

STENANTHIUM LEIMANTHOIDES AND *S. DENSUM* (MELANTHIACEAE)  
REVISITED, WITH THE DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT

The genus *Stenanthium*, distributed through much of eastern United States, has previously been circumscribed with four species. Herbarium and field research on *Stenanthium densum* and *S. leimanthoides* (Melanthiaceae) support the recognition of two new segregate species, *S. macrum* and *S. tennesseense*. Data are presented on morphology, phenology, habitat, and distribution of each of these four species. Selected specimen records, distribution maps, field photographs, and a key to these four species are provided.

RESUMEN

El género *Stenanthium*, distribuido por el este de los Estados Unidos, ha sido circunscrito previamente con cuatro especies. Investigaciones de Herbario y campo en *Stenanthium densum* y *S. leimanthoides* (Melanthiaceae) soportan el reconocimiento de la segregación de dos nuevas especies, *S. macrum* y *S. tennesseense*. Se presentan datos de su morfología, fenología, hábitat, y distribución de cada una de estas cuatro especies. Se aportan citas de especímenes seleccionados, mapas de distribución, fotografías de campo, y una clave de estas cuatro especies.

INTRODUCTION

Plants of *Stenanthium leimanthoides* (A. Gray) Zomlefer & Judd (= *Zigadenus leimanthoides* A. Gray) have traditionally been identified by their branched racemose inflorescences compared to the simple racemes of *S. densum* (Desr.) Zomlefer & Judd [= *Z. densus* (Desr.) Fern.] (Chapman 1897; Small 1933; Fernald 1950; Gleason 1952; Radford et al. 1968; Correll & Johnston 1970; Zomlefer & Judd 2002). *Stenanthium leimanthoides* inhabits shrub balds and boggy habitats in the southern Appalachian Mountains of West Virginia, Virginia, and North Carolina, and boggy or seepage habitats on the Coastal Plain of Delaware, New Jersey, and New York. The species was added to the flora of the Maryland Coastal Plain in 2007 (Knapp et al. 2011). Plants disjunct to central Tennessee, also with branched racemes, have traditionally been assigned to *S. leimanthoides* despite some morphological inconsistencies (Chester et al. 1993; Tennessee Flora Committee 2015).

*Stenanthium densum* has been recorded from wet savannas and seepage slopes on the Atlantic and Gulf Coastal Plain (i.e., no inland/upland populations), from Virginia south to Florida and Mississippi. However, during the twentieth century it became apparent that a significant number of populations from the Gulf Coastal Plain from Georgia to Texas bore branched racemes; accordingly, they were identified as *S. leimanthoides* (Anderson 1995; Carter et al. 2009; Morris 2012). Diggs et al. (2006) described the inflorescence of Gulf Coast *S. densum* (their concept included *S. leimanthoides*) as a raceme or panicle of racemes, and “while distinct in some areas, the two entities intergrade (size, inflorescence morphology, flowering time) in the Gulf Coast area.” They posited that “Plant size, which is determined by age and environment, appears to affect inflorescence morphology—smaller plants tend to have simple racemes, while larger plants develop panicles”; a concept originally suggested by McDearman (1984, 1994). Schwartz (2002) also synonymized *leimanthoides* within *densum* in her treatment of *Zigadenus* for the *Flora of North America*.

However, all *Stenanthium densum* specimens seen from the Atlantic Coastal Plain possess simple racemes (i.e., no robust plants with branched racemes occur). This throws into question the true identity of the Gulf Coastal Plain paniced plants. Anderson (1995) recognized the large plants with branched inflorescences in northwestern Florida as distinct from *S. densum*. He stated that “The taxonomic relationships are complicated further because the type specimens of *Z. leimanthoides* are relatively small plants from the mountains of North Carolina, whereas plants from the Florida Coastal Plain are very robust (they may represent a separate taxon).”

Carter et al. (2009) and Morris (2012) also recognized Gulf Coastal Plain *S. leimanthoides* as distinct from *S. densum*. In this paper we re-examine the identity of *S. leimanthoides* relative to *S. densum*.

#### METHODS

Field work by the senior author conducted in the 1990s and 2000s throughout the southern Atlantic Coastal Plain and the Gulf Coastal Plain provided data on morphology, habitat, and distribution of *Stenanthium* taxa and gave impetus to this study. Specimens of *S. leimanthoides* and *S. densum* were borrowed from BRIT, DUKE, FSU, GH, IBE, MISSA, NCU, TENN, and VDB. We contacted a number of botanists with field and herbarium knowledge of these taxa to fill in distribution gaps.

We assessed nine potential morphological characters: basal sheaths and their fibers, leaf width, inflorescence branching, pedicel bract shape and length, pedicel length, tepal length, and capsule length. For each character, 25 measurements or evaluations were made.

#### RESULTS

##### Morphology

One character considered to be useful in separating *S. leimanthoides* from *S. densum* is the basal gland on the tepals: "small" and "yellow" in *S. leimanthoides* and "obscure" in *S. densum* according to Gleason (1952); "with a deeper yellowish spot" in *S. leimanthoides* and "usually with a very small gland at base when fresh" in *S. densum* according to Fernald (1950). We observed that dried specimens of northern *S. leimanthoides*, and plants from central Tennessee, did indeed show a basal blotch of a darker hue than the rest of the tepal, and very slightly raised above the tepal surface. In living plants this blotch is pale yellow and indistinct. In contrast, we were unable to discern *any glands at all* in dried specimens or living plants of *S. densum* or Gulf Coast *S. leimanthoides* (pers. obs. and photographs). Pedicel length was eliminated from analysis after it became evident that length varied positively with age of the inflorescence or inflorescence branch (pers. obs.).

