

TAXONOMY OF THE *LIATRIS PILOSA* (GRAMINIFOLIA) COMPLEX (ASTERACEAE: EUPATORIEAE)

Guy L. Nesom

Botanical Research Institute of Texas
509 Pecan Street
Fort Worth, Texas 76102-4060, U.S.A.
gnesom@brit.org

Jon M. Stucky

Department of Botany
North Carolina State University
Raleigh, North Carolina 27695

ABSTRACT

Liatris graminifolia Willd. is the name generally used for the grass-leaved gayleather of the south-eastern United States. Gray (1884), Gaiser (1946), and Wilbur (1962) observed that the name *Liatris pilosa* (Aiton) Willd. apparently applies to this species and has priority; Fernald and Griscom (1938) dissented, but the present study concurs that *L. pilosa* should replace *L. graminifolia* as the correct name. A lectotype from BM is designated for *Liatris* (*Serratula*) *pilosa*. This specimen probably was collected in New Jersey or Delaware and apparently represents a particularly hairy populational variant of the species that occurs in the area but that intergrades there with plants more characteristic of the species in the broader Atlantic coast region. Two taxa that have been identified as varieties of *L. graminifolia* are here treated at specific rank: *Liatris elegantula* (Greene) K. Schum. occurs on the Gulf coastal plain in Mississippi (rare), Alabama, Florida, and Georgia; *Liatris virgata* Nutt. (= *Liatris regimontis*, *Lacinaria smallii*) occupies an intermediate geographic position, ranging in South Carolina and Georgia northward through western North Carolina into Virginia. These three taxa differ consistently in involucre morphology and the range of *L. virgata* is geographically juxtaposed between *L. pilosa* and *L. elegantula*. Intermediates have not been observed in areas of sympatry at the range margins. *Liatris cokeri* Pyne & Stucky is a fourth member of this group, possibly most closely related to *L. virgata*. A taxonomic summary is provided, including nomenclature, distribution maps, ecological summaries, and a key.

RESUMEN

Liatris graminifolia Willd. es el nombre que se usa generalmente para la planta del Sureste de los Estados Unidos. Gray (1884), Gaiser (1946), y Wilbur (1962) observaron que el nombre *Liatris pilosa* (Aiton) Willd. aparentemente se aplica a esta especie y tiene prioridad; Fernald and Griscom (1938) disintieron, pero en el presente estudio se concluye que *L. pilosa* debe reemplazar a *L. graminifolia* como nombre correcto. Se designa un lectotipo de BM para *Liatris* (*Serratula*) *pilosa*. Este espécimen probablemente fue colectado en Nueva Jersey o Delaware y aparentemente representa una variante poblacional particularmente pelosa de la especie que se encuentra en el área pero que se intergrada con plantas más características de la especie en la región Atlántica costera más amplia. Dos taxa que han sido identificados como variedades de *L. graminifolia* se tratan aquí con rango específico: *Liatris elegantula* (Greene) K. Schum. vive en la llanura costera del Golfo en Mississippi (rara), Alabama, Florida, y Georgia; *Liatris virgata* Nutt. (= *Liatris regimontis*, *Lacinaria smallii*) ocupa una posición geográfica intermedia, yendo desde Carolina del Sur y Georgia por el Oeste de Carolina del Norte hasta Virginia. Estos tres taxa difieren consistentemente en la morfología involucral y el rango de *L. virgata* está yuxtapuesto geográficamente entre *L. pilosa* y *L. elegantula*. No se han observado intermedios en áreas de simpatria en los extremos de área. *Liatris cokeri* Pyne & Stucky es un cuarto miembro de este grupo, posiblemente más relacionado con *L. virgata*. Se ofrece un resumen taxonómico que incluye nomenclatura, mapas de distribución, resúmenes ecológicos, y una clave.

