

TOWARDS A REVISION OF THE *ERYNGIUM INTEGRIFOLIUM* COMPLEX (APIACEAE)

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ABSTRACT

A preliminary taxonomic treatment of the *Eryngium integrifolium* Walt. complex is presented. We recognize five species, with two additional taxa treated at varietal rank, based on a morphometric analysis as well as ecological and biogeographic evidence, pending further phylogenetic review. *Eryngium ludovicianum* Morong is recognized at species rank, along with a new combination for *E. integrifolium* var. *lanceolatum* Wolff. at species rank, two undescribed species from the inland southeast, and three varieties recognized within *E. integrifolium* sensu stricto, which is restricted here to the outer Atlantic and Gulf coastal plains and inland bogs and seeps of the Blue Ridge and Piedmont. New nomenclature: ***Eryngium altamaha* Kees, Weakley, & Poindexter, sp. nov.**; ***Eryngium mississippiense* Kees, Weakley, & Poindexter, sp. nov.**; ***Eryngium integrifolium* var. *maficolum* Kees, Weakley, & Poindexter, var. nov.**; ***Eryngium integrifolium* var. *piedmontanum* Kees, Weakley, & Poindexter, var. nov.**; ***Eryngium lanceolatum* Kees, Weakley, & Poindexter, comb. et stat. nov.** A Principal Component Analysis (PCA) of 22 morphometric traits is provided, along with a Linear Discriminant Analysis (LDA), Multivariate Analysis of Variance (MANOVA), and Pairwise Adonis Test using 19 quantitative vegetative and inflorescence characters chosen based on the PCA results. We provide a new taxonomic key to the complex as well as a range map, diagnoses for newly described taxa, and notes on habitat, phenology, nomenclature, and conservation status for all taxa treated.

Eryngium L. is the largest genus in the Apiaceae, comprising around 250 species, perennial and annual herbs, tropical and temperate. It is a taxonomically complex genus, with an evolutionary history of rapid radiations, hybridization, and long-distance dispersal (Calvino et al. 2010). Weakley (2022) has recognized 18 taxa in the southeastern USA — 4 naturalized and 14 native. Nearly all native southeastern USA *Eryngium* species occur primarily in grassland and open woodland habitats, often in wetland, and a number are closely associated with the endangered longleaf pine ecosystem (Weakley 2022). The highest diversity is in panhandle and peninsular Florida, aligned with major centers of vascular plant endemism on the North American Coastal Plain. The North American Coastal Plain is a biodiversity hotspot rich in imperiled vascular plant endemics (many of which are grassland species), which continues to yield new species, and more careful taxonomic investigation of species complexes in the region is critically needed — rare plants rarely receive protection without formal taxonomic recognition (Noss et al. 2015; Noss et al. 2021).

Eryngium integrifolium Walt. sensu lato is endemic to the southeastern USA and occurs in a wide range of open wetland habitats, including longleaf pine savannahs, sandhill seeps and pocosin margins, forested seepages and wet terraces, mountain bogs, wet prairies, wet flatwoods, and roadside ditches, and generally in wet, acid soils. Its range is highly fragmented, with major population centers

on the outer Atlantic Coastal Plain and East Gulf Coastal Plain (centered on the Florida panhandle), West Gulf Coastal Plain, and the Post Oak Savannah region of Texas, widely scattered inland. It has been variously treated as a single species, a single species with three varieties (Wolff 1913), and two distinct species — one mostly southern Gulf Coastal Plain and the other more widely distributed. Morphologically *E. integrifolium* is easily differentiated from all other southeastern species by its branched inflorescences of blue-flowered heads and unlobed, toothed, elliptic to linear-lanceolate cauline leaves less than 10 cm long (Weakley 2022). It sometimes occurs sympatrically with *E. baldwinii*, *E. yuccifolium*, *E. synchaetum*, *E. aquaticum*, and *E. prostratum*.

At least seven different names have been subsumed under the current concept of *Eryngium integrifolium*. Calvino & Levin (FNA, submitted) and Weakley (2022) both have treated *E. integrifolium* as a single species with no infraspecific taxa. The species complex was originally described under the name *E. integrifolium* in Walter's (1788) *Flora Caroliniana*. It was subsequently treated as *E. virgatum* in Lamarck's 1798 *Systema Vegetabilia*, and as *E. ovalifolium* in Michaux's *Flora Boreali-Americana*, though neither Lamarck nor Michaux designate a type specimen. Walter's *Flora* treated only three species, *E. integrifolium*, *E. foetidum*, and *E. aquaticum*; Roemer & Schultes' description for *E. americanum* apparently corresponds to *E. integrifolium* sensu stricto, although it includes a confusing reference to procumbent stems, which I have only rarely observed in material of *E. integrifolium*.

Morong (1887) described *Eryngium ludovicianum*, designating a type specimen from northwestern Louisiana. The holotype has narrow, linear-lanceolate leaves with remote teeth and smaller heads than typical *E. integrifolium* and clearly fits the concept of *E. ludovicianum* presented here. Small (1903) maintained *E. ludovicianum* at species rank, without citing collections, but mentioning smaller head diameter in addition to the obvious vegetative distinctions between the two species, and a range from Texas east to Georgia. Wolff (1913) treated *E. ludovicianum* at varietal rank under *E. integrifolium*, following Roemer & Schultes, but described a new entity, var. *lanceolatum*, citing an illustration from Rusk Co., Texas. I was unable to locate the plate cited as the type var. *lanceolatum*, but given the locality and Wolff's description, var. *lanceolatum* most likely refers to the entity treated here as *E. lanceolatum*. Subsequent treatments, including Calvino & Levin (FNA, submitted) and Weakley (2022), have lumped all three entities into *E. integrifolium*.

We here present rationale for the recognition of all three entities (*Eryngium ludovicianum*, *E. integrifolium*, and *E. lanceolatum*) at species rank, as well as two distinctive species described here from the interior South (*E. altamaha*, *E. mississippiense*). Two additional taxa, of the Piedmont and Blue Ridge eastward, are recognized at varietal rank under a narrower concept of *E. integrifolium*. Further investigation may reveal that several of the entities treated here at varietal rank or as informal variants may warrant specific rank.

MATERIALS AND METHODS

Herbarium loans were obtained from BRIT, UNA, MMNS, AHNC, APSC, LSU, and DUKE, and specimens were examined at NCU and MMNS herbaria for vegetative and mericarp measurements. 119 physical specimens were measured in total for our morphometric analysis. We have reviewed all digitized specimen images available in SERNEC virtually in order to determine relative ranges of the five taxa; 309 additional specimens are cited here for county-level distributions, by barcode or catalog number (where available). Geographic range and habitat preference were considered in addition to morphometrics in diagnosing taxa — allopatry and parapatry were considered as additional evidence for distinctiveness. Characters used in the morphometric analysis were length/width ratio, teeth/length, teeth/side, petiole length, and teeth/cm at midlength for upper and midculm-blades and terminal bracts, and length/width of the largest tooth/lobe on the terminal bracts. A Principal Component Analysis was performed using the `corr` and `ggcorrplot` packages in R to analyze morphometric measurements; we

then conducted a multiple discriminant analysis (LDA) and MANOVA in R using dplyr, and an additional Pairwise Adonis test to evaluate distinctions between individual species pairs.

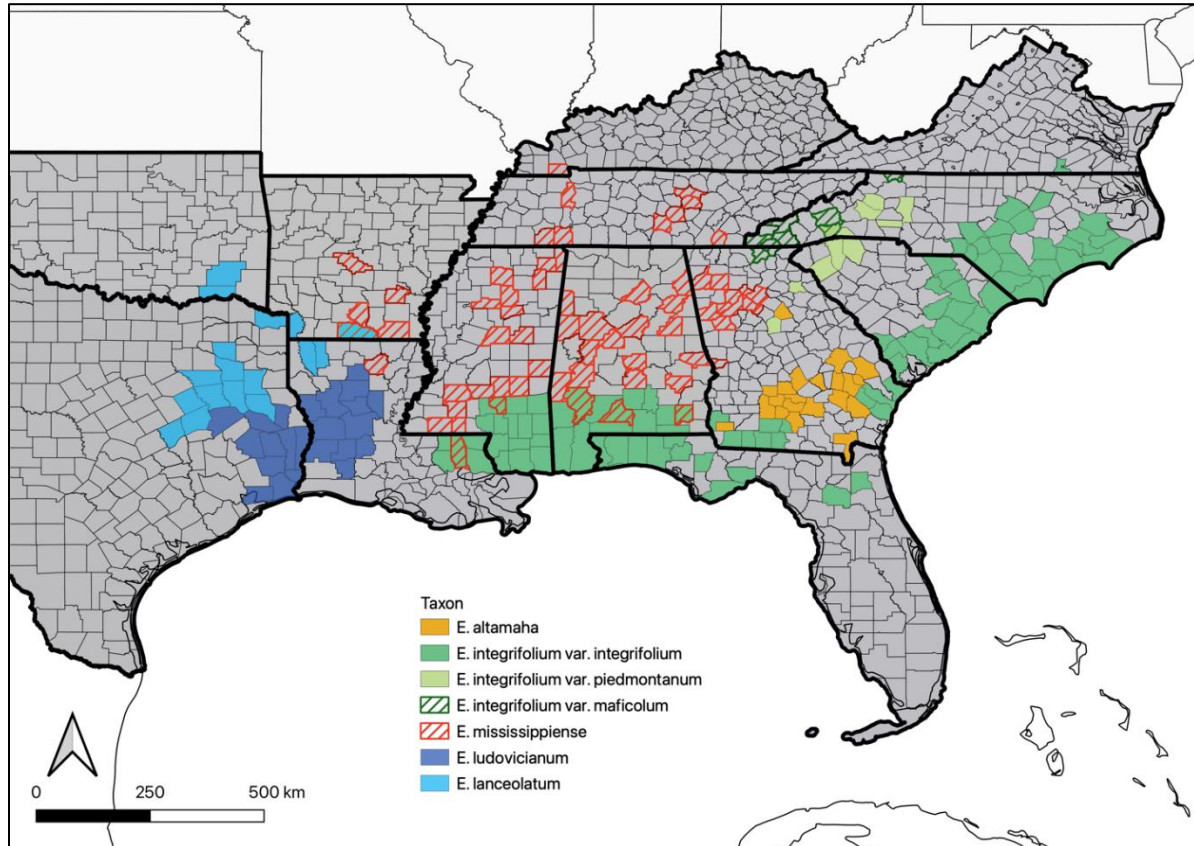


Figure 1. Distribution of the *Eryngium integrifolium* complex.