Table 1 displays characters that we found most informative in discriminating among the *Stenanthium* taxa under study. Basal sheath fibers are the remains of former leaf bases which remain loosely to tightly attached to the stem base. The color purple here is interpreted as "red-purple," not violet which has a much bluer tint. Leaf width measurements are of the widest blade of each plant. Pedicel bracts occur at the junction of the pedicel and the inflorescence rachis; we measured only bracts on the central rachis, not on branches. Capsule length includes the attenuate tip. "Northern *leimanthoides*" includes plants from lowlands of New York to Maryland and from the Appalachians of West Virginia to North Carolina. "Tennessee *leimanthoides*" includes plants from the Eastern Highland Rim and Cumberland Plateau of Tennessee. "Gulf Coast *leimanthoides*" includes plants from southern Georgia to eastern Texas. *Stenanthium densum* includes plants with unbranched inflorescences from the Coastal Plain of southeastern Virginia to central Florida and southeastern Mississippi.

The two major divisions in Table 1 are: "Northern *leimanthoides*"–"Tennessee *leimanthoides*" on the one hand, and "Gulf Coast *leimanthoides*"–"*S. densum* sensu stricto" on the other. Six characters serve to place each specimen into one division or the other. Basal sheath color, presence of basal sheath fibers, number of pedicels per centimeter of central raceme, tepal color post-anthesis, presence of tepal gland, and flowering dates cleanly distinguish between two groups of taxa. Thus, "Tennessee *leimanthoides*" aligns with "northern *leimanthoides*," differing in pedicel bract length and leaf width. Likewise, "Gulf Coast *leimanthoides*" aligns with *S. densum*, differing in larger size and in inflorescence branching.

Range disjunction (Fig. 1) coupled with morphological differences (in plant height, leaf width, and pedicel bract length) between the two northern taxa supports species level discrimination, as separate evolutionary entities based on morphology and biogeography.

The two Coastal Plain taxa differ in plant height, leaf width, and branched (vs. unbranched) inflorescences. In the field, the robust aspect of "Gulf Coast *leimanthoides*" is striking. However, this species occupies precisely the same seepage bog habitats (specimen label data and pers. obs.). The range maps of "Gulf Coast *leimanthoides*" (Fig. 2) and *S. densum* (Fig. 3) show that the former is in the minority in Georgia, but westward it becomes the majority in terms of numbers of populations and individuals, thus suggesting a gradual replacement distribution pattern. Curiously, branched inflorescences have been documented in Greenville County,

TABLE 1. Character states of **1**) *Stenanthium leimanthoides* from southern Appalachians plus Maryland to New York; **2**) *S. leimanthoides* (branched inflorescences) from central Tennessee; **3**) *S. leimanthoides* (branched inflorescences) from the Coastal Plain of Georgia and panhandle Florida west to Texas; **4**) *S. densum* from the Coastal Plain of Virginia to peninsular Florida and Mississippi. Measurements are in millimeters and n=25, unless otherwise stated.

Character state	Northern " <i>leimanthoides</i> "	Tennessee " <i>leimanthoides</i> "	Gulf Coast " <i>leimanthoides</i> "	<i>S. densum sensu stricto</i>
Basal sheath color	Brown, occasionally purplish brown	Brown, occasionally purplish brown	Purple	Purple
Basal sheath fibers	Densely clothed with fibers (rare specimens may be stripped of fibers during collecting)	Densely/moderately clothed with fibers (rare specimens may be stripped of fibers during collecting)	Without fibers (3/36 specimens have moderate number of fibers)	Without fibers (5/120 specimens have sparse to moderate fibers)
Width of largest leaves, mean	7.7	4.8	7.1	4.3
Plant height, mean	71.6 cm	87.8 cm	114.6 cm	67.8 cm
Inflorescence branched	Yes	Yes (11/12 specimens branched)	Yes	No (1/120 specimens branched)
Number of pedicels per 5 cm of central raceme, mean	32	32	42.5	44.5
Pedicel bract shape and length, mean	Attenuate, 4.5	Attenuate to acute, 3.3	Attenuate to acute, 3.7	Acute, 3.2
Tepal color post-anthesis, living plants	Dull green or olive; no purple tinge	Dull green or olive; no purple tinge	Dull white with purple tinge on margin or purple tinged throughout	Dull white with purple tinge on margin or purple tinged throughout
Tepal length, mean	3.7	3.8	3.6	3.4
Tepal gland	Present	Present	Absent	Absent
Capsule length	9.6	10.4	13.3	11.0
Flowering dates	22 Jun–5 Aug	1 Jun–26 Jul	15 Apr–9 Jun	8 Mar–19 Jun

Virginia [Fernald and Moore 15078 (GH), the specimen otherwise with the dimensions of *S. densum*], and unbranched inflorescences were reportedly found in Henderson and Tyler counties, Texas (MacRoberts et al. 1999)—suggesting that there may be incomplete genetic separation or developmental anomalies or variation that makes inflorescence branching a less than 100% effective character. It would be extremely useful to obtain data on potential interbreeding of these two taxa on the Gulf Coast. The senior author found mixed populations of both Coastal Plain entities at two sites in southern Mississippi (Jackson County, *Sorrie 9153* NCU), one in southern Alabama (Mobile County, *Sorrie 9159* NCU), and one in the panhandle of Florida during the course of field work in 1996–98. In one Mississippi population “intermediate” plants were seen; there was no obvious intergradation at the other sites (BAS, field notes). There is a critical need to voucher additional populations to determine the extent of intergradation between “Gulf Coast *leimanthoides*” and *S. densum*, and whether such intergradation is significant. Meanwhile, we prefer to recognize “Gulf Coast *leimanthoides*” at species level, as separate evolutionary entities with different but overlapping distributions, nearly always maintaining their separate morphological features even in their region of sympatry.