Liatris graminifolia Willd. is the name generally applied to the grass-leaved gayfeather, a taxon of the southeastern U.S.A. (e.g., Radford et al. 1968; Cronquist 1980; Figs. 1 and 2). Gaiser (1946) recognized five infraspecific taxa: var. *graminifolia*, var. *elegantula* (Greene) K. Schum., var. *lasia* Fernald & Griscom, var. *dubia* (W.P.C. Barton) A. Gray, and var. *smallii* (Britton) Fernald & Griscom. Of these five, var. *dubia* and var. *lasia* both are representative of the Atlantic coast species, as is var. *graminifolia*; var. *elegantula* is treated here at specific rank; and var. *smallii* is treated here as a synonym of another formally recognized species. Fernald (1950) recognized *L. graminifolia* var. *graminifolia*, var. *racemosa* (DC.) Venard (as a replacement name for var. *dubia*), var. *lasia*, var. *smallii*, and var. *virgata* (Nutt.) Fernald. We observe that Fernald's concept of var. *virgata* (1949, 1950) was artificial and that var. *racemosa* represents the same taxon as the type of var. *virgata*. The only recent treatment of the genus in the area that includes all of these variants is Cronquist (1980), who reduced the formally recognized taxa to *L. graminifolia* vars. *graminifolia* and *elegantula*. In our assessment, these two and two more, *L. graminifolia* var. *virgata* sensu stricto and *L. cokeri* Pyne & Stucky, constitute the evolutionary entities of this complex. *Liatris cokeri* is a species of the fall-line sandhills of southern North Carolina and adjacent South Carolina (Stucky & Pyne 1990). Our treatment recognizes four taxa, each at specific rank: **L. pilosa** (Aiton) Willd., **L. elegantula** (Greene) K. Schum., **L. virgata** Nutt., and **L. cokeri**.

Taxonomic rank

It is clear that *Liatris pilosa*, *L. elegantula*, *L. virgata*, and *L. cokeri* are closely related among themselves. Morphological differences among them, mostly in involucre features, are relatively small but they are consistent and a series of principal components analyses (Stucky 1990, 1992) indicates that *L. cokeri*, *L. pilosa*, and *L. virgata* are distinct. *Liatris elegantula* was not included in the analyses by Stucky, and it has consistently been treated as a variety of *L. graminifolia* since Gaiser reduced it in rank. In addition to morphology, the decision regarding the rank of these taxa rests on biology. *Liatris cokeri* is completely sympatric with *L. pilosa* but contiguous or nearly so with *L. virgata* (Figs. 1 and 2). *Liatris virgata* is geographically juxtaposed between *L. pilosa* and *L. elegantula* and probably forms a reproductive barrier between them. From the sample of specimens studied and mapped here, it appears that the degree of sympatry between *L. virgata* and *L. elegantula* may be greater than between *L. virgata* and *L. pilosa*; in neither instance, however, have we seen collections that would clearly indicate that hybridization, intermediacy, or introgression occurs in the areas of sympatry (see comments below). Each of these taxa has been treated at varietal rank, but the nomenclature for treating them as species is already established.

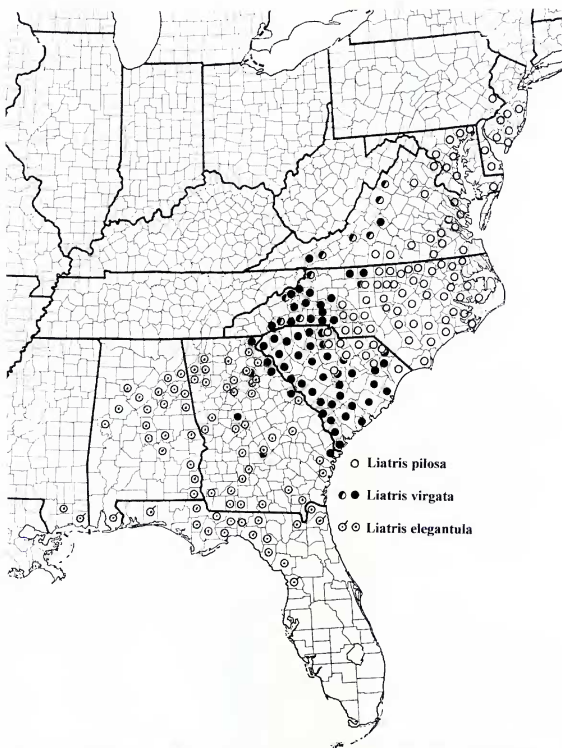


FIG. 1. Geographic distribution of *Liatris pilosa*, *Liatris virgata*, and *Liatris elegantula*. Records are from specimens studied from DOV, NCU, SMU/BRIT, TEX/LL, USCH, and VDB. Tagged symbols for *L. elegantula* in Florida are from Wunderlin and Hansen (2004), in Alabama and Mississippi from Gaiser (1946). Some records for *L. virgata* (half-filled circles) are added from Stucky & Pyne (1990).

