

# INFRAGENERIC CLASSIFICATION OF *LIATRIS* (ASTERACEAE: EUPATORIEAE)

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## ABSTRACT

The 37 currently recognized species of *Liatris* are placed in formal positions within an infrageneric taxonomic system modified from one proposed by Gaiser in 1946. Five sections are recognized: (1) sect. *Liatris* (including ser. *Liatris*, ser. *Punctatae*, and ser. *Elegantes*), (2) sect. **Vorago** Nesom, sect. nov., (3) sect. *Suprago* (Gaertner) DC., (4) sect. **Pilifilis** Nesom, sect. nov., and (5) sect. **Graminifolium** Nesom, sect. nov. (including ser. *Garberae*, ser. *Pauciflorae*, ser. *Virgatae*, ser. *Graminifoliae*, and ser. *Scariosae*).

## RESUMEN

Las 37 especies usualmente reconocidas de *Liatris* se colocan en posiciones formales en un sistema taxonómico infragenérico modificado a partir del propuesto por Gaiser en 1946. Se reconocen cinco secciones: (1) sect. *Liatris* (que incluye las ser. *Liatris*, ser. *Punctatae*, y ser. *Elegantes*), (2) sect. **Vorago** Nesom, sect. nov., (3) sect. *Suprago* (Gaertner) DC., (4) sect. **Pilifilis** Nesom, sect. nov., y (5) sect. **Graminifolium** Nesom, sect. nov. (incluyendo ser. *Garberae*, ser. *Pauciflorae*, ser. *Virgatae*, ser. *Graminifoliae*, y ser. *Scariosae*).

Gaiser (1946) provided the only taxonomic overview of the genus *Liatris* since reviews by de Candolle (1836) and Gray (1884). Regional treatments by Alexander (1933), Fernald (1950), and Cronquist (1980) included most or many of the species, and recent studies have investigated various taxonomic problems (Godfrey 1948; Menhusen 1963; Cruise 1964; Johnson 1971; Thomas 1975; Bowles et al. 1988; Pyne & Stucky 1990; Stucky & Pyne 1990; Stucky 1991, 1992; Godt & Hamrick 1996; Allison 2001; Nesom & O'Kennon 2001; Anderson 2002; Mayfield 2002; Kral & Nesom 2003; Gandhi et al. 2003; Nesom & Stucky 2004; Ward 2004; Nesom 2005a, 2005b). Apart from Gaiser's monograph, however, only Alexander and Fernald formally arranged species into infrageneric groups. King and Robinson (1987) offered pertinent observations regarding possible relationships within the genus but did not attempt to provide a formal infrageneric taxonomic structure. Observations made in connection with preparation of a species-level taxonomic treatment of *Liatris* (Nesom 2005a) for the Flora of North America volumes are formalized here toward additional perspective on interrelationships within the genus.

The closest relatives of *Liatris* are *Carphephorus* Cass. (7 species; including *Litrisa* Small—1 species and *Trilisa* (Cass.) Cass.—2 species), *Garberia* A.

Gray (1 species), and *Hartwrightia* A. Gray ex S. Wats. (1 species), which (with *Liatris*) constitute subtribe Liatrinae King & H. Robinson of tribe Eupatorieae Cass. (King & Robinson 1987). Specializations of *Hartwrightia* apparently obscured an understanding of its relationship until the study of Robinson and King (1977). The Liatrinae is essentially restricted to the eastern and southeastern U.S.A.; one species (*Liatris garberi*) occurs on the Bahama islands as well as in Florida and several species are essentially Great Plains entities, one of them reaching into northern Mexico. The subtribe is a well-defined group, characterized by the following features: base chromosome number of  $x = 10$ ; leaves alternate, usually in a basal rosette, at least in early stages (fide King & Robinson 1987); corollas rose-purple, with cells laxly subquadrate to short-oblong and usually without sinuous walls, lobes mamillate or papillose on inner surfaces; carpodium indefinite or lacking; cypselar duplex trichomes with cells diverging from near the base; and pappus bristles with barbels indefinitely (vs. linearly) arranged. Within the Liatrinae, *Liatris* is characterized by its usually cormose habit, usually spiciform to racemiform capitulescence, relatively long corolla lobes (long lobes also are characteristic of *Garberia*), and oblong-ovate and apically rounded (non-retuse) anther appendages (also found in *Trilisa*). Concepts of the other genera have been generally accepted, except for *Carphephorus*.

Most recent authors (e.g., Hebert 1968; Correa & Wilbur 1969; Cronquist 1980) have treated *Carphephorus* broadly to include *Litrisa* and *Trilisa*. Radford et al. (1968), in contrast, treated *Carphephorus* and *Trilisa* separately, and King and Robinson (1987) opted for narrower generic concepts, observing that (p. 279) "the broader concept of *Carphephorus* [sensu lato], though natural, is difficult to define in contrast to *Liatris*" and that "actual differences between *Carphephorus*, *Trilisa*, and *Litrisa* have been underestimated by the various authors favoring synonymy." A molecular-phylogenetic study (Schmidt & Schilling 2000), which included two species of *Trilisa* (*C. odoratissimus* and *C. paniculatus*), two of *Carphephorus* sensu stricto (*C. pseudoliatris* and *C. corymbosus*), and three of *Liatris*, suggests that *C. pseudoliatris* is more closely related to *Liatris* than to the others, but too few species of Liatrinae were included to make this a reliable conclusion. A preliminary report on Liatrinae phylogeny (Schilling & Cox 2000) appears to confirm the phylogenetic distinction of *Trilisa* and *Litrisa*. King and Robinson (1987, p. 272), observed that "the genus *Liatris* stands unmistakably outside of the complex including *Carphephorus*, *Litrisa*, and *Trilisa*."