**Phenology.**—Table 1 shows a nearly non-overlapping range of flowering dates between the two northern/inland taxa and the two Coastal Plain taxa. Even allowing for differences in length of growing season, there is a striking difference in timing of the former taxa (late) vs. the latter (early).

**Taxonomy.**—The following taxonomic treatment includes four species of *Stenanthium*, based on modern evolutionary species concepts. We assert that the four entities here recognized are each separately evolving evolutionary lineages, based on multiple fields of evidence: they are phenetically distinguishable based on multiple characters, diagnosable, ecologically and biogeographically distinct, and largely or completely reproductively isolated from one another by phenology and other factors (de Quieroz 2007).

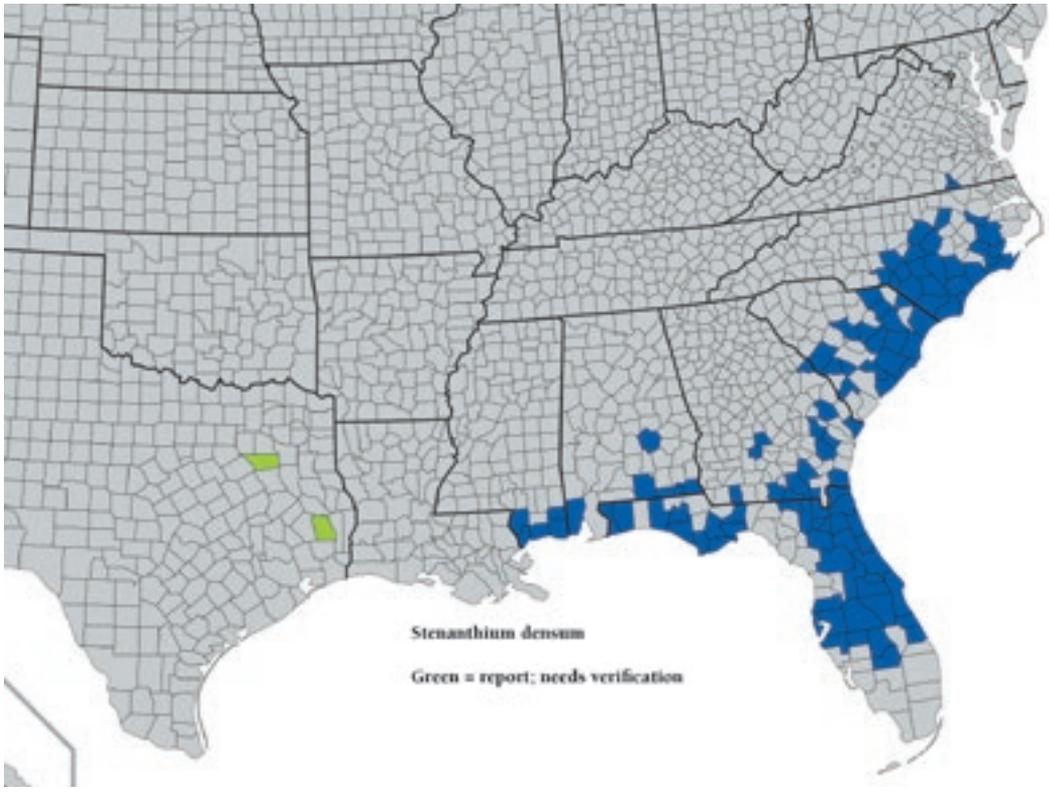


Fig. 1. Known distribution of *Stenanthium densum*, based on herbarium records.

***Stenanthium leimanthoides*** (A. Gray) Zomlefer & Judd. (Fig. 4). See Zomlefer & Judd (2002) for publication data of basionym and lectotype.

Selected specimens examined. **DELAWARE.** New Castle Co.: 2 mi W of Wilmington, M. Crane's swamp, 11 Jul 1866, *Commons s.n.* (GH). **MARYLAND.** Cecil Co.: NE of Belvedere 0.8 km, freshwater seepage underlain by terraced gravel deposits, 4 Aug 2009, *Knapp et al. 2968* (FLAS, US). **NEW JERSEY.** Burlington Co.: low ground, 3 Jul 1866, *Parker s.n.* (F). Camden Co.: prope Haddonfield, 20 Jul 1837, *Durand s.n.* (GH, NY). Monmouth Co.: meadows near Shark River, 22 Aug 1854, *Hexamer s.n.* (GH). **NEW YORK.** Nassau Co.: *Bicknell s.n.* (NY). **NORTH CAROLINA.** Avery Co.: Grandfather Mountain, Sept 1843, *Gray s.n.* (GH); sheltered niches along ridgeline summit of Grandfather Mountain, elev. ca. 6000 ft, perianth becoming green and functional after anthesis, Jul 1953, *Barrell s.n.* (GH); dry rocky soil, thicket on mountainside 2 mi NE of Linville, 5 Aug 1922, *Randolph & Randolph 1203* (GH); **Burke Co.:** Table Mountain, 1835, *Curtis s.n.* (GH, NY). **Yancey Co.:** Mount Mitchell State Park, Commissary Ridge on old railroad grade, elev. 5800 ft, 25 Jul 1971, *McLeod 1375* (NCU). **PENNSYLVANIA.** [no county]: near Philadelphia, 22 Jun 1889, *Greenman 1250* (GH). **VIRGINIA.** Grayson Co.: Big Spring Bog, 26 Jul 1981, *S. & M. Bentley s.n.* (FARM). **WEST VIRGINIA.** Grant Co.: Dolly Sods, top of the mountain, growing with sphagnum moss in wet bog, 6 Aug 1977, *Farley s.n.* (MUHW). **Randolph Co.:** open riverbank, Shavers Fork below Cheat Bridge, 26 Jul 1997, *Grafton s.n.* (MUHW). **Tucker Co.:** Bear Rocks area of Dolly Sods, windswept plateau, 5 Aug 1995, *Suiter s.n.* (MUHW).