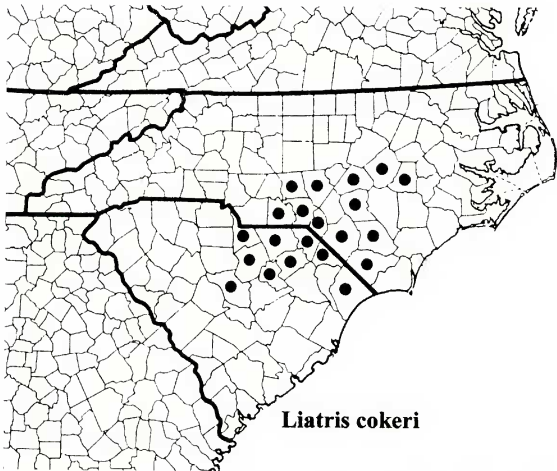


Fig. 2. Geographic distribution of *Liatris cokeri*. Records are from specimens studied from NCU, SMU/BRIT, USCH, and VDB.

Identification of the species

With the maps and following key, we believe that identifications can be made with accuracy and consistency. All key contrasts are not mutually exclusive, but they contribute toward an understanding of distinctions among the taxa. Species descriptions are provided in a treatment of the genus for the forthcoming Flora of North America volumes of Asteraceae (Nesom in prep.).

KEY TO THE SPECIES OF THE *LIATRIS PILOSA* COMPLEX

1. **Phyllaries apically rounded**; lamina relatively thin, eglandular or with superficial to shallowly inset punctate glands, **completely bordered by a narrow, hyaline rim**; involucre turbinate (obconic) to turbinate-campanulate.
2. Stems glabrous to sparsely or moderately pilose distally or over whole stem; leaf laminae glabrous to sparsely pilose on abaxial surface; heads relatively densely arranged, on **internodes (1–)2–5(–7) mm** long; **peduncles 0–10(=17, =80 in proximal region of capitulescence) mm** long; involucre (7–)8–10 mm long, phyllaries in (3–)4–5(–6) series; **florets (6–)7–12(=13)**, mostly 9–13 in N.J. and Del. _____ ***Liatris pilosa***
2. Stems glabrous; leaf laminae glabrous; heads relatively loosely arranged, on internodes (2–)5–10(–14) mm long, peduncles 0–2(–7) mm long; involucre 6–8 mm long; phyllaries in 3–4(–5) series; florets (7–)8–11(–13) _____ ***Liatris elegantula***

1. Phyllaries apically angular, lamina relative thin or thick, with inset or superficial glands, bordered on the lateral margins but not at the apex by a narrow, hyaline rim; involucre cylindrical-campanulate.
3. Heads densely arranged, on internodes 1–2(–5) mm long, often secund; phyllary apex sharply acuminate-acute, distinctly involute, lamina relatively thin, glands consistently present and superficial at least on proximal portion; florets 4–7(–9) per head; basal and lower cauline leaves 2–5 mm wide, gradually reduced in length distally _____ ***Liatris cokeri***
3. Heads loosely arranged, on internodes 6–15(–20) mm long, not secund; phyllary apex sharply acute to obtuse-angled with a thickened apiculum, not markedly involute, lamina relatively thick, usually with evidently sunken punctate glands, without superficial glands; florets 7–10(–12) per head; basal and lower cauline leaves 4–9(–12) mm wide, quickly reduced in width and length distally _____ ***Liatris virgata***

