (PH). Isotype.



Figure 20. *Boltonia delmaria*. Sussex Co., Delaware. Naczi 12076 (VDB). Isotype.

Figure 21. *Boltonia delmaria*. Sussex Co., Delaware. Naczi 8877 (DOV).

Nesom: *Boltonia glastifolia*, *B. cuneata*, *B. angustifolia*, *B. delmaria*



Figure 22. *Boltonia delmaria*. Sussex Co., Delaware. McAvoy 5306 (DOV).

Figure 23. *Boltonia delmaria*. Sussex Co., Delaware. Hirst 604 (DOV).



Figure 24. *Boltonia glastifolia*. Hort. Kew ed. 1: 19, fig. 3. 1768. Holotype.



Figure 25. *Boltonia glastifolia*. James City Co., Virginia. Fernald & Long 11466 (US). Isoeotype.



Figure 26. *Boltonia glastifolia*. New Kent Co., Virginia. Fernald & Long 13815 (GH).

Figure 27. *Boltonia glastifolia*. Charles City Co., Virginia. Fernald & Long 13813 (US).

Figure 28. *Boltonia glastifolia*. Charles City Co., Virginia. Fernald & Long 13817 (US).

Figure 29. *Boltonia glastifolia*. Virginia Beach City, Virginia. Fleming 11543 (WILLI).



Figure 30. *Boltonia glastifolia*. Chesapeake City, Virginia. Fleming 11529 (GMUF).

Nesom: *Boltonia glastifolia*, *B. cuneata*, *B. angustifolia*, *B. delmaria*



Figure 31. *Boltonia glastifolia*. Camden Co., North Carolina. Radford 11532 (BYU).



Figure 32. *Boltonia glastifolia*. Currituck Co., North Carolina. Godfrey 51009 (DUKE).

Figure 33. *Boltonia cuneifolia*. Nassau Co., Florida. Wilbur 69500 (DUKE).

Nesom: *Boltonia glastifolia*, *B. cuneata*, *B. angustifolia*, *B. delmaria*

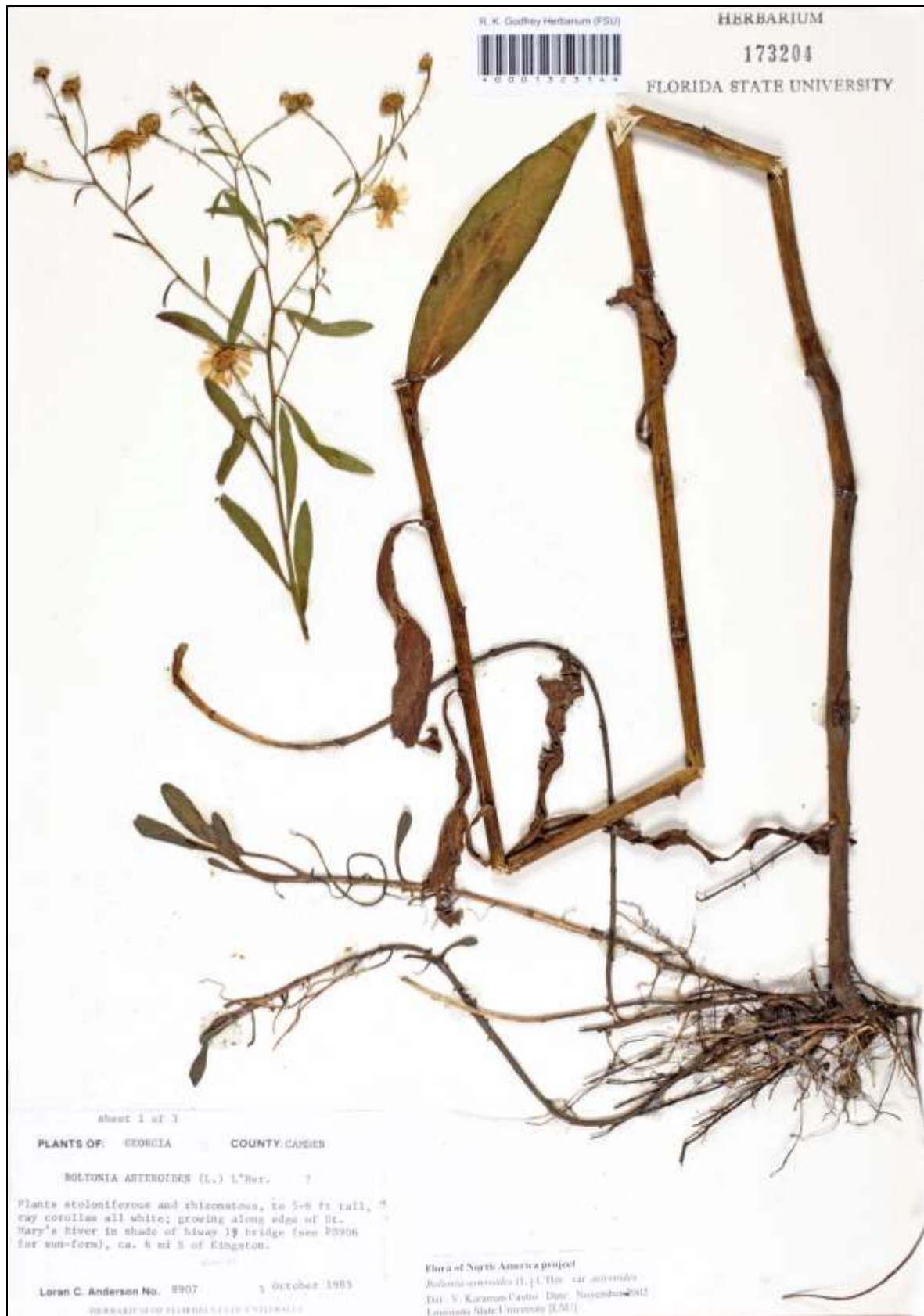


Figure 34. *Boltonia cuneifolia*. Camden Co., Georgia. Anderson 8907 (FSU).

Figure 35. *Boltonia cuneifolia*. Camden Co., Georgia. Anderson 8906 (FSU).



Figure 36. *Boltonia cuneifolia*. Camden Co., Georgia (probably). Baldwin s.n. (PH).

Figure 37. *Boltonia cuneifolia*. Chatham Co., Georgia. Anderson 8905 (FSU).



Figure 38. *Boltonia cuneifolia*. Chatham Co., Georgia. Melling s.n. (GAS).

Figure 39. *Boltonia cuneifolia*. McIntosh Co., Georgia. Harper 2003 (US).

Figure 40. *Boltonia cuneifolia*. McIntosh Co., Georgia. Harper 2003 (GH).



Figure 41. *Boltonia cuneifolia*. McIntosh Co., Georgia. Eyles 7622 (NCSC).



Figure 42. *Boltonia cuneifolia*. Berkeley Co., South Carolina. Ravenel s.n. (GH). Holotype of *B. ravenelii* on the left.



Figure 43. *Boltonia cuneifolia*. Berkeley Co., South Carolina. Ravenel s.n. (BRU). Possible isotype of *B. ravenelii*.

Figure 44. *Boltonia cuneifolia*. Georgetown Co., South Carolina. Nelson 21621 (USCH).



Figure 45. *Boltonia cuneifolia*. Georgetown Co., South Carolina. Nelson 26285 (USCH).

Figure 46. *Boltonia cuneifolia*. Georgetown Co., South Carolina. Nelson 18698 (USCH).



Figure 47. *Boltonia cuneifolia*. Jasper Co., South Carolina. Anderson 8902 (FSU). Voucher, n = 9II.