***Stenanthium tennesseense*** Sorrie & Weakley, sp. nov. (Fig. 5). TYPE: TENNESSEE. Grundy Co.: boggy meadow between Tracey City and Coalmont, 3 Aug 1947, *R.E. Shanks, A.J. Sharp, and E. Clebsch 5203* (HOLOTYPE: TENN!).

Similar to *S. leimanthoides*, but plants taller (mean 87.8 mm vs. 71.6 mm), leaves narrower (mean 4.8 mm vs. 7.7 mm), pedicel bracts shorter (mean 3.3 mm vs. 4.5 mm), and capsules longer (mean 10.4 mm vs. 9.6 mm).

Description. Perennial herb from a bulbous base, fibers from old leaf bases dense to moderately dense. Basal sheath brown (occasionally purplish brown). Leaves basal and near-basal, the few distal leaves much reduced; basal leaves 3–7 mm wide (mean 4.8) and up to 50 cm long. Stem simple, 65–108 cm tall (mean 87.8). Inflorescence a paniced raceme, branches 1–several. Tepals 6, ± elliptic, 3.0–4.0 mm long, white, fading

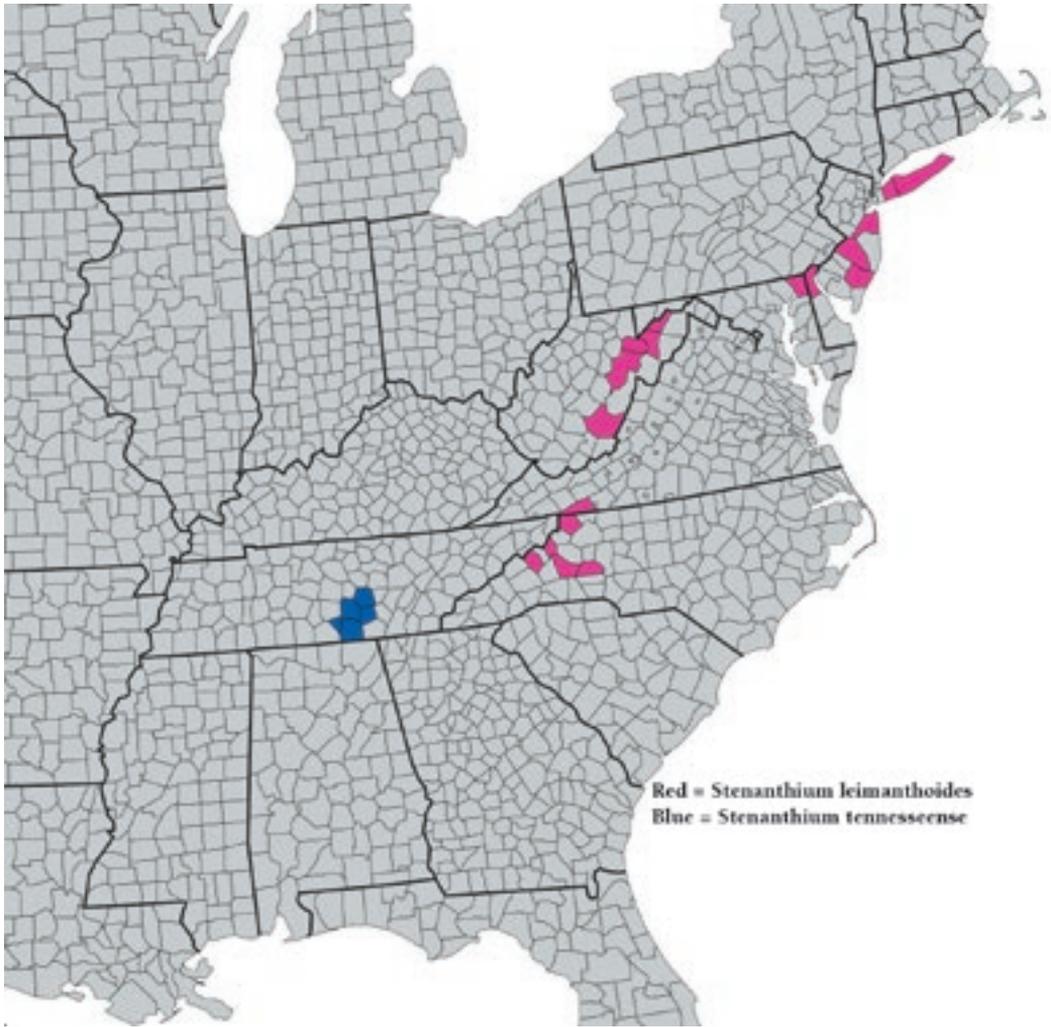


FIG. 2. Distribution of *Stenanthium leimanthoides* (red) and *Stenanthium tennesseense* (blue).

greenish post-anthesis. Tepal gland basal, very slightly raised, yellowish. Capsules narrowly conic, 8–13 mm long, (mean 10.4), greenish to brownish.