Liatris pilosa*: the oldest correct name for *L. graminifolia

Liatris pilosa (Aiton) Willd. 1803 (based on *Serratula pilosa* Aiton 1789) is the oldest name in the *L. graminifolia* complex but was treated by Gaiser as a synonym of *L. graminifolia* var. *dubia*. Fernald (1950) did not include the name *L. pilosa* in his account of the genus. Gray (1856) had treated *L. pilosa* as a distinct, montane species ("Mountains of Virginia and southward"), but he later (1884) regarded *L. pilosa* as a questionable synonym of *L. graminifolia* var. *dubia*. Fernald and Griscom (1935) examined the "fragments of a head from Aiton's type" of *Serratula pilosa* (from GH, perhaps obtained by Gray from type material at BM), but they concluded that "*Serratula pilosa* has nothing to do with *Liatris graminifolia*" – emphasizing the "long pedunculate" heads (from the type description) and the "linear and acute ... involucre bracts" (from the GH fragments). Gray (1884) had observed these same features and noted that *L. pilosa* represents a 'state' of *L. graminifolia* with "unusually narrow involucre scales." Gaiser's lengthy discussion of the typification of *L. pilosa* (1946, pp. 257–258) indicated that she regarded it as conspecific with *L. graminifolia*, and her placement of it in the synonymy of var. *dubia* seems to have been more of a nomenclatural error than reluctance to use the name because of uncertainty about its identity. Wilbur (1962) accepted *L. pilosa* as the correct name for the species, perhaps based on Gaiser's comments, while acknowledging the different interpretation by Fernald and Griscom; he noted that it seemed undesirable to provide new combinations for infraspecific taxa prior to critical study of infraspecific variation.

After a detailed survey of variation within *Liatris graminifolia* in the context of a study of the whole genus, and with the opportunity to study type material of *Liatris pilosa* from BM, we also conclude that the name *L. pilosa* does indeed apply to the species and must replace *L. graminifolia* as the correct name. Gaiser (1946, pp. 257–258) quoted notes from E.G. Baker of the National Herbarium, who apparently also examined type material of *Serratula pilosa* and whose observations regarding its morphology agree with ours. Some plants

from New Jersey and Delaware, at the northern extremity of the range of the species, which have prominently pilose stems and leaf lamina and a tendency to produce long peduncles, are similar to the BM type. We have seen collections of this "morphotype" from Atlantic, Camden, and Cumberland cos., New Jersey, and Sussex and Kent cos., Delaware. The lanceolate, apically acute phyllaries of the *Serratula pilosa* type are unusual for the species over most of its range but this feature appears sporadically in plants of the New Jersey-Delaware region.

Some plants in New Jersey corresponding to *Liatris pilosa* sensu stricto occur in populations of relatively uniform morphology (David Snyder, pers. comm.): these plants have "lower branches up to 11 cm long with up to 5 heads. The branching is most pronounced on the lower half of the stem but the heads of the upper are long peduncled (up to 4 cm long). The branches are strictly ascending. Stems, peduncles, and leaf bases are densely hirsute." On the other hand, plants more similar to those in eastern Virginia and North Carolina apparently are at least as common or more so in New Jersey (Atlantic, Burlington, Cape May, Ocean cos.!) and Delaware (Sussex and Kent cos.!) as the prominently hairy ones. Plants from this region with stems and leaf lamina glabrous or sparsely hairy but with slightly larger heads were identified as *L. graminifolia* var. *dubia* by Gaiser (1946), who cited collections from New Jersey, Delaware, Maryland, District of Columbia, Virginia, and Pennsylvania (Bucks Co.). Our study substantiates the observation that some populations of this region are distinct in their combination of characters, but the tendencies for relatively densely pilose stems and leaves, long-pedunculate heads, more florets per head, and inner phyllaries with subacute apices apparently are only loosely correlated among themselves. We have not been able to meaningfully sort the variation, but this is an area that needs to be investigated more closely.

Liatris elegantula

Plants of *Liatris elegantula* have consistently glabrous stems and leaves, relatively short and distinctly turbinate (obtriangular) involucre with a reduced number of phyllaries (evidenced by fewer series), and the heads tend to be more widely spaced than in *L. pilosa*. Records for this taxon cited by Gaiser (1946) from southwestern Alabama (Baldwin Co.) and adjacent Mississippi (Jackson Co.) have not been examined in this study.

Treatment of *Liatris elegantula* at specific rank is perhaps the most divergent proposal of the current overview. It is most similar to *L. pilosa* in involucre morphology, but small differences between the two are consistent and the geographic hiatus is real. *Liatris elegantula* and *L. pilosa* might be treated as conspecific, as has been generally done, or *L. elegantula*, *L. pilosa* and *L. virgata* might all be considered as a single species, but this would not account for apparent reproductive isolation in areas of sympatry (comments above) or a possible close relationship between *L. virgata* and *L. cokeri*.