The evolutionary and taxonomic coherence of *Liatris* is supported by the apparent ease with which hybrids are formed between species. A pattern of occurrence is not evident. Interspecific hybrids within *Liatris* have been reported across sectional boundaries (as delimited here) within *Liatris*: *Suprago-Graminifolium* (Gaiser 1946; Hadley & Levin 1967; Levin 1967); *Liatris-Graminifolium*, *Liatris-Pilifilis*, and *Liatris-Suprago* (Gaiser 1951; Hadley &

Levin 1967; Levin 1973); and *Liatris-Vorago* (Allison 2001; Mayfield 2002; Hardig et al. submitted). A list of *Liatris* interspecific hybrids and their putative parents is given in the FNA treatment (Nesom 2005a). There is no readily apparent morphological evidence, however, that hybridization has occurred between species of any of the generic-level taxa of Liatrinae, including the segregates of *Carphephorus*.

### Overview of *Liatris* infrageneric taxonomy

Alexander (1933) did not assign rank to species groups that he recognized for *Laciniaria* (= *Lacinaria* = *Liatris*). Gaiser (1946) used the conventions initiated by Alexander (plural adjectives for group names) but modified the species constitution for some of the groups. Although she specifically referred to the species groups as “series” (placed within two sections) (Table 1), Gaiser did not validate the infrageneric nomenclature by providing Latin diagnoses for the groups, nor did she make direct or indirect reference to Alexander’s names. Fernald (1950) credited Gaiser as combining author of the names she had proposed at the rank of series, using unranked basionyms of Alexander from 1933.

The current study arranges 37 species of *Liatris* in five sections. Figure 1 is essentially a diagrammatic representation of the classification presented below, or it might be read as an essentially unresolved cladogram. A few phyletic generalizations are noted in the following discussion, but lack of morphological evidence limits resolution of relationships.

Among the five sections, sects. *Liatris* and *Vorago* have a more western distribution (essentially extra-Floridian, extra-Atlantic) and constitute a lineage characterized by a distinctive foliar feature—the margins are distinctly whitish-thickened and the surface of this tissue is minutely pebbly-scabrous, an apparently specialized feature not occurring elsewhere in the genus or Liatrinae. Sect. *Liatris* is the only group within the Liatrinae with plumose pappus bristles and is interpreted here as monophyletic on the basis of this apparent synapomorphy. The level of morphological differentiation among the three series of sect. *Liatris*, however, is greater than among the groups treated here as series within sect. *Graminifolium*.

Sects. *Graminifolium*, *Suprago*, and *Pilifilis* have been considered together to constitute sect. *Suprago* (Gaiser 1946; King & Robinson 1987; presumably characterized by the shared plesiomorphy of barbellate pappus bristles), but no specialized morphological feature is evident that would link these groups as a single clade. Gaiser recognized ser. *Pycnostachyae*, ser. *Spicatae*, and ser. *Tenuifoliae* as distinct groups, but the first two are treated here without formal rank within sect. *Suprago*. The two species of ser. *Tenuifoliae* are treated here as sect. *Pilifilis*. Sect. *Graminifolium* includes the species that have an internally pilose corolla tube (with exceptions, as noted below): within the section, ser. *Scariosae* and ser. *Graminifoliae* were recognized as formal groups by Gaiser,

TABLE 1. Gaiser's classification (1946) of *Liatris*.Section **Euliatris**Ser. **Elegantes**: *L. elegans*Ser. **Punctatae**: *L. punctata*, *L. densispicata*, *L. mucronata*, *L. angustifolia*, *L. bracteata*Ser. **Cylindraceae**: *L. cymosa*, *L. ohlingerae*, *L. cylindracea*Ser. **Squarrosae**: *L. squarrosa*Section **Suprago**Ser. **Spicatae**: *L. spicata*, *L. lancifolia*, *L. microcephala*, *L. acidota*, *L. garberi*Ser. **Pycnostachyae**: *L. pycnostachya*Ser. **Graminifoliae**: *L. graminifolia*, *L. helleri*, *L. regimontis*, *L. gracilis*, *L. turgida*Ser. **Pauciflorae**: *L. chapmanii*, *L. pauciflora*, *L. secunda*Ser. **Tenuifoliae**: *L. tenuifolia*, *L. laevigata*Ser. **Scariosae**: *L. scariosa*, *L. aspera*, *L. scabra*, *L. ligulistylis*, *L. borealis*, *L. earlei*

although the species compositions of both are modified here; additionally, ser. *Virgatae*, ser. *Pauciflorae*, and ser. *Garberae* are recognized as constituents of sect. *Graminifolium* in the current classification.