Selected specimens examined. **TENNESSEE. Coffee Co.:** open grassy swamps, oak barrens E of Tullahoma, 24 Jun 1938, *Svenson 9683* (BRIT, GH); Tullahoma, 10 Jul 1886, *Gattinger s.n.* (DUKE, F, NY); SE of Manchester, 3 Aug 1947, *Sharp and Shanks 5276* (TENN); just N of Manchester by I-24, 21 Jun 1974, *Kral 53219* (NY); peaty powerline just W of Arnold Space Center HQ, 6 Jun 1989, *Kral 76578* (VDB); wet open area under powerline near Gate 3, Arnold Engineering Development Center, 10 Jun 1980, *Horn 7* (VDB); Arnold Engineering Development Center, under powerline on access road 3 mi, W of main gate, 1 Jun 1992, *DeSelm s.n.* (TENN); Arnold Engineering Development Center, roadside wet barrens on hwy. 55 between Manchester and Tullahoma, several hundred flowering stems, 18 Jun 1993, *Pyne 93-132* (MO); low places in oak barrens just N of Manchester, 21 Jun 1974, *Kral 53219* (VDB); sandy peaty clearings in low oak barrens 1 mi. N of Tullahoma, 2 Jun 1982, *Kral 68708* (VDB); May Prairie State Natural Area, Hillsboro Road, mesic oak barrens, 25 Jun 1997, *Pyne 97-025* (APSC, NCU). **Franklin Co.:** Carter Mountain, remnant of swamp in clear-cut 0.8 mi from Rowe Gap Church, 1 Jul 1987, *Jones 4995* (EKY, TENN); same place 4 Jun 1987, *Jones 4840* (VDB). **Grundy Co.:** swamp on N rim of Savage Gulf, Savage Gulf Natural Area, 26 Jul 1977, *Wofford & Webb 77-223* (TENN); Savage Gulf, swamp on north rim, 13 Jun 1979, *Eagar & Nossi s.n.* (VDB); boggy meadow between Tracey City and Coalmont, 3 Aug 1947, *Shanks, Sharp, and Clebsch 5203* (holotype, TENN); peat of swale in oak-pine, 5 mi. W of Altamont, 12 Jun 1991, *Kral 78911* (VDB). **Moore Co.:** SW of Tullahoma, Cumberland Springs WMA, growing in barrens along highway 130, 31 Jul 2002,

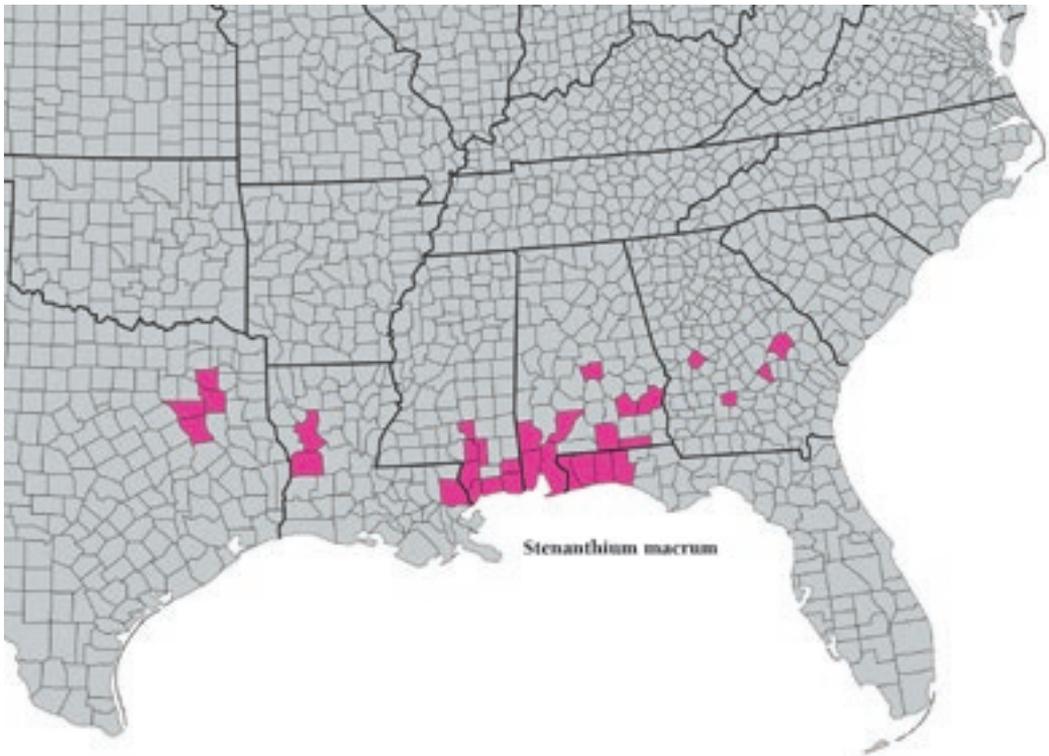


Fig. 3. Known distribution of *Stenanthium macrum*.