Liatris virgata* and *L. cokeri

Liatris virgata has mostly been identified within *Liatris graminifolia* sensu lato, and as observed by Stucky (1992), this name has not been included in most of the pertinent taxonomic literature for the genus, even as a synonym, although one of its synonyms (*L. graminifolia* var. *smallii*) has sometimes been correctly applied. A principal components analysis (Stucky 1992) indicates that *L. virgata* and *L. graminifolia* (*L. pilosa*) are morphologically distinct. The name *L. regimontis* (Small) K. Schum., now understood to be a synonym of *L. virgata*, mostly had been applied to the species segregated by Stucky and Pyne (1990) as *L. cokeri*.

The range of *Liatris virgata* is essentially contiguous with *L. elegantula* on the southwestern margin and with *L. pilosa* on the northeastern margin, but some overlap occurs in both areas (Fig. 1). Although *L. virgata* has been collected in close proximity to both of its closest relatives and all three species flower in generally the same period of time, our observations indicate that the taxa are discrete even in areas of sympatry. For example, from York Co., S.C., we have studied five collections of *L. virgata* (Nelson 4994, Kennemore 917, 997, 1046, 1486, all USCH) and three of *L. pilosa* (Nelson 4989, 4998, 5024, all USCH)—all eight of these were collected within Kings Mountain National Military Park. From Richland Co., S.C., we have studied 20 collections of *L. virgata* (USCH, NCU, BRIT) and a single one of *L. pilosa* (Nelson 11244, USCH), south of its primary range. Field and herbarium studies are needed to further the understanding of the geographic and evolutionary relationship between *L. virgata* and its close relatives. If hybridization and intergradation prove to be more significant than observed in the current study, treatment of these three taxa as conspecific might be more appropriate.

Spacing of the heads and phyllary morphology are features that provide the most immediate recognition of *Liatris virgata*. Contrasted with *L. pilosa* and *L. elegantula*, the phyllary lamina is thicker and the glands are distinctly sunken into the tissue, and the apex is generally angular (vs. rounded) and lacks the narrow hyaline rim that borders the lateral margins. In Richland Co., S.C., from which numerous collections are available, the apex shape varies from sharply acute to obtuse, but even the obtuse angle is distinct, as the tip characteristically ends in a thickened and slightly raised (keel-like) apiculum or mucro. Similar variation occurs over the range of the species, although a tendency for obtuse apices apparently is more common on the coastal plain.

Variation in *Liatris virgata* also occurs in involucreal size and configuration. Larger-headed plants (including the types of *Lacinaria smallii* and *Lacinaria regimontis*) are mostly montane and piedmont. Larger heads are more elongate-cylindric and have phyllaries in 5-6(-7) series with more consistently sharply acute apices, while smaller heads have 3-5(-6) series. Number of florets tends to be slightly higher in larger heads.

Finally, we note that the distribution of *Liatris virgata* from outer coastal plain into montane habitats is unusual, but *L. pilosa* and *L. elegantula* both occur on the piedmont as well as their primary coastal plain range, and other species of *Liatris* range widely across habitats and ecological zones (e.g., *L. squarrulosa* Michx. and *L. aspera* Michx.). Further study of *L. virgata* may demonstrate geographic patterns of differentiation that we have not been able to delimit.

Stucky and Pyne (1990) observed that apparent intermediates between *Liatris virgata* and *L. cokeri* occur on the coastal plain of North Carolina and South Carolina. In the present study, however, we have identified some of those putative intermediates as *L. cokeri*, and we have not confirmed the occurrence of *L. virgata* where the putative intermediates occur in North Carolina (Stucky & Pyne 1990, Fig. 10). *Liatris cokeri* is characterized by phyllaries with acute-angled apices, and this is likely an indication of close relationship to *L. virgata*. Indeed, evolutionary relationships within the *L. pilosa* complex, as outlined here, may be that of two sister pairs—*L. pilosa*-*elegantula* and *L. virgata*-*cokeri*.