**Morphological trends**

Parallel trends in morphological specialization can be observed within *Liatris*. Although the other genera of Liatrinae produce heads in corymbiform arrangements, the ancestral arrangement within *Liatris* apparently is spiciform to racemiform, and the open, broadly corymbiform capitulescences of *L. ohlingerae* (sect. *Graminifolium*) and *L. cymosa* (sect. *Liatris*) are interpreted here as independently and secondarily derived. As observed by King and Robinson (1987), a nearly complete reduction of the anther appendages seems to have been correlated with these modifications in head arrangement (appendage reduction also has occurred in *L. elegans*); increase in head size also has been a concomitant. Marked increase in head size also has occurred in ser. *Punctatae*, and size of heads (especially as gauged by number of florets) often varies widely among species, particularly in sect. *Graminifolium*. Parallel foliar venation apparently has developed independently in sect. *Liatris* and sect. *Suprago*. Reduction or loss of glandular punctation has occurred in sect. *Suprago*, several groups of sect. *Graminifolium*, sect. *Liatris*, and sect. *Vorago*. Elongation of the putatively primitive corm has occurred independently in sect. *Liatris* (e.g., *L. elegans*, *L. punctata*), sect. *Suprago* (e.g., *L. pycnostachya* var. *lasiophylla*, *L. spicata*), and sect. *Graminifolium* (e.g., *L. garberi*, *L. savannensis*). Chromosome numbers in *Liatris* and Liatrinae are mostly  $2n = 20$  (Gaiser 1949, 1950a, 1950b); within *Liatris*, polyploidy occurs in ser. *Punctatae* (see below) and perhaps other groups.

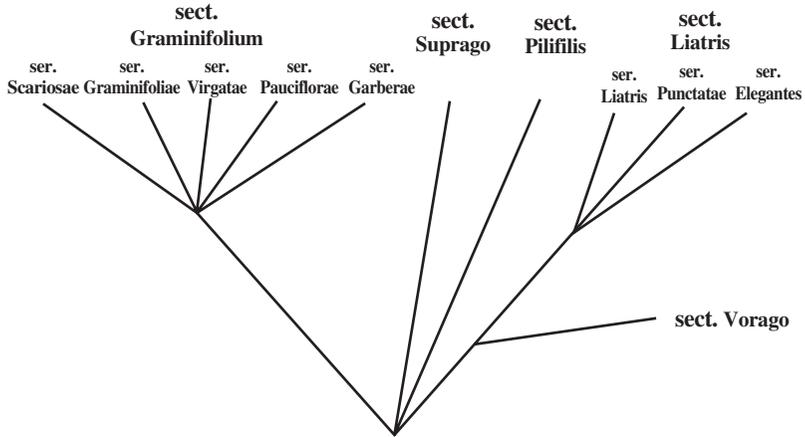


FIG. 1. Infrageneric taxonomic structure of *Liatris*.

### Corms or roots?

Interpretation of the morphological nature of the perennating structures of *Liatris* and their descriptive terminology have been inconsistent. Gaiser (1946, p. 168-169) interpreted them as thickened underground stems and referred to them as corms. She noted that "During the first summer of the seedling's growth there develop a few radical leaves above what appears as a slightly thickened tap-root, but at the end of the season an apical bud is developed from a small crown and this, in the second year, produces the first flowering stalk. During successive summers the stem thickens, becoming globular or remaining ovoid in most species. ..." She referred to the more elongate structures, such as produced by *L. punctata*, both as "rhizomes" and as "rootstocks" and also was inconsistent in description of the globose structures: for example, she noted for *L. spicata* (p. 178) "Rootstock globose in young plants, enlarged and shallow in old plants by separation of parts permitting considerable vegetative propagation." Other botanists also have described them variously: Gray (1884), "a tuberous or mostly globose and corm-like stock;" Fernald (1950), "a roundish corm or tuber ...;" Bailey and Bailey (1976), "a corm, or less often ... a rhizome or an elongated root crown;" Cronquist (1980), "a thickened, usually cormlike rootstock" but noting that they appear to have characteristics of both corm and root; King and Robinson (1987), "a thickened, usually corm-like, penetrating rootstock ..." Kerster (1968) and Levin (1973) made age estimates of *Liatris* individuals by counting annual growth rings from radial sections of "corms," but they did not detail their interpretation of them as stems rather than roots; annular secondary growth may occur in both kinds of organs.

While these structures quickly become woody and nodes are difficult to discern, they are here regarded as corms and rhizomes, rather than roots with adventitious buds, because of several reasons. (1) New, ascending-erect stems may be produced from various lateral points (nodes) of somewhat elongated, vertically oriented corms. From the somewhat flattened tops of older, much enlarged corms (e.g., in *L. punctata* var. *mucronata*), up to 30 buds (stems) are sometimes produced. (2) In some taxa there are various stages of transition between the globose structures and much-elongated structures, which appear to function as horizontal rhizomes. Such elongation can be observed in *Liatris pycnostachya* var. *lasiophylla* and *L. punctata* var. *punctata*. Some of the longer rhizomes produce new erect stems at intervals; the lowermost portions of such new stems may expand in circumference, become woody, and appear like caudex branches. (3) All of the other Liatrinae (except perhaps the shrubby *Garberia*) apparently produce rhizomes with fibrous roots. In some species of *Carphephorus*, there is little if any rhizome and the stems and fibrous roots originate from the highly condensed crown area. A taproot is never evident, except perhaps very early in ontogeny, as noted above by Gaiser for *Liatris*.

#### CLASSIFICATION

***Liatris*** Gaertner ex Schreb., Gen. Pl. 2:542. 1791 (nom. cons.). TYPE SPECIES: *Liatris squarrosa* (L.) Michx. = *Serratula squarrosa* L. (typ. cons.)