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RESULTS

Our morphometric analysis provides strong support for the existence of 7 morphologically distinct and geographically correlated entities in the *Eryngium integrifolium* complex. The multiple discriminant analyses showed highly significant morphological differentiation between the taxa in the *E. integrifolium* group. Overall classification success was 78.7%, with a p-value <0.001 recovered from the MANOVA. P-values were also < 0.001 for 18 of 19 characters used in the LDA, suggesting

that nearly all characters used in the analysis (measurements of length/width, petiole, and marginal teeth of mid-cauline leaves, distal cauline leaves, and inflorescence bracts, and inflorescence bract lobing) have significant discriminatory power. Head and mericarp measurements (mentioned in Small) were not recorded in the data set, but might provide additional support for *E. ludovicianum* and *E. altamaha*, which tend to have slightly smaller heads and smaller mericarps with sparser scales.

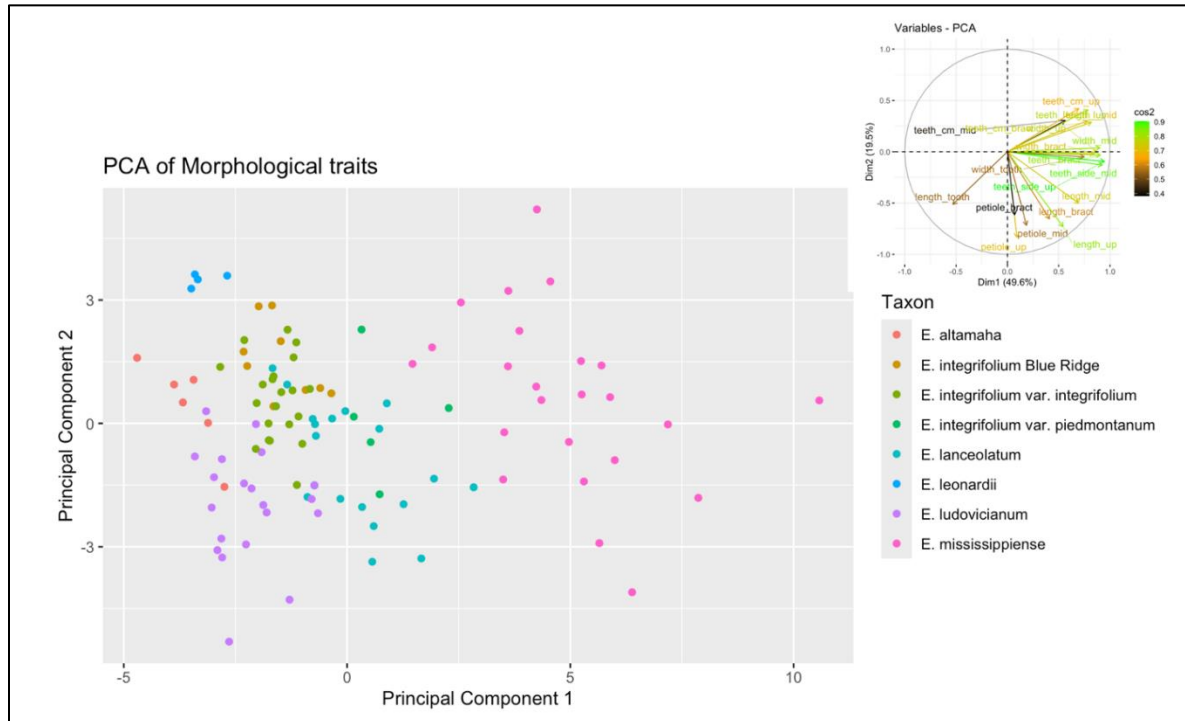


Figure 2. PCA of 22 morphometric traits.

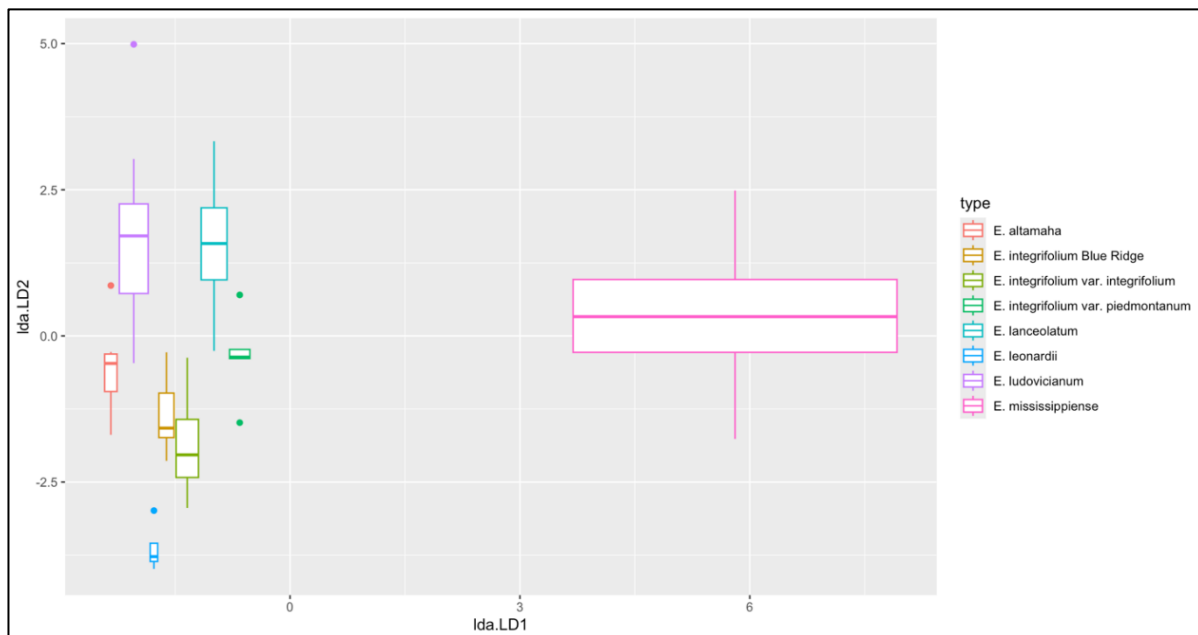


Figure 3. Boxplot of LDA of 19 morphometric traits.

Collections fall into three major clusters along the second Principal Component axis (Fig. 1), with little overlap – *Eryngium ludovicianum* and *E. altamaha* of the West Gulf Coastal Plain and GA, respectively, oriented negative, *E. mississippiense* positive, and *E. lanceolatum* and the four *E. integrifolium* entities (*E. “leonardii”*, *E. integrifolium* Blue Ridge, *E. integrifolium* var. *piedmontanum*, *E. integrifolium* var. *integrifolium*) between the two. *E. integrifolium* “Blue Ridge” is embedded in *E. integrifolium* var. *integrifolium*. Although most specimens sort easily, *E. integrifolium* var. *piedmontanum* and *E. integrifolium* var. *integrifolium* both show some degree of morphological overlap with *E. “lanceolatum.”* There is also a small overlap between *E. ludovicianum* var. *ludovicianum* and *E. altamaha*. Both species pairs are widely disjunct, separated by the Mississippi River and several major phylogeographic breaks, with the intervening space occupied by *E. mississippiense* and *E. integrifolium* var. *integrifolium*. One group of collections by Steve Leonard from Perry Co., Mississippi (denoted “*E. leonardii*” in morphometric analyses), are isolated in the PCA.

Incorrect *a posteriori* assignment by the LDA appears to be largely explained by species pairs which are widely geographically disjunct and therefore likely unrelated (see Fig. 2). The pairwise Adonis test (see Table 1) returned comparatively high p-values for *Eryngium integrifolium* var. *piedmontanum* and *E. lanceolatum* ($p=0.0458$), *E. altamaha* and *E. “leonardii”* ($p=0.0141$), *E. integrifolium* var. *piedmontanum* and *E. mississippiense* ($p=0.0080$), *E. ludovicianum* var. *E. ludovicianum* and *E. altamaha* ($p=0.0027$), and between the four *E. integrifolium* sensu stricto entities ($0.02 > p > 0.01$); all other p-values were < 0.002 . The moderately significant value for *E. altamaha* and *E. “leonardii”* may be an artifact of comparatively poor sampling of these two entities, as they are very easily differentiated even in vegetative condition. *Eryngium integrifolium* var. *piedmontanum* is morphologically intermediate between *E. mississippiense* and *E. integrifolium* “Blue Ridge,” and it is possible that it is derived from hybridization between montane *E. integrifolium* populations and a likely more recent eastward dispersal of *E. mississippiense*.