Estes 03806 (TENN); 4 mi W of Tullahoma, swampy places in woods, 5 Jun 1936, *McVaugh 4447* (GA). **Warren Co.:** low wet area along route 55, just N of Morrison, 10 Jun 1999, *Rhinchart s.n.* (TENN).

*Etymology.*—The species is endemic to Tennessee.

*Conservation.*—*Stenanthium tennesseense* should be of conservation concern, as it only occurs in five counties, four with current or recent records and Grundy with historical records only. There are only 20 known collections, suggesting that *S. tennesseense* warrants a status survey to assess its population status.

***Stenanthium densum*** (Desr.) Zomlefer & Judd. (Fig. 6). See Zomlefer & Judd (2002) for publication data of basionym and holotype.

Selected specimens examined. **ALABAMA. Covington Co.:** Conecuh National Forest, Bass Road, pitcher plant bog, 9 May 2014, *Diamond 25079* (TROY). **Houston Co.:** (TENN). **Mobile Co.:** May 1845, *Sullivan s.n.* (GH). **FLORIDA. Franklin Co.:** 11.8 mi E of Carrabelle Beach on U.S. 98, 20 Apr 1991, *Mears s.n.* (FLAS). **Hardee Co.:** 3 mi S of Zolfo Spring along railroad track, 24 Apr 1980, *Wunderlin, Hansen, & Semple 8607* (FLAS). **Hillsborough Co.:** Hulsey Meadow, formerly open wet pineland, burned over and cleared, 16 Apr 1966, *Lakela 29566* (NCU). **Lake Co.:** roadside of hwy. 98 between Lakeland and Dade City, 3 Apr 1970, *Wofford 10403* (TENN). **Nassau Co.:** along route 200 about 17 mi SW of Callahan, 7 Apr 1962, *Will, Jr. s.n.* (NCU). **GEORGIA. Camden Co.:** exposed roadside along route 252 about 4 mi W of White Oak, 18 Apr 2001, *McNeilus 01-63* (TENN). **Echols Co.:** low exposed area along route 94 about 3 mi W of Clinch County line, 22 Aug 1993, *McNeilus 93-1907* (TENN). **Richmond Co.:** *Olney s.n.* (GH). **Wilcox Co.:** low moist savanna between US 280 and railroad, 3.6 mi W of Rochelle, 3 Jul 1960, *Browne, Jr. 2553* (NCU). **MISSISSIPPI. Hancock Co.:** about 5 mi NE of Santa Rosa, low wet flatwoods, 26 Apr 1981, *McDaniel 24974* (TENN). **Jackson Co.:** Pecan, route 90 near Alabama state line, 16 Apr 1988, *Hill 19127* (GH); Mississippi Sandhill Crane National Wildlife Refuge, wet savanna just N of old headquarters, 30% of plants with branched inflorescences, 16 Apr 1997, *Sorrie 9153* (NCU). **NORTH CAROLINA. Brunswick Co.:** upland bog-clearing, 14 mi N of Southport, Orton Plantation, 17 May 1941, *Godfrey, Pl. Exs. Gr. 1123* (GH, TENN). **Carteret Co.:** Croatan National Forest, savannah, Millis Road, 23 May 1978, *Dorr 1461* (NCU). **Moore Co.:** Southern Pines, 12 Jun 1920, *Bequaert 3534* (GH). **Wake Co.:** Mitchell's Mill, eastern part of Wake County, 29 Sep 1932, *Coker & Totten s.n.* (NCU). **SOUTH CAROLINA.** [no county], "cette espece croit dans las lieux plus eleves et moins humides, Basse Caroline," *Michaux s.n.* (GH photo)



FIG. 4. *Stenanthium leimanthoides*. A. Cecil Co., Maryland. Photo W. Knapp. Note that corollas fade to greenish color. B. Grayson Co., Virginia. Photo Wilson.

of specimen at P). **Beaufort Co.:** sandy field, Beaufort, 26 Apr 1917, *Churchill s.n.* (GH). **Charleston Co.:** sold by Negroes in market under name of “Black Snakeroot,” *Robinson s.n.* (GH). **Williamsburg Co.:** Savannah near US 521, 3 mi NW of Greeleyville, 21 Apr 1957, *Radford 21273* (NCU). **VIRGINIA. Greensville Co.:** sphagnous bog about 1 mi NW of Dahlia, 7 Jun 1946, *Fernald & Moore 15078* (GH) [specimens show branched and unbranched inflorescences].

***Stenanthium macrum*** Sorrie & Weakley, sp. nov. (Figs. 3, 7). TYPE: ALABAMA. MOBILE CO.: S of Theodore in sunny moist field, common locally with *Dichromena latifolia* and *Calopogon tuberosus*, 1 May 1965, R. Deramus 420 (HOLOTYPE: NCU!; ISOTYPES: IBE!, VDB!).

Similar to *S. densum*, but plants much taller (mean height 115 cm vs. 68 cm), leaves much broader (mean width of largest leaves 7.1 mm vs. 4.3 mm) and inflorescence branched (vs. unbranched).

**Description.** Perennial herb from a bulbous base, lacking fibers from old leaf bases (rarely possessing moderate numbers of fibers). Basal sheath purple. Leaves basal and near-basal, the few distal leaves much reduced; basal leaves 5–12 mm wide (mean 7.1) and up to 50 cm long. Stem simple, 70–155 cm tall (mean 115). Inflorescence a paniced raceme, branches 1–several. Tepals 6, ± elliptic, 3.0–4.4 mm long, white, fading purplish post-anthesis. Tepal gland absent. Capsules slender-conic, 11–16 mm long (mean 13.3), purplish to brownish.