*Lacinaria* J. Hill, Veg. Syst. 4 (ed. 2):49, t. 46. 1762 (nom. rej.); non *Laciniaria* J. Hill (1769), an orthographic variant. LECTOTYPE (J. Hill, Hort. Kew. 70. 1769), *Liatris squarrosa* (L.) Michx.

*Psilothamnus* Necker, Elem. Bot. 1:69. 1790 (nom. inval.).

*Suprago* Gaertner, Fruct. Sem. Pl. 2(3):402. 1791. LECTOTYPE: (Cassini, Dict. Sci. Nat. 51:384. 1827), *Liatris spicata* (L.) Willd.

*Calostelma* D. Don in Sweet, Brit. Flower Gard. ser. 2, 2:184. 1833. TYPE SPECIES: *Liatris elegans* (Walter) Michx.

*Ammopursus* Small, Bull. Torrey Bot. Club 51:392. 1924. TYPE SPECIES: *Liatris ohlingerae* (Blake) B.L. Rob.

#### KEY TO THE SECTIONS

1. Leaf margins whitish, thickened, and minutely scabrous; phyllaries foliaceous and subequal to weakly or strongly graduate, hyaline margins absent or extremely narrow (apices hyaline in ser. *Elegantes*); pappus bristles plumose or barbellate.
  2. Pappus bristles plumose. \_\_\_\_\_ **1. Sect. *Liatris***
  2. Pappus bristles barbellate. \_\_\_\_\_ **2. Sect. *Vorago***
1. Leaf margins greenish, slightly thickened or not, smooth; phyllaries not foliaceous, usually strongly graduate, usually completely bordered by purplish, hyaline margins; pappus bristles barbellate.
  3. Basal and lower cauline leaves 3–5-veined, parallel venation of basal leaf bases persistent as fibrous vestiges; corolla tubes glabrous within. \_\_\_\_\_ **3. Sect. *Suprago***
  3. Basal and lower cauline leaves 1-veined, parallel venation of leaf bases usually not persistent-fibrous; corolla tubes glabrous or pilose within.
    4. Corolla tubes glabrous within, stems glabrous; staminal filaments pilose. \_\_\_\_\_ **4. Sect. *Pilifilis***

4. Corolla tubes pilose within, or if glabrous (in *L. ligulistylis*, *L. scariosa*, *L. microcephala*, *L. ohlingerae*, and *L. garberi*) then stems puberulent to puberulent-pilose; staminal filaments glabrous. \_\_\_\_\_ **5. Sect. Graminifolium**

**1. Section *Liatris*.** TYPE SPECIES: *Liatris squarrosa* (L.) Michx.

Leaves 3–5-veined; leaf margins thickened, whitish, and minutely pebbly-scarious; parallel venation of leaf bases not fibrous-persistent; laminae punctate-glandular to weakly punctate-glandular. Capitulescence mostly racemoid-spiciform, cymoid in one species of ser. *Punctatae* (heads commonly solitary in *L. compacta*). Heads sessile to subsessile or pedunculate. Involucres cylindrical to campanulate-cylindric; phyllaries indurate to thin-herbaceous, appressed to loose or spreading, apices rounded to acute or acuminate, green or petaloid, margins usually without a scarious border. Corolla lobes hispid-hirsute or glabrous on adaxial surface; corolla tubes glabrous within; staminal filaments glabrous. Pappus bristles plumose.

Species of sect. *Liatris* are characterized by white-indurate, minutely scarious leaf margins, cylindrical heads with foliaceous, subequal phyllaries (strongly to weakly graduate in ser. *Punctatae*), plumose pappus bristles, and a primarily central North American distribution.

KEY TO THE SERIES

1. Leaves with 3–5 parallel nerves; leaves and phyllaries weakly glandular-punctate or not at all; phyllaries weakly graduate to subequal, usually loose and spreading (strongly graduate and appressed in *L. cylindracea*), apices green; corolla lobes hispid on adaxial surface. \_\_\_\_\_ **1a. Ser. *Liatris***
1. Leaves 1-nerved; leaves and phyllaries glandular-punctate; phyllaries strongly graduate and appressed or subequal and loose or spreading; corolla lobes glabrous.
  2. Phyllaries not foliaceous, strongly to weakly graduate, mostly appressed, apices green. \_\_\_\_\_ **1b. Ser. *Punctatae***
  2. Phyllaries somewhat foliaceous, weakly graduate to subequal, loose or spreading, apices petaloid. \_\_\_\_\_ **1c. Ser. *Elegantes***

**1a. Series *Liatris*.** TYPE SPECIES: *Liatris squarrosa* (L.) Michx.

*Lacinaria* unranked *Squarrosae* Alexander in Small, Man. Southeastern Fl. 1331. 1933. *Liatris* ser. *Squarrosae* (Alexander) Gaiser ex Fernald, Gray's Man. ed. 8, 1375. 1950. TYPE SPECIES: *Liatris squarrosa* (L.) Michx.

*Liatris* sect. *Euliatris* series *Squarrosae* Gaiser, Rhodora 48:393. 1946 (nom. nud., without Latin descr.).

*Liatris* sect. *Euliatris* series *Cylindraceae* Gaiser, Rhodora 48:373. 1946 (nom. nud., without Latin descr.).

*Liatris* ser. *Cylindraceae* Gaiser ex Fernald, Gray's Man. ed. 8, 1375. 1950 (nom. nud., without Latin descr.).