Given the wide biogeographic disjunction and clear ecological differentiation between the four *Eryngium integrifolium* entities and *E. lanceolatum*, the small morphological overlap between the two taxa (primarily with the problematic var. *piedmontanum*) is perhaps attributable to pseudoconvergence. Reviewing specimens across the range revealed little introgression between *E. integrifolium*, *E. mississippiense*, and *E. altamaha*, suggesting that strong species boundaries are maintained even where they occur in close proximity, and morphological distinctions between the three species, particularly *E. mississippiense*, are well-supported by our LDA and pairwise Adonis test. Investigation of additional herbarium material, however, reveals potential introgression between *E. lanceolatum* and the western race of *E. mississippiense* (see discussion below); material in northwestern Louisiana and southern Arkansas, while clearly not *E. ludovicianum*, is difficult to assign and some specimens may key to *E. integrifolium* var. *piedmontanum*.

For the entities included here under *Eryngium integrifolium* sensu stricto, the high degree of morphological overlap, reflected in higher (but still significant) p-values, is consistent with treatment at varietal rather than species rank, although their apparent allopatry suggests this is a problematic taxonomic decision. Molecular analyses may reveal that they are justifiably recognized at specific rank. It also seems likely that there is significant differentiation between Atlantic and Gulf populations of var. *integrifolium* and that the Blue Ridge and upper Piedmont entities are more closely allied to *E. mississippiense* than to typical *E. integrifolium*, or basal to both.

Given the lack of any distinction in habitat preferences or biogeography, the dwarf, small-leaved plants denoted *E. integrifolium* “*leonardii*” in morphometric analyses presumably represent outliers in the already variable *E. integrifolium* sensu stricto and are here considered as an informal, unmapped variant. Examination of additional herbarium material reveals similar small-leaved plants at sporadic locations in the East Gulf Coastal Plain range and fairly continuous variation.

Although they are embedded in the PCA, the LDA and pairwise Adonis test provide some support for the distinction between *Eryngium integrifolium* “Blue Ridge” and var. *integrifolium*. *Eryngium integrifolium* “Blue Ridge” is perhaps most easily distinguished from var. *integrifolium* by its basal leaves, which tend to be narrower, more serrate, and held erect-ascending. Basal leaves are not preserved in any herbarium collections of *E. integrifolium* “Blue Ridge” and only in very few collections of var. *integrifolium*, as they wither well before anthesis, and were therefore not accounted for in our morphometric analysis. *Eryngium integrifolium* “Blue Ridge” is recognized here at varietal rank (as *E. integrifolium* var. *maficolum*), since these populations are separated from var. *integrifolium* by var. *piedmontanum*, which is well-supported by our morphometric analyses, widely disjunct, and they occur in dissimilar habitats (mafic seeps in “Blue Ridge” vs. highly acidic Coastal Plain bogs in var. *integrifolium*).

Eryngium altamaha and *E. ludovicianum* have somewhat similar habitat preferences (often associated with Miocene sandstone outcrops) in addition to superficial similarity in vegetative and floral morphology, but they are allopatric by over 500 miles, separated by extensive populations of *E. integrifolium* and *E. mississippiense*. Given that both have quite specific habitat preferences and very limited long-distance dispersal capacity, it is possible that the far-disjunct distribution of the two is relictual or representative of long-distance dispersal, but it seems more likely that they are only distantly related. *Eryngium integrifolium* (var. *integrifolium*) is known to have $n=8$ (Bell & Constance 1957) but other ploidy levels have not been recorded for the species. The coarser vegetative features of *E. mississippiense* are suggestive of polyploid derivation.

TAXONOMIC KEY

1. Bracts of terminal whorl pinnately 3-7-lobed, lobes linear to filiform; mid-culm blades narrowly lanceolate to linear, (5.5-)6.2-15(-18)× as long as wide; leaf margins remotely serrate (1-4 teeth per cm at midlength), teeth sharp, irregular, sometimes spinose; stems slender, wiry; [w Gulf Coastal Plain, or Inner Coastal Plain of GA].
 2. Mid-stem blades 2.3-3.5cm (\bar{x} = 3.0cm), usually with long spinose teeth basally; stems often flexuous and diffusely branching from near base; [e of the Mississippi River; GA] **E. altamaha**
 2. Mid-stem blades (3.2-)4.1-5.9(-8.9)cm (\bar{x} = 5.2cm), serrate to shortly spinose-serrate; stems erect, mostly single, branched above (branched throughout in robust plants of *E. lanceolatum*, then with stout, erect stems); [w of the MS River; LA, AR, TX].
 3. Leaves mostly linear-lanceolate, widest at about 1/3-1/2 length, 0.3-0.8(-1.2)cm wide; leaf teeth (1-)2-3(-4) per cm at mid-length, remote, varying from crenate-serrate (lower leaves) to spinose-serrate **E. ludovicianum**
 3. Leaves mostly deltate-lanceolate, widest near base, (0.7-)0.9-1.6(-1.8)cm wide; leaf teeth (3-)4-6 per cm at mid-length, regularly serrate or dentate (uppermost sometimes ±spinose-serrate) **E. lanceolatum**
1. Bracts of terminal whorl 3(-5)-lobed basally or unlobed, serrate, lanceolate to ovate; mid and upper cauline leaves mostly ovate to lanceolate, (1.5-)2-3(-4)× as long as wide; leaf margins serrulate to crenate-dentate (3-8 teeth per cm at mid-length), teeth frequently blunt or rounded; stems stout to slender, erect; [collectively widespread].
 4. Bracts of terminal whorl finely serrate, teeth (5-)7-14(-19) per side, ovate or elliptic; cauline leaves ovate to elliptic, (1.6-)2-4.3(-4.4) cm wide at mid-stem, serrulate (teeth >25 per side); plants robust: stems stout, heads commonly 20--50+; [inner Gulf Coastal Plain, Sedimentary Appalachians, and Piedmont] **E. mississippiense**
 4. Bracts of terminal whorl 3-lobed (or coarsely toothed), the terminal lobe with 1-3(-6) additional teeth per side, lanceolate to linear; cauline leaves mostly lanceolate or narrowly elliptic-ovate, (0.7-)0.9-1.8(-2.1) cm wide at mid-stem, serrate or crenate-serrate (teeth (6-)9-22(-26) per side, rarely more in

E. lanceolatum); plants smaller: stems slender to moderately stout, heads usually <25; [bogs and seepage slopes, mostly Coastal Plain, rarely Piedmont and Mountain bogs].

5. Mid-stem blades deltate-lanceolate, (3.4-)4-6(-6.7) × as long as wide, regularly serrate with small straight-sided teeth; petioles (1.6-)1.9-2.9(-3.6)cm, spreading; [w of the MS River] **E. lanceolatum**
5. Mid-stem blades blades elliptic-ovate, 2-3(-3.7)× as long as wide, sharply serrate (teeth curved or acuminate) to crenate-serrate; petioles (0.8-)0.9-1.6(-1.9)cm at mid-culm, usually sheathing the stem for most of their length; [e of the MS River].
6. Mid-stem blades sharply serrate, teeth 12-22(-26) per side; bracts of terminal whorl with irregular long teeth (or weakly 3-parted), teeth (3-)4-6(-8) per side (ignore 2° and 3° bracts); leaves and inflorescence branches often lax; [NC, SC; upper Piedmont and low mountains] **E. integrifolium** var. **piedmontanum**
6. Mid-stem blades sharply serrate to shallowly crenate-serrate, teeth (6-)9-12(-14) per side; bracts of terminal whorl tricuspidate, central lobe with an additional 1-2(-4) teeth per side (rarely merely coarsely serrate in var. *maficolum*); leaves and inflorescence branches stiff; [of the Coastal Plain from VA to w. LA, or of the Blue Ridge Mountains of NC and GA]
7. Basal leaves (withering by flowering) typically ascending, obovate to narrowly ovate-elliptic, often serrate to near apex; teeth of midstem leaves slender, acuminate (edges forming a ~15-30° angle); inflorescence branches erect; [plants of Mountain bogs of NC and GA, usually over mafic substrates] **E. integrifolium** var. **maficolum**
7. Basal leaves (withering by flowering) flat against soil surface, broadly ovate-elliptic or ovate, obscurely crenate in lower half to subentire; teeth of midstem leaves teeth usually rounded to bluntly acute (edges forming a 45-75° angle, the outer strongly convex); inflorescence branches spreading-ascending; [plants of the Coastal Plain from VA to e. LA, over acidic substrates] **E. integrifolium** var. **integrifolium**

1. ERYNGIUM ALTAMAHA Kees, Weakley, & Poindexter, **sp. nov.** **TYPE: Georgia.** Charlton Co.: Along GA Hwy 84, 31 Aug. 1978, *S.B. Jones 23085* (holotype: NCU, isotypes: GA, NCSC, LSU, MO).