NOMENCLATURE AND TYPOLOGY

***Liatris pilosa* (Aiton) Willd., Sp. Pl. 3:1636. 1803.** *Serratula pilosa* Aiton, Hort. Kew. 3:138. 1789. *Lacinaria graminifolia* (Willd.) Kuntze var. *pilosa* (Aiton) Britton, Mem. Torrey Bot. Club 5:314. 1894. *Lacinaria pilosa* (Aiton) A. Heller, Muhlenbergia 16. 1900. LECTOTYPE, here designated: U.S.A. Cultivated plant, without collection data but the original stock probably from New Jersey or Delaware, probably collected by William Young, Jr. prior to 1783 (BM-Banks Herbarium, photo, fragment of lectotype GH). A handwritten inscription on the back of the lectotype sheet reads "Hort Kew. 1785" and matches the handwriting of Jonas Dryander (Marshall 1978), who assumed the primary responsibilities of describing and naming plants for the Hortus Kewensis after the death of Daniel Solander in 1782. The publication itself, however, credited authorship solely to William Aiton (see Britten 1912). Photos of the lectotype have been deposited at BRIT, GH, NCSC, NCU, and US.

The protologue of *Serratula pilosa* described the plants as "foliis linearibus pilosis, floribus axillaribus longe pedunculatis" and noted "Nat. of North America. Introd. 1783, by Mr. William Young." William Young, Jr. lived in Philadelphia and made forays into "the Carolinas" as he collected horticultural stock for English gardeners (Harshberger 1917). It seems a reasonable surmise that the material of *L. pilosa* was collected by Young in the region of his home, probably close by in New Jersey or Delaware, where plants of this morphology are known to occur (as also true for the type of *L. dubia*, see below; Keller and Brown [1905] noted records in New Jersey and Delaware for "*Liatris graminifolia pilosa*"). The type specimen presumably was grown in cultivation at Kew Gardens, as Young was supported as "Botanist to their Majestys" in collecting horticultural possibilities. Young informally used the name *Serratula pilosa* for gayfeather material in his plant collection (Young 1985).

***Liatris graminifolia* Willd., Sp. Pl. 3:1636. 1803.** *Lacinaria graminifolia* (Willd.) Kuntze, Revis. Gen. Pl. 1:349. 1891. TYPE: Original not located. U.S.A. NORTH CAROLINA. New Hanover Co. edge of Wilmington, common in the open pine woods skirting the Cypress Tree Park, 24 Oct 1948, E.O. White s.n. (NEOTYPE (Gaiser 1950, p. 414); GH, internet image; ISONEOTYPES. [MO] noted by Gaiser to have been deposited at NY and US). The collection date apparently was miscited by Gaiser as "25 Oct.," because the GH specimen reads "24 Oct" and corresponds in

all other details with the citation. Many authors, including Gaiser (1946), have interpreted Willdenow's name as a new combination based on a name of Thomas Walter (*Anonymos graminifolius* Walter, Fl. Carol. 197. 1788), but as noted by Wilbur (1962) and others, Walter's names using "Anonymos" as the genus are interpreted as invalid (ICBN 2000: Arts. 20.4, 43.1). Willdenow's protologue cited "*Anonymos (graminifolius)* ... Walt. carol. 197." and "Habitat in Carolina. 4 (vs.)" and it fully quoted Walter's description. Despite Willdenow's apparent suggestion that he saw material corresponding to Walter's type, such a specimen apparently has not been relocated. Gaiser (1946, p. 255) noted that observations had been made on a BM specimen labeled "*Chrysosoma affinis* F. 309 (supposedly referring to Fraser) and with Nuttall's annotation *Liatris* in pencil," which she interpreted as authentic type material, but she later rejected this interpretation in favor of a neotype. The only specimen in the Willdenow herbarium identified as *Liatris graminifolia* (B-Willdenow fiche 14838) is a plant of *Liatris spicata* (L.) Willd. var. *spicata* with a label that notes "Habitat in Pennsylvania;" the label also cites "*Anonymos graminifolia* W. carol. 197," but it seems unlikely that Willdenow would have intended this collection as the type for *L. graminifolia*, which he explicitly understood was from "Carolina."