Leaves 3–5-nerved. Phyllaries foliaceous, weakly graduate to subequal, loose or spreading, apices green. Corolla lobes hispid on adaxial surface.

*Species included.*—*Liatris compacta* (Torrey & A. Gray) Rydb., *L. cylindracea* Michx., *L. hirsuta* Rydb., *L. squarrosa* (L.) Michx.

The strongly graduate, appressed phyllaries of *Liatris cylindracea* are similar to those of ser. *Punctatae*, but the 3–5-veined leaves and hirsute corolla lobes of ser. *Liatris* make this a strongly defined and easily recognizable group within the ‘western’ clade (which has white-indurate, minutely scabrous leaf margins and plumose pappus bristles).

**1b. Series *Punctatae*** (Alexander) Gaiser ex Fernald. *Lacinaria* unranked *Punctatae* Alexander in Small, Man. Southeastern Fl. 1331. 1933. *Liatris* ser. *Punctatae* (Alexander) Gaiser ex Fernald, Gray's Man. ed. 8, 1375. 1950. TYPE: *Liatris punctata* Hook.

*Liatris* sect. *Euliatris* series *Punctatae* Gaiser, *Rhodora* 48:346. 1946 (nom. nud., without Latin descr.).

Leaves 1-nerved. Phyllaries not foliaceous, strongly to weakly graduate, appressed to slightly loose, apices green. Corolla lobes glabrous.

*Species included.*—*Liatris aestivalis* Nesom & O'Kennon, *L. bracteata* Gaiser, *L. cymosa* (H. Ness) K. Schum., *L. glandulosa* Nesom & O'Kennon, *L. punctata* Hook. (including *L. mucronata* DC. and *L. densispicata* [Bush] Gaiser).

Ser. *Punctatae* apparently is the only group of *Liatrinae* in which polyploidy is prevalent (Gaiser 1950b, 1954). Except for *L. punctata*, which ranges from Canada into northern Mexico, the species are largely Texas-centered. Several taxonomic problems remain to be resolved within *L. punctata* sensu lato.

**1c. Series *Elegantes*** (Alexander) Gaiser ex Nesom, comb. et stat. nov. BASIONYM: *Lacinaria* unranked *Elegantes* Alexander in Small, Man. Southeastern Fl. 1331. 1933. TYPE SPECIES: *Liatris elegans* (Walter) Michx.

*Liatris* sect. *Euliatris* series *Elegantes* Gaiser, *Rhodora* 48:340. 1946 (nom. nud., without Latin descr.). Calostelma D. Don in Sweet, Brit. Flow. Gard. ser. 2, 2:184. 1833. TYPE SPECIES: *Liatris elegans* (Walter) Michx.

Leaves 1-nerved. Phyllaries foliaceous, weakly graduate to subequal, loose or spreading, apices petaloid. Corolla lobes glabrous.

*Species included.*—*Liatris elegans* (Walter) Michx.

**2. Section *Vorago*** Nesom, sect. nov. TYPE SPECIES: *Liatris oligocephala* J. Allison.

Folia 1-nervia (*L. oligocephala*) vel leniter 1–3-nervia (*L. tenuis*); margines incrassati, candidi, scabrelli; nervatura parallela basium foliorum non fibrosi-persistens. Capitulescentia spiciformis (*L. tenuis*) aut cymiformis capitulis 1-aliquot (*L. oligocephala*). Capitula sessiles vel subsessiles vel pedunculata. Involucra campanulati-cylindrica; phyllaria indurata, virida, plerumque incohaerentia vel patentia, sine marginibus angustis hyalinis, apicibus acutis vel acuminatis. Corollae lobis glabris, tubis glabris interne; stamina filamentis glabris. Pappus setis plerumque barbellatis.

Leaves 1-veined (*L. oligocephala*) or 1- to weakly 3-veined (*L. tenuis*); leaf margins thickened, whitish, and minutely pebbly-scabrous; parallel venation of leaf bases not fibrous-persistent; lamina not punctate-glandular or only weakly punctate. Capitulescence spiciform (*L. tenuis*) or heads solitary to few and in a cymoid arrangement (*L. oligocephala*). Heads sessile to sessile or pedunculate. Involucres campanulate-cylindric; phyllaries indurate, green, usually loose or

spreading, apices acute to acuminate, margins without a hyaline border. Corolla lobes glabrous; corolla tubes glabrous within; staminal filaments glabrous. Pappus bristles mostly barbellate.

*Species included.*—*Liatris oligocephala* J. Allison, *L. tenuis* Shinners.

These species are similar to some in sect. *Liatris* in their whitish, thickened, and minutely scabrous leaf margins, cylindrical heads, and indurate and loose or spreading, subequal to weakly graduate, somewhat foliaceous, triangular phyllaries with acute to acuminate apices and without hyaline margins. Their generally western (non-Floridian) geographical position within the genus also suggests ancestry similar to sect. *Liatris*. Pappus bristles of both species, however, are barbellate.

In the original description of *Liatris tenuis*, Shinners (1959) noted its general similarity to *L. squarrosa* (ser. *Liatris*) but rejected a hypothesis of close relationship because of the disparity in pappus bristle morphology. Still, the weakly 3-veined leaves of *L. tenuis* suggest that it may be closest to species of ser. *Liatris*, perhaps as a sister element.