Plants wiry, diffusely branched, flexuous, heads numerous; leaves <3.5cm long, narrowly lanceolate, with elongate basal teeth or lobes, petioles slender, spreading; primary and secondary array bracts pinnately dissected, segments filiform; bracts subtending individual florets tricuspidate; mericarps densely beset with scales.

Plants caespitose, stems one to several, from fibrous roots, rhizomes absent; stems and branches slender, often flexuous; leaves simple, alternate, coriaceous, proximal cauline usually withering by flowering, with a few spinose teeth basally, otherwise entire; mid-cauline 2.3-3.5cm long, (0.15-)0.2-0.6cm wide, coarsely and remotely serrate, teeth (2-)5-7(-10) per side, the lowermost elongate and spinose; upper cauline 1.5-2.4(-3.7)cm long, 0.1-0.4cm wide, coarsely and remotely spinose-serrate; petioles narrowed abruptly from base, scarcely sheathing stem; inflorescence cymose, heads numerous, terminal and usually with multiple additional inflorescences from leaf axils, often branching from near base; terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these filiform, pale, 1(-2)× pinnately dissected; heads subtended by a single whorl of 4-8 linear bracts, rigid or pliable, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide or slightly broader; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also moderately to densely beset with pale, appressed scales, deep brown or black surface usually visible beneath.



Herbarium of The University of Georgia
CHARLTON COUNTY
FLORA OF GEORGIA
Eryngium integrifolium Walt.
Along GA hwy 94 between St. George and road
to Camp Cornelia. Moist acid roadside.
Purplish-blue corollas.
w/ J. Bruce, N. Coile, K. Kirkman, M. Muir,
R. Lugato, H. Neufeld
Samuel B. Jones 23085 31 August 1978

Figure 4. Holotype of *Eryngium altamaha* (NCU).

The name *Eryngium altamaha* refers to the Altamaha grit outcrops, with which this novel taxon is frequently associated, and to the Altamaha River drainage basin, which is the core of its distribution.

Concept map. < *E. ludovicianum* Morong – Small (1903); < *E. integrifolium* Walter var. *ludovicianum* H. Wolff – Wolff (1913); < *E. integrifolium* Walter – Weakley (2022), FNA (2022); < *E. virgatum* Lamarck – Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. – Michaux (1803).

Distribution. *E. altamaha* is apparently endemic to the state of Georgia, occurring in the Inner Coastal Plain, associated with the Altamaha Grit and other undifferentiated Miocene geology, and very rarely (and perhaps only historically) disjunct in Piedmont bogs. It occurs primarily in Atlantic watersheds (Altamaha, Ocmulgee, Suwanee, Satilla), with one outlier in the Flint River drainage basin.

Habitat. Seepages and bogs in longleaf pinelands, particularly over Miocene sandstone.

Taxonomic Comments. This highly distinctive species has been confused with *E. ludovicianum* in prior treatments; Small (1903) gave the range of *E. ludovicianum* from TX to GA, presumably based on *E. altamaha*, although neither *E. ludovicianum* nor *E. altamaha* is known from MS, AL, or FL. *Eryngium altamaha* resembles *E. baldwinii* Sprengel in its weaker stems, very thin stems and inflorescence branches, and small leaves with strong basal leaf teeth or lobes (unique in the *E. integrifolium* complex), and may be derived from ancestral hybridization between *E. baldwinii* and the Atlantic race of *E. integrifolium* var. *integrifolium*; cytology for this species is unknown, but allotetraploid derivation is plausible.

Conservation. Owing to the highly restricted range and imperiled habitat, we suggest that a G1G2 conservation rank is appropriate for this taxon (see NatureServe ranking criteria in Faber-Langendoen et al. 2012). *Eryngium altamaha* is currently known mostly from historical collections. We are aware of fewer than five photographic records (on iNaturalist) within the past two decades and a handful of collections from the 1990s. Little protected, well-managed habitat exists within its range.

2. ERYNGIUM INTEGRIFOLIUM Walt., Fl. Carol. 112. 1788. **NEOTYPE** (Ward 2008): **South Carolina.** Berkeley Co.: Savannah 14 mi SW of Monks Cornder and about 6 mi NE of Summerville, 31 Aug 1950, *Wilbur & Webster 2861* (GH; isoneotypes: MICH, NY, US).

Eryngium virgatum Lam., Encycl. 4(2): 757. 1798. Protologue: "J'ai observé cette espèce dans l'herbier du citoyen Jussieu, où elle se trouve sans indication de lieu natal (V. s.)." The description corresponds to typical *E. integrifolium*.

Eryngium ovalifolium Michx., Fl. Bor.-Amer. 1: 163. 1803. Protologue: Hab. in subhumidis sylvaticis et pratensibus Carolinae. Floret Julio." Michaux cited "*E. americanum?* Walt." — his distribution and morphological description (dentate, oval leaves, tricuspidate bracts) closely corresponds to var. *integrifolium*.

Eryngium americanum Walt. ex Spreng., Syst. Veg., ed. 15 bis [Roemer & Schultes] 6: 337. 1820. Sprengel cited "Walt. Fl. Carol. p. 112" but Walter's species were *E. foetidum*, *E. aquaticum*, and *E. integrifolium* — Sprengel apparently meant his epithet to be "integrifolium" as his description mostly matches that of Walter.

2a. ERYNGIUM INTEGRIFOLIUM var. **INTEGRIFOLIUM**

Eryngium integrifolium var. *typicum* H. Wolff., Pflanzenr. (Engler) 4, Fam. 228: 161. 1913 [nom. illeg.]. Wolff cited collections from Alabama, Florida, Georgia, North Carolina, South Carolina, and Texas.

Plants caespitose, stems single, from fibrous roots, rhizomes absent; stems erect; basal leaves ovate-elliptic, subentire or weakly crenate proximally; stem leaves simple, alternate, coriaceous;

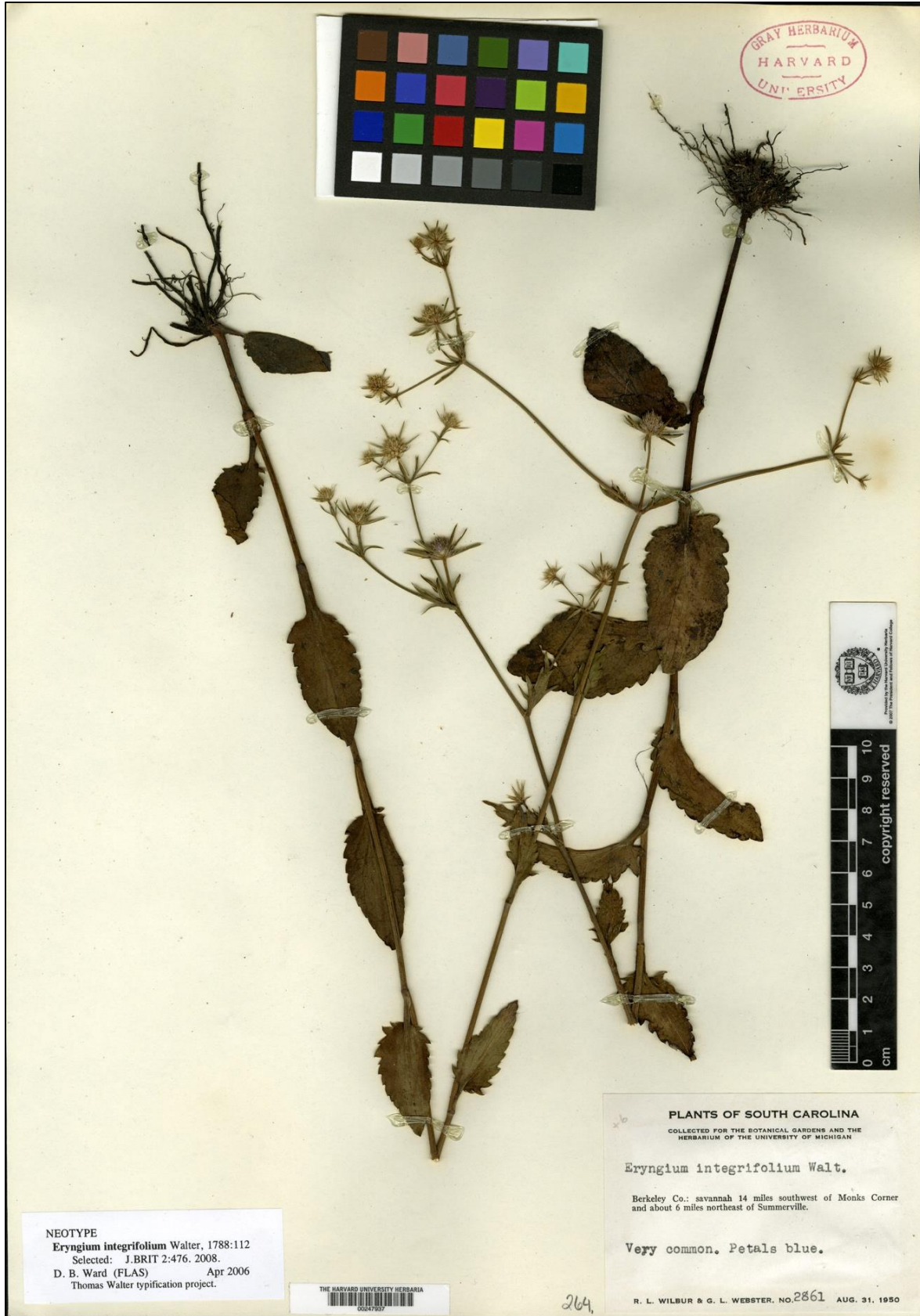


Figure 5. Neotype of *Eryngium integrifolium* (GH).

proximal cauline usually withering by flowering, subentire or weakly crenate-serrate at most in proximal half; mid-cauline (1.5-)3.3-4.7(-6.7)cm long (smaller in Gulf material), (0.9-)1-1.8(-2.4)cm wide, crenate-serrate, teeth (7-)8-12(-14) per side, teeth usually rounded to bluntly acute; upper cauline (1.4-)2.3-3.5(-4.0)cm long, (0.3-)0.5-1.3(-1.4)cm wide, crenate-serrate to bluntly serrate; petioles 0.8-)0.9-1.6(-1.9)cm, moderately broad, with hyaline margins, sheathing stem for full length; inflorescence cymose, terminal and occasionally from upper leaf axils (especially in Atlantic plants), branches stiffly spreading-ascending, heads 3-15(-25 in Atlantic material, rarely); terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these tricuspidate, central lobe narrowly lanceolate with an additional 1-2(-4) coarse, irregular teeth per side; heads subtended by a single whorl of 4-8 linear bracts, rigid, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also densely beset with pale, appressed scales mostly obscuring dark brown or black surface.