Liatris dubia W.P.C. Barton, Veg. Mater. Med. U.S. 2:223, t. 49. 1819. *Liatris graminifolia* Willd. var. *dubia* (W.P.C. Barton) A. Gray, Manual, ed. 2, 185. 1856. TYPE: U.S.A. [perhaps NEW JERSEY or DELAWARE, in the region where plants of this morphology occur]. This is the only element of potential type material used by the author and presumably stands as the HOLOTYPE (ICBN 2000, Art. 9.1). No collection data were cited, but Barton, a Philadelphia resident, apparently drew the illustration from a live plant, judging from the realistic dimensionality of the drawing, even though the broad leaves and elongate involucre suggest that considerable artistic license was in play. The description and illustration portray a plant with hairy stems and peduncles, linear-lanceolate lower leaves, and loosely arranged, long-pedunculate heads with elongate, "subacute" phyllaries. Gray (1848) mentioned "var. *dubia*" under *L. graminifolia*, but he did not provide a basis of reference to the basionym until the second edition in 1856. Fernald and Griscom (1935) noted that *L. dubia* was "suggestive of Aiton's plant" (i.e., *L. pilosa* s. str.).

Liatris pilosa (Aiton) Willd. var. *laevicaulis* DC., Prodr. 5:131. 1836. TYPE: U.S.A. Nov. Caesar [Nova Caesarea - NEW JERSEY]. 1835, [no other data], Mr. Torrey (HOLOTYPE: G-DC, fide!). This plant has long peduncles, apparently glabrous stems, long, narrow phyllaries apparently with sub-acute apices, and (fide de Candolle) 7-8 florets per head.

Liatris propinqua Hook., Bot. Mag. 67 (n. ser. 14): t. 3829. 1840. TYPE: [U.S.A., cultivated in England]. With regard to its origin, Hooker noted only "Sent from the Horticultural Society's garden of Edinburgh in the autumn of 1839, under the name of *L. paniculata*." The illustration shows a plant with relatively large, turbinate-cylindric, sessile to subsessile heads in a loosely spiciform array, acute phyllaries, and narrowly oblanceolate, punctate leaves prominently ciliate on the proximal margins. The stems and leaf lamina are not described or depicted as being hairy. The common name given by Hooker to this plant, "Sharp-scale spiked *Liatris*," referred to the acute phyllaries. **The identification seems reasonable as *L. pilosa*, especially in view of the prominently ciliate leaves,** but the sparsely pubescent (or glabrous?) stems, acute phyllaries, and relatively few florets ("subdecemfloro," from the description) leave open the possibility that it might be *L. virgata*. The name (*L. propinqua*) is ambiguous in reference until a type specimen is located or designated.

Liatris graminifolia Willd. var. *lasia* Fernald & Griscom, Rhodora 37:183. 1935. TYPE: U.S.A. NEW JERSEY. Camden Co.: Lindenwold, dry sandy soil, 29 Sep 1923, J.M. Fogg, Jr. 622 (HOLOTYPE: GH).

Flowering (Aug-)Sep-Oct(-Nov). Old fields, pine barrens, scrub oak-pine sandhills, openings in pine, oak, and oak-hickory woods, tidal marsh edges, sandy fields, dune hollows, wet sand near beach, edge of tidal marsh sand to

sandy clay-loam; ca. (0–)10–500 m. Delaware, Maryland, New Jersey, North Carolina, Pennsylvania, South Carolina, Virginia.

Liatrix elegantula (Greene) K. Schum., Bot. Jahresber. (Just) 29:569. 1903. *Lacinaria elegantula* Greene, Pittonia 4:316. 1901. *Liatrix graminifolia* Willd. var. *elegantula* (Greene) Gaiser, Rhodora 48:254. 1946. TYPE U.S.A. ALABAMA. Lee Co.: Auburn, 18 Oct 1896, F.S. Earle (HOLOTYPE: ND-G).

Flowering Aug–Oct(–Nov). Longleaf pine-scrub oak, pine, live oak-pine, deciduous oak-pine, deciduous flatwoods, sandhills, savanna edges, edge of cypress depressions, depression meadows, live oak-pine-palmetto hammocks, sandy clay or loam, rarely clay; 5–300(–450) m. Alabama, Florida, Georgia, Mississippi.