*Liatris oligocephala* is similar to *L. tenuis* in features of the involucre, corolla, and pappus, but because no synapomorphy is evident, it seems likely that these two species originated independently from the ancestral stock of sect. *Liatris*. Thus, sect. *Vorago*, as delimited here, may not be monophyletic. As noted by Allison (2001), the glabrous achene surfaces of *L. oligocephala* represent a specialized state unique in the genus. Leaf margins are thickened and whitish but vary from “pebbly” (Allison 7817, VDB) to smooth (Allison 8134, VDB). Phyllary margins are mostly without a hyaline border, but a weakly developed proximal border sometimes is evident.

The name of the section (“vorago,” Latin, gulf) alludes to the range of the two species on the Gulf Coastal Plain as well as to the considerable morphological “gulf” between them.

**3. Section *Suprago* (Gaertner) DC.** *Suprago* Gaertner, Fruct. Sem. Pl. 2(3):402. 1791. *Liatris* section *Suprago* (Cass.) DC., Prodr. 5:129. 1836. LECTOTYPE: (Cassini, Dict. Sci. Nat. 51:384. 1827), *Liatris spicata* (L.) Willd.

*Lacinaria* unranked *Spicatae* Alexander in Small, Man. Southeastern Fl. 1332. 1933. *Liatris* ser. *Spicatae* (Alexander) Gaiser ex Fernald, Gray's Man. ed. 8, 1372. 1950. TYPE SPECIES: *Liatris spicata* (L.) Willd.

*Liatris* sect. *Suprago* series *Spicatae* Gaiser, Rhodora 48:177. 1946 (nom. nud., without Latin descr.).

*Lacinaria* unranked *Pycnostachyae* Alexander in Small, Man. Southeastern Fl. 1331. 1933. *Liatris* ser. *Pycnostachyae* (Alexander) Gaiser ex Fernald, Gray's Man. ed. 8, 1373. 1950. TYPE SPECIES: *Liatris pycnostachya* Michx.

*Liatris* sect. *Suprago* series *Pycnostachyae* Gaiser, Rhodora 48:237. 1946 (nom. nud., without Latin descr.).

Leaves 3–5 veined; leaf margins slightly thickened, green, smooth; parallel venation of bases of basal leaves conspicuously persisting as fibrous vestiges;

lamina punctate-glandular to weakly punctate-glandular. Capitulescence spiciform to narrowly racemiform. Heads sessile to subsessile. Involucres cylindrical; phyllaries thin-herbaceous, appressed to loose or spreading, apices rounded to acute, green (petaloid-recurving in *L. pycnostachya*), margins usually with a narrow scarious border. Corolla lobes glabrous; corolla tubes glabrous within; staminal filaments glabrous. Pappus bristles barbellate (subplumose in *L. acidota*). TYPE SPECIES: *Liatris spicata* (L.) Willd.

*Species included.*—*Liatris acidota* Engelm. & A. Gray, *L. lancifolia* (Greene) Kittell, *L. pycnostachya* Michx., *L. spicata* (L.) Willd.

Sect. *Suprago* is distinct in its 3–5-veined leaves, parallel veins at the bases of the basal leaves conspicuously persisting as fibers, and internally glabrous corolla tubes. The species are relatively scattered in geographic distribution but are mostly “western” like those of sect. *Liatris*; none are primarily “Floridian.” In addition to features of sect. *Suprago* noted in the description, cauline leaves tend to be abruptly reduced to bracts above midstem. Even within *L. spicata*, however, the distal cauline leaves of *L. spicata* var. *resinosa* are abruptly reduced while those of var. *spicata* are only gradually reduced. Similar reduction of distal cauline leaves also occurs in other groups of *Liatris*.

**4. Section *Pilifilis*** Nesom, sect. nov. *Lacinaria* unranked *Tenuifoliae* Alexander in Small, Man. Southeastern Fl. 133l. 1933. TYPE SPECIES: *Liatris tenuifolia* Nutt.

*Liatris* sect. *Suprago* series *Tenuifoliae* Gaiser, *Rhodora* 48:286. 1946 (nom. nud., without Latin descr.).

Folia 1-nervia; margines leniter incrassati, virides, laeves; nervatura parallella basium foliorum plerumque non fibrosi-persistens. Capitulescentia spiciformis vel leniter racemiformis. Capitula sessiles vel subsessiles vel pedunculata. Involucra cylindrica; phyllaria tenuiter herbacea, virida (non petaloidea), appressa, apicibus obtusis vel retusis plerumque apiculatis, marginibus angustis hyalinis. Corollae lobis glabris, tubis glabris interne; stamina filamentis pilosis. Pappus setis barbellatis.

Leaves 1-veined; leaf margins slightly thickened, green, smooth; parallel venation of leaf bases usually not fibrous-persistent but sometimes weakly so; lamina punctate-glandular to weakly punctate-glandular. Capitulescence spiciform to slightly racemiform. Heads sessile to subsessile or pedunculate. Involucres cylindrical; phyllaries thin-herbaceous, green (not petaloid), appressed, apices obtuse to retuse and usually apiculate, margins with a narrow scarious border. Corolla lobes glabrous; corolla tubes glabrous within; staminal filaments pilose. Pappus bristles barbellate.

*Species included.*—*Liatris laevigata* Nutt., *L. tenuifolia* Nutt.

The pilose staminal filaments of these two species set them apart from others in the genus. It seems reasonable to speculate that this is homologous with production of hairs from internal petal tissue near the corolla base in sect. *Graminifolium*. Basal leaves of *L. laevigata* and *L. tenuifolia* show a tendency to be fibrous-persistent, like those in sect. *Suprago*, but the leaves are 1-veined.