Concept map. < *E. integrifolium* Walter var. *typicum* Wolff - Wolff (1913); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2022); < *E. virgatum* Lamarck - Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. - Michaux (1803); < *E. americanum* Walter ex Sprengel - Roemer & Schultes (1820).

Distribution. *E. integrifolium* var. *integrifolium*, as here circumscribed, has a bimodal distribution on the Outer East Gulf (MS, FL panhandle, AL) and Atlantic (NC, SC, GA, n. FL) Coastal Plains, with scattered populations in n. peninsular FL and the NC and SC sandhills.

Habitat. Hillside seepage bogs, pitcherplant bogs, sandhill-pocosin ecotones, and occasionally roadside ditches in longleaf pinelands, on acidic, sphagnous soils.

Taxonomic comments. There is some differentiation between Gulf and Atlantic populations of var. *integrifolium*. Atlantic plants are more robust, tending toward larger leaves with more obtuse apices, and more diffuse inflorescences, frequently with axillary cymose inflorescences from upper and mistem leaves. Extremely small-leaved plants occur sporadically in the Gulf Coastal Plain distribution (one collection by Steve Leonard was analyzed in our PCA and LDA labeled “*E. leonardii*”) but likely do not warrant formal recognition.

Conservation. We suggest that a G4 conservation rank is appropriate for this taxon. This typical coastal plain variant is narrowly endemic to the East Gulf and Atlantic Coastal Plains and associated with imperiled longleaf pine and bog communities, although fairly abundant within remnants of these imperiled communities.

2b. ERYNGIUM INTEGRIFOLIUM var. **MAFICOLUM** Kees, Weakley, & Poindexter, **var. nov.** **TYPE:** **North Carolina.** Clay Co.: Chatuge Lake, 3.5 mi E of Hayesville, 21 Aug. 1956, *A.E. Radford 16312* (holotype: NCU, isotype: TENN-V);

Stems erect, inflorescence sparse, upper leaves much reduced, branches few and stiffly spreading-ascending; leaves small, ovate or narrowly ovate-elliptic, mid and upper cauline irregularly serrate with slender, acuminate teeth, basal and proximal serrate or crenate serrate, usually throughout; primary and secondary bracts usually tricuspidate, often with 2-3 additional pairs of teeth; bracts subtending florets tricuspidate; mericarps densely beset with scales.

Plants cespitose, stems single, from fibrous roots, rhizomes absent; stems erect; basal leaves ovate-elliptic to narrowly obovate, held erect-ascending, usually serrate to near apex; stem leaves simple, alternate, coriaceous; proximal cauline usually withering by flowering, serrate to crenate-serrate; mid-cauline (2.4-)2.8-3.6(-4.7)cm long, 0.7-1.5cm wide, sharply serrate, teeth (6-)8-10(-16) per side, teeth usually slender, acuminate; upper cauline (2.0-)2.2-3.2(-3.7) cm long, (0.3-)0.5-1.3(-



Figure 6. Holotype of *Eryngium integrifolium* var. *maficolum* (NCU).

1.4) cm wide, irregularly and very sharply serrate, teeth slender, acuminate; petioles moderately broad, with hyaline margins, sheathing stem, or proximal often spreading-ascending and narrower; inflorescence cymose, terminal, branches stiffly spreading-ascending, heads 3-15; terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these tricuspidate, central lobe narrowly lanceolate with an additional 1-3(-4) coarse, irregular teeth per side; heads subtended by a single whorl of 4-8 linear bracts, rigid, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also densely beset with pale, appressed scales mostly obscuring dark brown or black surface.

The epithet alludes to this variety's association with mafic geology, rather than the acidic substrates with which all other entities in the complex are associated.

Concept Map. < *E. integrifolium* Walter var. *typicum* Wolff - Wolff (1913); >> *E. integrifolium* Walter var. *ludovicianum* Wolff - Wolff (1913); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2022); < *E. virgatum* Lamarck - Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. - Michaux (1803); < *E. americanum* Walter ex Sprengel - Roemer & Schultes (1820).

Distribution. *E. integrifolium* var. *maficolum* is restricted to scattered sites in the high-elevation Blue Ridge of NC and GA, frequently associated with mafic geology.

Habitat. Mountain bogs and seeps, typically over mafic rock.

Taxonomic notes. Although poorly differentiated morphologically from *E. integrifolium* var. *integrifolium*, the ecology and biogeography of this species suggests an affinity with *E. integrifolium* var. *pedmontanum* and possibly *E. mississippiense*, rather than with Coastal Plain populations. Plants of Henderson and Buncombe cos., North Carolina, with very narrow, sharply serrate leaves have been confused with *E. ludovicianum* in some treatments; these plants are co-distributed with narrow endemics such as *Sarracenia jonesii* and could represent another (likely extinct) semi-cryptic taxon within *E. integrifolium*.

Conservation. We suggest that a T1 conservation rank is appropriate for this taxon (S1 in NC and S1 in GA). *Eryngium integrifolium* var. *maficolum* is known from fewer than ten sites globally, and most of these are represented only by historic collections and are likely no longer extant. Much of the habitat for this species has been destroyed by wetland drainage, reservoir construction, and suburban development, which continue to threaten remaining occurrences.

2c. ERYNGIUM INTEGRIFOLIUM var. **PIEDMONTANUM** Kees, Weakley, & Poindexter, **var. nov.**

TYPE: South Carolina. Greenville Co.: State Hwy 14 at Berry's pond, 31 Aug 1956, *O.M. Freeman* 63693 (holotype: NCU).

Stems moderately stout, erect, heads few, inflorescence branches often lax (especially in bud); leaves ovate or narrowly ovate-elliptic, sharply and somewhat irregularly serrate, petioles sheathing; 1° and 2° bracts coarsely toothed, narrowly lanceolate, sometimes weakly 3-parted basally; bracts subtending individual florets tricuspidate; mericarps densely beset with scales.

Plants caespitose, stems single, from fibrous roots, rhizomes absent; stems erect; basal leaves ovate-elliptic, subentire or crenate-serrate; cauline leaves simple, alternate, coriaceous, ascending; proximal usually withering by flowering, subentire to crenate-serrate or serrate; mid-cauline (3.2-)4.1-6.2(-6.7)cm long, 1.2-2.1(-3.2)cm wide, sharply serrate, teeth 12-22 per side, teeth usually slender, acuminate; upper cauline 3.1-3.5(-4.5)cm long, 1-1.4cm wide, irregularly and very sharply serrate, teeth slender, acuminate; petioles moderately broad, with hyaline margins, sheathing stem, or proximal



Figure 7. Holotype of *Eryngium integrifolium* var. *piedmontanum* (NCU).

sometimes spreading-ascending and narrower; inflorescence cymose, terminal, branches stiffly spreading-ascending, and often with a few additional axillary inflorescences from distal leaf axils, heads 7-15(-21); terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these narrowly lanceolate, coarsely toothed (sometimes 3-parted), teeth (3-)4-6(-8) per side; heads subtended by a single whorl of 4-8 linear bracts, rigid, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also densely beset with pale, appressed scales mostly obscuring dark brown or black surface.

Var. *piedmontanum* is a Piedmont near-endemic, thus the epithet.

Distribution. Upper Piedmont of nw. SC and sw. NC, south to the lower Piedmont of GA, and (perhaps only historically) lower-elevation mountains of NC (Henderson Co.); in Atlantic-draining river basins north and east of the distribution of *E. mississippiense*, and between sandhills var. *integrifolium* and montane var. *maficolum*.

Habitat. Acidic Piedmont bogs and seepages.

Concept Map. < *E. integrifolium* Walter var. *typicum* Wolff - Wolff (1913); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2024); < *E. virgatum* Lamarck – Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. – Michaux (1803); < *E. americanum* Walter ex Sprengel – Roemer & Schultes (1820).