Liatrix virgata Nutt., J. Acad. Nat. Sci. Philadelphia 7:72. 1834. *Liatrix graminifolia* Willd. var. *virgata* (Nutt.) Fernald, Rhodora 51:104. 1949. TYPE: U.S.A. GEORGIA. [probably Nov 1815], I. Nuttall s.n. (LECTOTYPE (Stucky 1992, p. 179): PH; probable type material, "Hb. Nuttall" s.n., NY! ex BM). Nuttall noted "Hab. In Georgia and North Carolina" in the protologue; the PH specimen shows "Geo." as the only collection data. Nuttall later (1841) described the habitat as "In the pine forests of Georgia, and near Newbern, N. Carolina"—the plants from near Newbern are almost certainly *Liatrix cokeri* Stucky & Pyne (see Stucky & Pyne 1990). Graustein (1967, pp. 100–101) noted that in mid October, 1815, Nuttall traveled by boat to Savannah, Georgia, and then northward along the Savannah River to Augusta and vicinity, through longleaf pine sandhill vegetation and north at least to "where hills of deciduous trees (oaks, hickories, &) and primitive soil commence." Nuttall's protologue noted that the capitulescence was a subpannulate and branched raceme and referred to the "long lealy pedicels of the flowers." Gaiser (1946) apparently saw the PH specimen (she referred to it as "isotype") and placed *L. virgata* in synonymy of *L. graminifolia* var. *dubia*, but the latter is here interpreted as a synonym of *Liatrix pilosa* sensu stricto. Fernald's concept of *L. graminifolia* var. *virgata* (1949, 1950) was artificial (including many citations from the Atlantic coast region, based on plants with strongly branched capitulescence), though he surely was aware that the type was from Georgia, having indicated that he saw the Nuttall collection or at least a photo of it. Details on morphology of the PH specimen are provided in Stucky (1992).

Liatrix spicata L. var. *racemosa* DC., Prodr. 5:130. 1836. *Liatrix graminifolia* Willd. var. *racemosa* (DC.) Venard, Rhodora 51:35. 1949. TYPE: U.S.A. GEORGIA. Savannah, 1832, no collector indicated (HOLOTYPE: G-DC, fide!). The description by de Candolle noted "capitulis distincte pedicellatis...caule glabro...foliis ciliatis...floribus in invol. 8." The G-DC sheet has 2 branches with heads of nearly identical morphology: one was broken off and the heads are borne on peduncles up to 5 cm long; the other is intact and the distal heads are sessile while the proximal ones are on peduncles ca. 1 cm long. The involucre are campanulate-cylindric, and the phyllaries are apically thickened and subacute, the outer slightly spreading.

Liatrix regimontis (Small) K. Schum., Bot. Jahresber. (Just) 26:378. 1900. *Lacinaria regimontis* Small, Bull. Torrey Bot. Club 25:473. 1898. TYPE: U.S.A. NORTH CAROLINA. Cleveland Co.: King's Mt., wooded slopes, 27–30 Aug 1894, J.K. Small s.n. (HOLOTYPE: NY!; ISOTYPE: NY!).

Lacinaria smallii Britton, Man. Fl. N. States 927. 1901. *Liatrix graminifolia* Willd. var. *smallii* (Britton) Fernald & Griscom, Rhodora 37:182. 1935. TYPE: U.S.A. VIRGINIA. Smyth Co.: along Dickey Creek on Iron Mtn., 2900 ft, 8 Aug 1892, J.K. Small s.n. (HOLOTYPE: NY!; ISOTYPE: MO!).

Flowering (Jul–)Aug–Oct(–Nov). Edge of swampy woods, creek margins, slopes, clearings, and edges of upland woods, rocky woods, pine-oak woods, mixed de-

ciduous woods, roadsides, Iredell soil, clay; ca. 50-1000 m. Georgia, North Carolina, South Carolina, Virginia.

Liatris cokeri Pyne & Stucky, *Sida* 14:205. 1990. TYPE: U.S.A. NORTH CAROLINA. Harnett Co.: 0.2 mi E jct NC Rte 27 and Co. Rd. 1243 along NC 27 on S side of road, sandy roadside and margin of longleaf pine/turkey oak/wiregrass association, 23 Sep 1989, J.M. Stucky 511 (HOLOTYPE: NCU; ISOTYPES: GH, NCSC, NCU, NY, US, USCH).

Flowering (Aug-)Sep-Oct. Sand ridges, sandy fields and roadsides, turkey-oak, longleaf pine-oak; 50-150 m. North Carolina, South Carolina.

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