**5. Section *Graminifolium*** Nesom, sect. nov. TYPE SPECIES: *Liatris pilosa* (Aiton) Willd. (= *Liatris graminifolia* Willd.).

Folia 1-nervia. (leniter 3–5-nervia in *L. savannensi*); margines leniter incrassati, virides, laeves; nervatura parallela basium foliorum non fibrosi-persistens. Capitulescentia racemi-spiciformis, raro cymiformis. Capitula sessiles vel subsessiles vel pedunculata. Involucra cylindrica vel campanulata; phyllaria tenuiter herbacea, virida, appressa, apicibus rotundatis vel acutis, marginibus angustis hyalinis. Corollae lobis glabris, tubis plerumque pilosis interne (glabris in *L. garberi*, *L. ligulistylis*, *L. microcephala*, ac *L. ohlingerae*); stamina filamentis glabris. Pappus setis barbellatis.

Leaves 1-veined (weakly 3–5 veined in *L. savannensis*); leaf margins slightly thickened, green, smooth; parallel venation of leaf bases not fibrous-persistent; lamina punctate-glandular to weakly punctate-glandular. Capitulescence racemoid-spiciform, rarely cymoid. Heads sessile to subsessile or pedunculate. Involucres cylindric to campanulate; phyllaries thin-herbaceous, green, appressed, apices rounded to acute, margins with a narrow scarious border. Corolla lobes glabrous; corolla tubes usually pilose within (glabrous in *L. ligulistylis*, *L. ohlingerae*, *L. microcephala*, and *L. garberi*); staminal filaments glabrous. Pappus bristles barbellate.

Section *Graminifolium* is characterized by the distinctive pilose vestiture produced within the corolla tubes in the region of filament insertion. This vestiture is hypothesized to have been lost in four species, each of which apparently is specialized in other features: *Liatris ohlingerae* and *L. ligulistylis* produce particularly large heads; *L. microcephala* has exceptionally short pappus bristles and short corollas, mostly due to loss of tube length; *L. garberi* is hypothesized to have reverted to a characteristically primitive root system (see comments below).

KEY TO THE SERIES

1. Phyllaries acute to obtuse (angular) at the apex.
  2. Stems glabrous; phyllaries oblong-triangular. \_\_\_\_\_ **5c. Ser. *Virgatae***
  2. Stems hirtellous or pilose-puberulent (usually glabrous in *L. pauciflora*); phyllaries usually obovate.
    3. Corms globose; stems hirtellous or glabrous; corolla tubes pilose within. \_\_\_\_\_ **5a. Ser. *Pauciflorae***
    3. Corms irregularly shaped, short-rhizomiform with tuberous-thickened fibrous roots; stems pilose-puberulent; corolla tubes glabrous within. \_\_\_\_\_ **5b. Ser. *Garberae***
1. Phyllaries rounded to obtuse-rounded at the apex.
  4. Stems glabrous or uncommonly sparsely pilose; basal leaves mostly oblanceolate; heads sessile to short-pedunculate in a spiciform capitulescence. \_\_\_\_\_ **5d. Ser. *Graminifoliae***
  4. Stems puberulent; basal leaves obovate-spatulate; heads usually pedunculate in a racemiform to corymbiform capitulescence. \_\_\_\_\_ **5e. Ser. *Scariosae***

**5a. Series *Pauciflorae*** (Alexander) Gaiser ex Nesom, comb. et stat. nov. BASIONYM: *Lacinaria* unranked *Pauciflorae* Alexander in Small, Man. Southeastern Fl. 1331. 1933. TYPE SPECIES: *Liatris pauciflora* Pursh.

*Liatriis* sect. *Euliatriis* series *Pauciflorae* Gaiser, *Rhodora* 48:279. 1946 (nom. nud., without Latin descr.).

Corms globose. Stems hirtellous or glabrous. Basal leaves mostly oblanceolate. Heads sessile to short-pedunculate in a spiciform capitulescence. Phyllaries obovate, apically acute to obtuse (angular). Corolla tubes pilose within.

*Species included.*—*Liatriis chapmanii* Torrey & A. Gray, *L. pauciflora* Pursh (including *L. secunda* Ell.), *L. provincialis* Godfrey

**5b. Series *Garberae*** Nesom, ser. nov. TYPE: *Liatriis garberi* A. Gray.

Cormi forma irregulares, brevi-rhizomiformes radicibus fibris crassis. Caules pilosi-puberuli. Folia basalia plerumque oblanceolata. Capitula sessiles vel brevipedunculata capitulescentia spiciformis. Phyllaria obovata, ad apices angulata, acuta vel obtusa. Corollae tubis interne glabris.

Corms irregularly shaped, short-rhizomiform with tuberous-thickened fibrous roots. Stems pilose-puberulent. Basal leaves mostly oblanceolate. Heads sessile to short-pedunculate in a spiciform capitulescence. Phyllaries obovate, apically acute to obtuse (angular). Corolla tubes glabrous within.