Taxonomic comments. Further study may reveal var. *piedmontanum* and var. *maficolum* warrant specific rank. Although these plants cluster with *E. integrifolium* s.s. in the PCA, var. *piedmontanum* is morphologically intermediate between *E. integrifolium* var. *integrifolium* and *E. mississippiense*, which may be due to pseudoconvergence or, alternatively, ancestral hybridization between disjunct Blue Ridge *E. integrifolium* and a more recent north and east dispersal of the apparently more vigorous *E. mississippiense*. *E. mississippiense* reaches its eastern limit in the Coosa and Chattahoochee drainages in the Georgia Piedmont, with the furthest southwest populations of *E. integrifolium* var. *piedmontanum* in Atlantic-draining basins. Some Arkansas material of *E. mississippiense* may key to var. *piedmontanum*.

Conservation. We suggest a T1 ranking for this taxon (SH in NC, S1 in SC, and SH in GA). *E. integrifolium* is extremely rare in the Piedmont and mountains, and most historic collections of var. *piedmontanum* are from bogs that have been drained and cleared for agriculture or urban development.

3. ERYNGIUM LANCEOLATUM Kees, Weakley, & Poindexter, **comb. et stat. nov.** *Eryngium integrifolium* var. *lanceolatum* H. Wolff, Pflanzenr. (Engler) 4, Fam. 228: 161. 1913. **Protologue:** "Texas: Rusk County, auf Waldwiesen (Vinzent, Texas Pl. n. 9 — blühend im August — Herb. Boissier); wahrscheinlich weiter verbreitet, bildet den Übergang zu var. γ)." This collection has not been located, but Geiser (1957) commented on the distribution of some of Vinzent's specimens. **EPITYPE** (designated here): **Texas.** Anderson Co.: 19 mi S of Athens, in bog, 8 Sep 1942, C.L. Lundell 11789 (BRIT; isoeotype: LL).

We identify the Vinzent collection based on Wolff's description and locality. Wolff cited another Texas specimen that corresponds to var. *lanceolatum* as treated here (under his *E. integrifolium* var. *typicum*, from Bowie Co., Heller 4089).

Stems slender to somewhat stout, erect, heads in sparse, cymose arrays; leaves deltate-lanceolate, regularly serrate or dentate, petioles divaricate, sometimes basally sheathing; primary and secondary bracts

Figure 8. Epitype of *Eryngium lanceolatum* (BRIT).

tricuspidate to pinnately dissected, sometimes additionally coarsely toothed, narrowly lanceolate or linear; bracts subtending individual florets tricuspidate; mericarps densely beset with scales.

Plants cespitose, stems one to several, from fibrous roots, rhizomes absent; stems wiry to somewhat stout, generally erect; leaves simple, alternate, coriaceous, proximal cauline usually withering by flowering; mid-cauline (3.4-)4.1-7.2(-8.2)cm long, (0.7-)0.9-1.7(-2.1)cm wide, moderately finely serrate, teeth 14-22(-32) per side, acute, straight-sided; distal cauline (2.7-)3.2-5.2(-5.5)cm long, (0.3-)0.4-0.9(-1.2)cm wide, finely serrate; petioles broadened basally, sheathing stem; inflorescence cymose, heads numerous, terminal and sometimes with additional inflorescences from distal leaf axils; terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these elliptic or lanceolate, often 3-parted basally, finely to coarsely serrate, teeth 1-4 per side; heads subtended by a single whorl of 4-8 linear bracts, rigid or pliable, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide or slightly longer; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also densely beset with pale, appressed scales obscuring deep brown or black surface.

Distribution. Endemic to the inner West Gulf Coastal Plain, ranging from eastern TX scattered to extreme se. OK, sw. AR, and nw. LA, loosely correlated with the Carrizo Sand formation and with the Post Oak Savannah ecoregion

Habitat. Muck bogs embedded in post oak or oak-pine woodlands, and occasionally in forested seepages and wet terraces eastward (nw. LA, sw. AR).

Concept Map. =? *E. integrifolium* Walter var. *lanceolatum* Wolff - Wolff (1913); >< *E. integrifolium* Walter var. *typicum* Wolff - Wolff (1913); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2024); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2022); < *E. virgatum* Lamarck – Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. – Michaux (1803); < *E. americanum* Walter ex Sprengel – Roemer & Schultes (1820).

Taxonomic comments. *E. lanceolatum* is replaced east of the Red River drainage basin by *E. mississippiense*, and in West Gulf Coastal Plain longleaf pinelands by *E. ludovicianum* sensu stricto. While there is overall little apparent introgression with *E. ludovicianum*, there is some material from Houston Co., Texas, included here under *E. ludovicianum*, which shows some intermediacy between the two taxa. While typical Texas and Oklahoma Post Oak Savannah material is highly distinctive, occurrences in sw. AR and nw. LA, included here under var. *lanceolatum*, are ambiguous and may represent introgression between *E. mississippiense* and *E. ludovicianum*.

Conservation. We suggest a G2G3 rank for this taxon (S1 in OK, S1 in AR, S1 in LA, and S1S3 in TX). While narrowly endemic, perhaps extirpated from much of its range, and associated with naturally rare and imperiled bog habitats, there are a handful of extant, well-managed occurrences in TX (Gus Engeling WMA).

4. ERYNGIUM LUDOVICIANUM Morong, Bull. Torrey Bot. Club 14: 51. 1887. *Eryngium virgatum* var. *ludovicianum* Morong in J.M.Coult. & Rose, Rev. N. Amer. Umbell. 96. 1888. *Eryngium integrifolium* var. *ludovicianum* (Morong) H. Wolff, Pflanzenr. (Engler) 4, Fam. 228: 161. 1913. **TYPE: Louisiana.** Natchitoches Parish: No other locality data, 9 Sep 1886, A.B. Langlois s.n. (holotype: NY).

The holotype is unambiguously identified as *E. ludovicianum*, although the specimen is somewhat damaged with only a few cauline leaves remaining. Wolff (1913) cited additional material from Georgia, which presumably represents *E. altamaha*.



Figure 9. Representative specimen of *Eryngium ludovicianum* (NCU).

Culms slender, inflorescence narrow, heads few; leaves linear-lanceolate, remotely serrate, distal spinose-serrate, proximal crenate; inflorescence bracts pinnately dissected, segments filiform; bracts below florets tricuspidate; mericarps densely beset with scales.

Plants caespitose, stems usually single, from fibrous roots, rhizomes absent; stems slender, erect, inflorescence much contracted, branches wiry; leaves simple, alternate, coriaceous, proximal cauline usually withering by flowering, remotely crenate to subentire; mid-cauline (3.2-)4.1-5.9(-8.9)cm long, 0.3-0.8(-1.2)cm, remotely serrate, teeth (7-)8-13(-17) per side, 1-3(-4) per cm at midlength; distal cauline (2.9)3.2-5.2(-5.9)cm long, (0.1-)0.2-0.4cm wide, remotely serrate or spinose-serrate, teeth (6-)7-10(-14) per side; petioles narrowed abruptly from base, scarcely sheathing stem; inflorescence cymose, heads few, terminal and occasionally with additional small inflorescences from distal leaf axils; terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these filiform, pale or green, 1(-2)x pinnately dissected; heads subtended by a single whorl of 4-8 linear bracts, rigid or pliable, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide or slightly broader; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also moderately to densely beset with pale, appressed scales, deep brown or black surface usually visible beneath.

Concept map. = *E. ludovicianum* Morong – Morong (1887), Small (1903); =*Eryngium virgatum* var. *ludovicianum* Morong – J.M. Coult & Rose (1888); < *E. integrifolium* Walter var. *ludovicianum* Wolff – Wolff (1913); < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2022); < *E. virgatum* Lamarck – Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. – Michaux (1803); < *E. americanum* Walter ex Sprengel – Roemer & Schultes (1820).

Distribution. *E. ludovicianum* var. *ludovicianum* is endemic to the West Gulf Coastal Plain of LA and East Texas, with a more southerly distribution than var. *lanceolatum*.

Habitat. Longleaf Pine woodlands and savannahs, in pitcherplant bogs, seepage slopes, and seepages over sandstone, generally in sphagnous and highly acidic soils embedded in open grasslands.

Conservation. We suggest a G2G3 conservation ranking is appropriate for *E. ludovicianum* (S2S3 in LA and S2S3 in TX); while there are a moderate number of collections from the Kisatchie NF in LA and Angelina NF in TX, most are more than 30 years old and is unclear how many are extant. *E. ludovicianum* var. *ludovicianum* appears to be rare and conservative throughout its highly limited West Gulf Coastal Plain distribution.

5. ERYNGIUM MISSISSIPPIENSE Kees, Weakley, & Poindexter, **sp. nov.** **TYPE: Mississippi.** Copiah Co.: Low right-of-way along US Hwy 51, 4 Aug 1966, *L.C. Temple 3809* (holotype: NCU; isotype: MISS).

Plants robust, stems stout, heads numerous; leaves broadly elliptic or ovate, serrulate, petioles dilated and sheathing; primary and secondary bracts ovate, unlobed, serrate; bracts subtending individual florets tricuspidate; mericarps densely beset with scales.