FIG. 5. *Stenanthium tennesseense*. Coffee Co., Tennessee. Photo M. Pyne.



Fig. 6. *Stenanthium macrum*. A & B. Jackson Co., Mississippi. Photos B. Sorrie.

Selected specimens examined. **ALABAMA. Autauga Co.:** M. & O. railroad right-of-way in bottoms of Bridge Creek, 9 Jun 1927, *Harper s.n.* (GH). **Baldwin Co.:** mesic roadside, 3 mi N of Gulf Shores on hwy. 59, 14 May 1971, *Evans 45982* (TENN). **Barbour Co.:** 30 May 2008, *Morris s.n.* (TROY). **Covington Co.:** low moist roadside just N of Mount Olive, 10 May 1967, *Jones, Jr. 12266* (BRIT, FSU). **Geneva Co.:** 6 mi S of Ganer, savannah bog and swales in sandhills, 4 Jun 1972, *Kral 47183* (VDB). **Mobile Co.:** 7.5 mi S of Theodore in sunny moist field, common locally with *Dichromena latifolia* and *Calopogon tuberosus*, 1 May 1965, *Deramus 420* (holotype NCU; isotypes IBE, VDB). **Monroe Co.:** bottoms ca. 4 mi S of Monroeville off US 84, 3 May 1972, *Kral 46271* (FSU, GH, VDB). **Pike Co.:** sandy peat of pineland creek swale by route 10, 3.4 mi NW of Clio, 7 Jun 1976, *Kral 58189* (VDB). **Washington Co.:** ca. 1.5 mi N of Wagarville, sandy peat of pineland bog, 1 Jun 1972, *Kral 47056* (AUA, VDB). **FLORIDA. Escambia Co.:** along creek S of Nine Mile Road, W of Pensacola, 27 May 1984, *Burkhalter 9390* (FLAS, FSU). **Okaloosa Co.:** Eglin Air Force Base, sunny seepage slope under power line along Turkey Creek, 9 Jun 1994, *Anderson 14944* (FSU). **Walton Co.:** shaded baygall bordering seepage slope, Blount Mill Creek drainage, 29 Jul 1994, *Anderson 15140* (FSU). **GEORGIA. Emanuel Co.:** springy place in sandhills, Fifteen Mile Creek, 3 Jul 1901, *Harper 989* (GH). **Taylor Co.:** 1876, *Neisler s.n.* (GH). **Turner Co.:** along branch swamp 5.1 mi ENE of Ashburn, 1970, *Faircloth 6714* (GA, NCU). **LOUISIANA. Natchitoches Par.:** Kisatchie National Forest, large clearcut N of FS 366, E of Kisatchie Bayou Camp, 9 Jul 1988, *Thomas 105524* (EKY, NLU). **St. Tammany Par.:** Money Hill TNC preserve, 27 Apr 2002, *Tran & Urbatsch 8* (LSU). **Vernon Par.:** Kisatchie National Forest, pitcher plant bog, *MacRoberts & MacRoberts 1646* (VDB). **MISSISSIPPI. Covington Co.:** low moist roadside just N of Mount Olive, 10 May 1967, *Jones, Jr. & Reynolds 12266* (MISS). **Forrest Co.:** Camp Shelby Training Site, abundant in long curving depression with *Sarracenia alata*, W side Poplar Creek, 1 Jun 2006, *Leonard 12275* (NCU). **George Co.:** *Sarracenia* bog, Lucedale, 16 May 1954, *Demaree 35202* (GH). **Hancock Co.:** Dead Tiger Savanna, common, 12 May 1984, *McDaniel 27693* (IBE). **Harrison Co.:** Landon, boggy pine barrens, 7 April 1913, *Lowe s.n.* (MISSA). **Jackson Co.:** pitcher plant bog 3 mi S of George Co. line on rte. 57, 24 Apr 1965, *Pullen 6527* (NCU). **Lamar Co.:** 2.5 mi S of Purvis, low area near longleaf pine woods, 6 May 1962, *McDaniel*



FIG. 7. *Stenanthium densum*. A & B. Hoke Co., North Carolina. Photos B. Sorrie. In 7a, note that corollas fade to purplish color.

3136a (IBE). **Pearl River Co.:** low pine woods, I-59 just S of Lumberton exit, 3 May 1967, Jones, Jr. 11980 (NCU). **TEXAS. Anderson Co.:** Gus Engeling Wildlife Management Area, Andrew's pitcher plant bog, 3 May 1998, MacRoberts & MacRoberts 3820 (LSUS). **Henderson Co.:** Bridges & Orzell 7180 (BRIT). **Smith Co.:** Swan, swamps, 16 May 1902, Reverchon 2772 (GH, MO). **Wood Co.:** "specimen from Highway Flower Show, McKinney," 17 May 1940, Stillwell s.n. (BRIT).

*Etymology.*—The epithet *macrum* refers to the tall plant height and large leaves. The plants are among the tallest spring-flowering herbs in Gulf Coast seepage bogs (see Figure 6a where they tower over *Sarracenia alata* (Wood) Wood).

*Conservation.*—*Stenanthium macrum* is widespread and has no real threats.

The following key will distinguish the four species of *Stenanthium* here recognized.