Plants caespitose, stems single, from fibrous roots, rhizomes absent; stems stout, erect; leaves simple, alternate, coriaceous, proximal cauline usually withering by flowering, crenate-serrate to subentire; mid-cauline (4.1-)5.3-8.4(-9.7)cm long, (1.7-)2.3-4.3(-4.4)cm wide, finely serrate or crenate, teeth (18-)25-38(-62) per side; distal cauline (2.4-)3.2-5.8(-7.8)cm long, 1-2.9(-3.5)cm wide, finely to moderately coarsely crenate-serrate; petioles broad, with hyaline margins, sheathing stem; inflorescence cymose, heads numerous (often 30-50+), terminal and usually with additional inflorescences from distal leaf axils, the inflorescence branches sometimes flexuous or arching, especially in bud; terminal inflorescence subtended by a single whorl of 2-3(-4) foliaceous bracts, these elliptic or lanceolate, finely to coarsely serrate, teeth 5-15 per side; heads subtended by a single whorl

Figure 10. Holotype of *Eryngium mississippiense* (NCU).

of 4-8 linear bracts, rigid or pliable, reflexed, white or bluish, with 1-2 teeth per side; heads pale blue at anthesis, hemispheric or subglobose, about as long as wide or slightly longer; individual florets each subtended by a single, spinose, tricuspidate bract; fruit a schizocarp of two mericarps; mericarps truncate apically, with a crown of scales, also densely beset with pale, appressed scales obscuring deep brown or black surface.

The epithet alludes to the type locality in Mississippi, where it is most common and widespread.

Concept Map. < *E. integrifolium* Walter - Small (1903), Weakley (2022), FNA (2024); < *E. virgatum* Lamarck – Lamarck (1798), J.M. Coult. & Rose (1888); < *E. ovalifolium* Michx. – Michaux (1803); < *E. americanum* Walter ex Sprengel – Roemer & Schultes (1820).

Distribution. *E. mississippiense* is endemic to the unglaciated southeastern USA, from sw. AR and TN south to extreme n. LA and sw. MS and w. to the piedmont of GA and AL Coastal Plain. It reaches its eastern limit in the Chattahoochee and Coosa drainage basins, replaced by *E. integrifolium* var. *piedmontanum* (and rarely *E. altamaha*) in adjacent Atlantic-draining watersheds in the GA Piedmont. West of the Mississippi River, *E. mississippiense* appears to intergrade southward with *E. ludovicianum*.

Habitat. *E. mississippiense* is unique among *E. integrifolium* segregates in that it is not tied to island-like Coastal Plain bog systems and similar Piedmont and Mountains microhabitats, instead occurring in a variety of semi-natural and natural habitats of small-stream terraces and second bottoms, now primarily in roadside ditches and rights-of-way, but probably originally associated with low hardwood flatwoods, streamsides and seepages in open oak-shortleaf pine woodlands, and wet meadows and terrace prairies. It is markedly less heliophytic and more robust, and associated with generally richer substrates than other *E. integrifolium* segregates.

Taxonomic comments. Chromosome counts for this species are unknown; however, the coarser vegetative and floral features of *E. mississippiense*, as well as its lack of introgression with numerous geographically associated entities in the complex, are suggestive of polyploid derivation. East of the Mississippi River, this species is very well-differentiated from *E. altamaha* and *E. integrifolium* with apparently very little introgression, even where sympatric. Material considered here to represent *E. mississippiense* from southern Arkansas is ambiguous, frequently with relatively narrower leaves and bracts, the bracts occasionally 3-lobed or 3-parted (but still more regularly serrate than *E. ludovicianum* or *E. integrifolium*); some of these plants may key to *E. integrifolium* var. *piedmontanum*, and they may represent introgression with *E. ludovicianum*.

Conservation. We suggest that a G3 rank is appropriate for this taxon (S2 in AR, S1 in TN, S2S3 in AL, S2S3 in MS, SH in LA, S1 in KY, and S1 in GA). While nowhere common, this taxon is less conservative ecologically than other members of the *E. integrifolium* complex and comparatively widespread, with a fair number of known occurrences in Mississippi and Arkansas, and probably is under-reported across the Inner Coastal Plain.

ACKNOWLEDGEMENTS

I thank Sushil Dahal (MSU) for providing R scripts used in our PCA, LDA, MANOVA, and pairwise test, and, along with Ryan Folk (MSU), for assisting me with the statistical component of this project. Morphometric data collection for this project was conducted while the primary author was a second-year undergraduate at UNC, with initial results submitted for BIOL 395H research credit.

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APPENDIX A – Specimens Cited

Specimens measured for morphometric analysis:

E. altamaha: **GEORGIA**: NCU00190653, DUKE10137184, NO 0088903, NO 0088910, LSU00105246, LSU00105244.

E. integrifolium var. *integrifolium*: **ALABAMA**: Conecuh Co.: NCU00190648, Washington Co.: NCU00190662; **FLORIDA**: Alachua Co.: NCU00190638, Wakulla Co.: NCU00314882, Walton Co.: NCU00190650, Santa Rosa Co.: NCU00314881, **GEORGIA**: Thomas Co.: NCU00190667, Worth Co.: NCU00190655, Brooks Co.: NCU00190678, Cook Co.: NCU00190641; **LOUISIANA**: St. Tammany Co.: LSU00048777, Tangipahoa Co.: LSU00214120, **MISSISSIPPI**: **NORTH CAROLINA**: Columbus Co.: NCU00165675, Carteret Co.: NCU00165672, Cumberland Co.: NCU00165678; **SOUTH CAROLINA**: Clarendon Co.: NCU00195025, Colleton Co.: NCU00195037, Allendale Co.: NCU00195001.

E. integrifolium var. *integrifolium* (“leonardii” variant): **MISSISSIPPI**: NCU00192914 (4 plants).

E. integrifolium var. *maficolum*: **NORTH CAROLINA**: Alleghany Co.: NCU00104897, NCU00165663, Cherokee Co.: NCU00179387, Clay Co.: NCU00314456, NCU00165673; **Henderson Co.:** NCU00165984, NCU00165993, NCU00165992; **Buncombe Co.:** NCU00165669, **Swain Co.:** NCU00094679.

E. integrifolium var. *piedmontanum*: **NORTH CAROLINA**: **Henderson Co.:** NCU00165994, NCU00165995; **Iredell Co.:** NCU00205996, NCU00205997, NCU00179388, **Lincoln Co.:** NCU00205998; **SOUTH CAROLINA**: **Greenville Co.:** NCU00195014, **Spartanburg Co.:** NCU00192907.

E. lanceolatum: **TEXAS**: **Freestone Co.:** NCU00176211, **Henderson Co.:** NCU00176213, BRIT489637; **Robertson Co.:** NCU00176214, BRIT489649; **Freestone Co.:** BRIT489630, BRIT489632, **Cherokee Co.:** BRIT489629, **Anderson Co.:** BRIT489627, BRIT489626, BRIT489625, BRIT489624, BRIT489623, **Nacogdoches Co.:** BRIT489643, **Smith Co.:** BRIT489652, **OKLAHOMA**: **Pushmataha Co.:** BRIT534265, **Choctaw Co.:** BRIT534264; **ARKANSAS**: **Union Co.:** ANHC016840, **Miller Co.:** ANHC000384.

E. ludovicianum: **LOUISIANA**: **Vernon Co.:** NCU00190657, LSU00058783, NCU00190669; **Natchitotes Co.:** LSU0043797, NCU00190558, LSU00043968, **Monroe Co.:** NCU00190559, **Beauregard Co.:** LSU00083073, LSU00056574, NCU00190536, **Rapides Co.:** LSU00048762, **Jackson Co.:** LSU00048761, **Allen Co.:** LSU00048754; **TEXAS**: **Hardin Co.:** NCU00176212, BRIT489634, **San Augustine Co.:** BRIT489650, **Polk Co.:** BRIT489647, **Newton Co.:** BRIT489645, **Jasper Co.:** BRIT489642, **Nacogdoches Co.:** BRIT489643, **Newton Co.:** LSU00139174, **Tyler Co.:** LSU00105249,

E. mississippiense: **ALABAMA**: **Hale Co.:** NCU00190636, **Tuscaloosa Co.:** UNA00037323, **Autauga Co.:** UNA00037377, **Lee Co.:** UNA00037347, **Shelby Co.:** UNA00059904; **ARKANSAS**: **Saline Co.:** ANHC01287, **Lincoln Co.:** ANHC000383.; **LOUISIANA**: **Ouachita Co.:** NLU0027846; **MISSISSIPPI**: **Copiah Co.:** NCU271875, MMNS017707, **Covington Co.:** NCU271875, **Lafayette Co.:** NCU290334, NCU00192913, **Lincoln Co.:** MMNS039620, **Grenada Co.:** MMNS011122, MMNS011123; **Lauderdale Co.:** MMNS021946, MMNS032093, **Simpson Co.:** MMNS023216, **Benton Co.:** NCU00192903, **Pike Co.:** NCU00192926; **TENNESSEE**: **Benton Co.:** NCU241782, **Coffee Co.:** NCU324209, **Putnam Co.:** NCU00439472.

Additional specimens examined for County-level distributions:

E. altamaha: **GEORGIA**: VSC0002232, VSC0002232, GA054361, EMORY 6369, GAS029074, EMORY 9892, LSU00105244, GA054343, GA054349, TENN-V-0243210, GA054363, GA054341, FLAS18426, FUGR0010556, GA054366, NO 0088910, DUKE10137184, GA054357, GA054362, APSC0067953, NO 0088903, LSU00105246, NCU00190653.