1. Basal sheaths brown (occasionally purple tinged), densely to moderately clothed with remnant fibers; inflorescence branched; number of pedicels per 5 cm of raceme 22–50 (mean 32); tepals fade to dull green or olive on living plants; summer-flowering (mainly Jun–Jul); southern Appalachian Mountains and on lowlands of New York–New Jersey–Delaware–Maryland, and disjunct in central Tennessee.
2. Pedicel bracts 3–6.5 mm long (mean 4.5) long; largest leaves 3–11 mm wide (mean 7.7); southern Appalachian Mountains and northern Atlantic Coastal Plain **S. leimanthoides**
2. Pedicel bracts 2.5–5.5 mm long (mean 3.3) long; largest leaves 2.5–7 mm wide (mean 4.8); central Tennessee **S. tennesseense**

1. Basal sheaths purple, fibers absent (occasionally sparse, rarely moderate); inflorescence unbranched or branched; tepals fade to purple on living plants; spring flowering (mostly Mar–May); southern Atlantic and Gulf Coastal Plain, from southeastern Virginia south to peninsular Florida and west to eastern Texas.
3. Plants short (mean 68 cm); largest leaves 3–5(–7) mm wide (mean 4.3); inflorescence simple; southern Atlantic Coastal Plain and East Gulf Coastal Plain, southeastern Virginia south to peninsular Florida, west to southern Mississippi \_\_\_\_\_ **S. densum**
3. Plants tall (mean 115 cm); largest leaves 4–10(–12) mm wide (mean 7.1); inflorescence branched (rarely simple); East Gulf Coastal Plain and West Gulf Coastal Plain, from Georgia to eastern Texas \_\_\_\_\_ **S. macrum**

## DISCUSSION

**Distribution Patterns.**—Distribution patterns of the four species examined in this study have strong parallels among other plant taxa. First, many species endemic to the Coastal Plain exhibit a distribution similar to that of *S. densum* (Sorrie & Weakley 2001). For example, *Bulbostylis ciliatifolia* (Ell.) Fern. var. *ciliatifolia*, which ranges from southeastern Virginia to southern Mississippi; *Eupatorium linearifolium* Walt., which ranges from southeastern Virginia to southern Louisiana; *Calopogon pallidus* Chapm., which ranges from southeastern Virginia to southeastern Louisiana; and *Digitaria serotina* (Walt.) Michx., which ranges from southeastern Virginia to southern Alabama.

Second, the disjunction within *S. leimanthoides* sensu stricto—from the Coastal Plain of the northeastern states to the southern Appalachian Mountains—is a documented phylogeographic pattern, matched by *Helonias bullata* L., *Xerophyllum asphodeloides* (L.) Nutt., and nearly matched by *Juncus caesariensis* Coville and *Kalmia buxifolia* (Berg.) Gift, Kron, & Stevens (Sorrie & Weakley 2001).

Third, the disjunction shown between *S. leimanthoides* and *S. tennesseense*—from the southern Appalachians to central Tennessee—is apparently uncommon but has been documented for several species. As examples we cite *Glyceria acutiflora* Torr. and *Vaccinium macrocarpon* Ait., both of which have a northeastern range which extends down the Appalachians, thence disjunct to central Tennessee (Pyne 2000).

**Species Biology.**—McDearman (1984, 1994) postulated that branched inflorescences in *Stenanthium leimanthoides* sensu lato result from a developmental delay as compared with simple racemes of *S. densum*. He stated: “In the mountains and northern Atlantic Coastal Plain, the first reproductive episode occurs in plants at larger size classes, resulting in a compound raceme (delayed reproduction). Southward on the Coastal Plain to west Florida, the onset of reproduction occurs at smaller size classes, associated with a single terminal raceme, and plants do not appear to attain sizes for reproductive effort to result in a compound raceme [i.e., *S. densum* sensu stricto]. Further westward from west Florida to Louisiana, plants reproduce at small classes and grow and survive to larger classes, resulting in individuals producing simple as well as compound racemes” (McDearman 1994).

Based on observations of mixed populations on the Gulf Coastal Plain—some plants with simple inflorescences, others branched—McDearman reasoned that plant development and age may account for large individuals with branched inflorescences. “Plant size at the first episode of reproduction is small, with correspondingly small reproductive effort, resulting in fewer flowers arranged on a single terminal raceme. With increasing plant size (and age), absolute reproductive increases, number of flowers increases, and inflorescence morphology shifts from a simple terminal raceme to a compound raceme” (McDearman 1994).

However, we have not been able to corroborate the scenario put forth by McDearman. All montane and northern Atlantic Coastal Plain plants (*S. leimanthoides* sensu stricto) we have observed produce branched inflorescences over a wide range of plant height (range 47–109 cm) and leaf width (range 3.0–11.0 mm). We are unable to detect meaningful size classes. Plants of the southern Atlantic Coastal Plain, ranging west to southern Mississippi, produce only simple racemes (*S. densum* sensu stricto), with a range of plant height (range 36–85 cm) and leaf width (range 2.0–8.0 mm) and no discernable size classes.

We concur that there appear to be plants of intermediate size between *S. macrum* and *S. densum*; however, to date they have been found only very locally at a few sites in Florida and Mississippi. The vast majority of populations of *S. densum* and *S. macrum* maintain their morphological differences throughout the overlap zone of southern Georgia to southern Mississippi.

In conclusion, our analyses point to a taxonomy based on morphology and biogeography, not on a developmental basis.

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