E. integrifolium var. *integrifolium*: **ALABAMA**: DUKE10137190, TROY000014544, BRIT70147, TROY000000980, NCU00190648, NCU00190648, USF227430, BRIT70158, TROY000042800, NCU00061679, NCU00190661, TROY000035937, NCU00190662, NCU00190662; **FLORIDA**: NCU00190638, USF246839, USF 228972, USF132392, USF210731, USF227660, USF180801, NCU00314881, USF13880, NCU00314882, USF210712, NCU00190650, NCU00190650, USF180866, USF201304; **GEORGIA**: VSC0009370, NCU00190678, LSU00105247, GA054354, NCU00174559, VSC0064362, NCU00190641, UCA001699, NCU00190641, EMORY9885, EMORY9894, RSA0377890, VSC0009378,

GAS025017, GA054368, AASU000102, NCU00190667, NCU00190667, RSA0377892, TTRS_000009537, GA054336, NCU00190655, RSA0070081, LSU00105251, **LOUISIANA:** NCU00190560, LSU00048763, LSU00048777, LSU00214120, BERA001831; **MISSISSIPPI:** NCU00190643, DUKE10137192, MISS0075774, MMNS006301, MMNS005688, MMNS005145, MISS0050317, DUKE10137193, NCU00072445, MISSA002288, MISS0050319, MISS0050327, MISS0050324, MMNS003769, MMNS030388, MISS0050335, USMS000024076; **NORTH CAROLINA:** NCSC00111327, CM203235, CM173436, DUKE10137071, NCU00165672, DUKE10137072, NCU00165675, DUKE10137074, DUKE10137073, NCU00165678, NCSC00111332, NCU00165983, NCSC00111333, DUKE10137078, DUKE10137079, CM271584, Dunham, W. 1888-07-00 (BDI), WEWO0001267, DUKE10137080, NCU00206000, CM173433, DUKE10137085, DUKE10137083, DUKE10137089, HBSH0000673, NCU00179381, NCSC00111340; **SOUTH CAROLINA:** NCU00195001, NCU00195049, BRIT47111, NCU00195013, NCU00195025, NCU00195037, NCU00195015, CLEMS0020609, USCH0002689, NCU00192943, USF120817, NY3464601, NCU00195003, NCU00192954, NCU00192931; **VIRGINIA:** GMUF-0029551.

E. integrifolium var. *maficolium*: **GEORGIA:** GA054333, GA054336; **NORTH CAROLINA:** NCU00104897, NCU00165663, NCU00165669, NCU00165669, DUKE10137070, NCU00179387, NCU00314456, NCU00165673, NCU00165674, NCU00165984, NCU00165993, NCU00165995, NCU00165994, NCU00094679, NCU00165992.

E. integrifolium var. *piedmontanum*: **NORTH CAROLINA:** PBRU00048876, NCU00205997, NCU00205996, NCU00179388, NCU00205998, UNCA337 (presumed, no image); **SOUTH CAROLINA:** NLU0028371, NCU00195014, NCU00192907; **GEORGIA:** GA054356, GA257326.

E. lanceolatum: **ARKANSAS:** ANHC000384, UAM017259 (likely *E. mississippiense* intergrade); **LOUISIANA:** NLU0027948; **TEXAS:** BRIT534264, BRIT53426, BRIT489627, BRIT489626, BRIT489625, BRIT489624, BRIT489623, PBRU00048872, BRIT489629, NCU00176211, BRIT489630, BRIT489632, NCU00176213, BRIT489637, TEX00281533, BRIT489643, BRIT489643, NCU00176214, BRIT489649, BRIT489652, BRIT489652, BRIT489654.

E. ludovicianum: **LOUISIANA:** LSU00048754, LSU00057273, LSU00083073, LSU00056574, NCU00190536, NLU0027944, APSC0029799, TENN-V-0160216, LSU00048761, NLU0027920, NLU0027916, NCU00190559, NCU00190558, LSU0043797, LSU00043968, LSU00048762, NLU0027895, NCU00190657, LSU00058783, NCU00190669, NCU00190657, LSU00043797; **TEXAS:** BRIT489628, TEX00281543, NCU00176212, BRIT489634, BRIT489638, BRIT489642, TEX00281544, BRIT489645, LSU00139174, BRIT489648, BRIT489647, BRIT489650, BRIT489650, LSU00105249.

E. mississippiense: **ALABAMA:** UNA00037377, UNA00037377, TROY000014019, UNA00054515, MISS0074694, NLU0028395, BRIT70141, GA195927, TROY000014020, TROY000000982, UNA00037342, NCU00190636, UNA00056385, BRIT70128, UNA00037342, BRIT70146, VSC0060410, UNA00037347, UNA00037347, GA195928, UNA00069357, BRIT70119, TROY000029149, UNA00059904, UNA00037323, UNA00037323; **ARKANSAS:** UAM017258, ANHC018840, ANHC000383, ANHC012873, ANHC016840; **GEORGIA:** GA054351, WGC03212, GA054327, GA054337, HWR-0000465, EMORY12852, GA054330, GA054381, DUKE10137183, GA257326, GA054356, FLAS244125, GA054335, GA054345; **KENTUCKY:** MUR17613; **LOUISIANA:** NLU0027846, LSU00214120; **MISSISSIPPI:** DUKE10137189, MISS0050311, MISS0050301, NCU00190631, MMNS017707, NCU00190631, NCU271875, MMNS011122, MMNS011123, NLU0028380, NCU290334, MMNS021946, MMNS032093, MISSA002293, MMNS039620, MISSA002295, NCU00192938, MMNS023216, MMNS023216, GA195942, APSC0136563, MISSA002297, MISS0050337, NCU00192913; **TENNESSEE:** NCU241782, NCU00192903, UCHT033534, NCU324209, TENN-V-0160050, TENN-V-0160051, NCU00439472, TENN-V-0160053, ANHC000385.

	pairs	Df	SumsOfSqs	F.Model	R2	p.adjusted
1	<i>E. integrifolium</i> v. <i>maficolum</i> vs. var. <i>piedmontanum</i>	1	26.82	3.97	0.249	0.0125
2	<i>E. integrifolium</i> v. <i>maficolum</i> vs. "leonardii"	1	25.91	7.15	0.394	0.0091
3	<i>E. integrifolium</i> v. <i>maficolum</i> vs. <i>E. altamaha</i>	1	28.22	6.05	0.317	0.002
4	<i>E. integrifolium</i> v. <i>maficolum</i> vs. <i>E. lanceolatum</i>	1	62.21	8.84	0.254	0.0013
5	<i>E. integrifolium</i> v. <i>maficolum</i> vs. <i>E. ludovicianum</i>	1	82.65	14.06	0.342	0.0013
6	<i>E. integrifolium</i> v. <i>maficolum</i> vs. <i>E. mississippiense</i>	1	274.51	18	0.367	0.0013
7	<i>E. integrifolium</i> v. <i>maficolum</i> vs. var. <i>integrifolium</i>	1	14.82	3.49	0.111	0.0141
8	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs "leonardii"	1	69.14	10.1	0.591	0.0156
9	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs <i>E. altamaha</i>	1	61.61	8.07	0.473	0.0125
10	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs <i>E. lanceolatum</i>	1	17.92	2.07	0.086	0.0458
11	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs <i>E. ludovicianum</i>	1	61.48	8.48	0.269	0.0013
12	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs <i>E. mississippiense</i>	1	77.04	4.33	0.138	0.008
13	<i>E. integrifolium</i> v. <i>piedmontanum</i> vs v. <i>integrifolium</i>	1	29.53	5.58	0.189	0.0013
14	<i>E. leonardii</i> vs <i>E. altamaha</i>	1	31.07	9.05	0.531	0.0141
15	<i>E. leonardii</i> vs <i>E. lanceolatum</i>	1	119.45	16.75	0.444	0.002
16	<i>E. leonardii</i> vs <i>E. ludovicianum</i>	1	112	19.63	0.471	0.002
17	<i>E. leonardii</i> vs <i>E. mississippiense</i>	1	261.51	15.47	0.373	0.0013
18	<i>E. leonardii</i> vs <i>E. integrifolium</i> var. <i>integrifolium</i>	1	45.25	12.14	0.345	0.0013
19	<i>E. altamaha</i> vs <i>E. lanceolatum</i>	1	95.17	12.83	0.358	0.0013
20	<i>E. altamaha</i> vs <i>E. ludovicianum</i>	1	43.67	7.16	0.23	0.0027
21	<i>E. altamaha</i> vs <i>E. mississippiense</i>	1	350.72	21.33	0.432	0.0013
22	<i>E. altamaha</i> vs <i>E. integrifolium</i> var. <i>integrifolium</i>	1	34.25	8.04	0.243	0.0013
23	<i>E. lanceolatum</i> vs <i>E. ludovicianum</i>	1	83.67	11.52	0.238	0.0013
24	<i>E. lanceolatum</i> vs <i>E. mississippiense</i>	1	293.14	20.63	0.335	0.0013
25	<i>E. lanceolatum</i> vs <i>E. integrifolium</i> var. <i>integrifolium</i>	1	94.39	15.68	0.292	0.0013
26	<i>E. ludovicianum</i> vs <i>E. mississippiense</i>	1	629.41	47.34	0.53	0.0013
27	<i>E. ludovicianum</i> vs <i>E. integrifolium</i> var. <i>integrifolium</i>	1	90.89	17.32	0.308	0.0013
28	<i>E. mississippiense</i> vs <i>E. integrifolium</i> var. <i>integrifolium</i>	1	478.92	39.71	0.48	0.0013

Table 1. Pairwise Adonis Test