*Species included.*—*Liatriis garberi* A. Gray

The thickened, fibrous roots of *Liatriis garberi*, arising from an abbreviated crown or short and irregular rhizome, are distinct in the genus and are similar to those of *Carphephorus* and *Hartwrightia*, presumably a primitive feature for the *Liatriinae*. If corms are an ancestral feature of *Liatriis*, as seems to be the case, then the root system of *L. garberi* may be secondarily derived. The internally glabrous corolla tubes of *L. garberi*, in the interpretation here, also are specialized (loss of pubescence). *Liatriis garberi* is more similar in stem vestiture to *L. pycnostachya* and *L. acidota* of sect. *Suprago* than to any species of sect. *Graminifolium*. Leaf bases of *L. garberi*, however, are not like those of sect. *Suprago* and the phyllaries are similar to those of ser. *Pauciflorae*. The restricted Floridian geography of *L. garberi* also suggests that its closest relatives are more likely found in the same area (i.e., ser. *Pauciflorae*, especially).

**5c. Series *Virgatae*** Nesom, ser. nov. TYPE SPECIES: *Liatriis virgata* Nutt.

Cormi globosi. Caules glabres. Folia basalia plerumque oblanceolata. Capitula sessiles vel brevipedunculata capitulescentia spiciformis. Phyllaria oblongi-triangularis, ad apices angulata. Corollae tubis interne pilosis.

Corms globose. Stems glabrous. Basal leaves mostly oblanceolate. Heads sessile to short-pedunculate in a spiciform capitulescence. Phyllaries oblong-triangular, apically acute to obtuse (angular). Corolla tubes pilose within.

*Species included.*—*Liatriis cokeri* Pyne & Stucky, *L. virgata* Nutt.

As suggested by Nesom and Stucky (2004), *Liatriis cokeri* and *L. virgata* may be sister taxa. Their angular phyllary apices possibly indicate relatively close ancestry with ser. *Pauciflorae*, although some plants in the northern range

of *L. pilosa* also produce angular phyllaries. The glabrous stems of *L. cokeri* and *L. virgata* are similar to those of ser. *Graminifoliae*.

**5d. Series *Graminifoliae*** Gaiser ex Nesom, ser. nov. *Liatris* sect. *Suprago* series *Graminifoliae* Gaiser, *Rhodora* 48:246. 1946 (nom. nud., without Latin descr.). *Liatris* ser. *Graminifoliae* Gaiser ex Fernald, *Gray's Man. ed.* 8, 1373. 1950 (nom. nud., without Latin descr.). Fernald attributed the basionym to Alexander, but “*Graminifoliae*” was not among the group-names used by Alexander. TYPE SPECIES: *Liatris pilosa* (Aiton) Willd. (= *Liatris graminifolia* Willd.).

Cormi globosi. Caules glabres vel sparsim pilosi. Folia basalia plerumque oblanceolata. Capitula sessiles vel brevipedunculata capitulescentia spiciformis. Phyllaria oblongi-triangularia, ad apices rotundata vel obtusi-rotundata. Corollae tubis interne pilosis.

Corms globose. Stems glabrous to sparsely pilose. Basal leaves mostly oblanceolate. Heads sessile to short-pedunculate in a spiciform capitulescence. Phyllaries oblong-triangular, apically rounded to obtuse-rounded. Corolla tubes pilose within.

*Species included.*—*Liatris elegantula* (Greene) K. Schum., *L. helleri* Porter (synonym = *L. turgida* Gaiser), *L. microcephala* (Small) K. Schum., *L. pilosa* (Aiton) Willd. (synonym = *L. graminifolia* Willd.), *L. savannensis* Kral & Nesom.

Prior to recent recognition of *Liatris savannensis* (Kral & Nesom 2003), plants of that species had been identified mostly as *L. spicata* (sect. *Suprago*). The leaves of *L. savannensis* are weakly 3-nerved, a feature of *L. spicata* and its close relatives but one not otherwise found in sect. *Graminifolium*, and *L. savannensis* might be investigated toward the possibility that genes from sect. *Suprago* were involved in its evolutionary origin.

Basal leaves of *Liatris helleri* (sensu lato, Nesom 2005b) range to relatively large size, similar to those of ser. *Scariosae*. *Liatris helleri*, however, is most similar overall to *L. pilosa*, and the geographic juxtaposition of *L. virgata* between *L. pilosa* and *L. elegantula* (Nesom & Stucky 2004) is perhaps indicative of a more distant relationship of the the latter two species.

*Liatris microcephala* is very similar to other species of ser. *Graminifoliae* but lacks the diagnostic pilose vestiture within the corolla tube. The tube, however, is much shortened (the whole head is shortened), and it is assumed here that loss of the vestiture accompanied other specializations toward reduction in corolla size. The characteristic tendency for short pappus bristles in *L. microcephala* also occurs in some populations of *L. helleri* (Nesom 2005b) but not elsewhere in the genus.

**5e. Series *Scariosae*** (Alexander) Gaiser ex Fernald. *Lacinaria* unranked *Scariosae* Alexander in Small, *Man. Southeastern Fl.* 1332. 1933. *Liatris* ser. *Scariosae* (Alexander) Gaiser ex Fernald, *Gray's Man. ed.* 8, 1374. 1950. TYPE SPECIES: *Liatris scariosa* (L.) Willd.

*Liatris* sect. *Euliatris* series *Scariosae* Gaiser, *Rhodora* 48:293. 1946 (nom. nud., without Latin descr.).

*Ammopursus* Small, Bull. Torrey Bot. Club 51:392. 1924. TYPE SPECIES: *Liatris ohlingerae* (Blake) B.L. Rob.

Corms globose. Stems hirtellous or pilose-puberulent (variably glabrous in *L. squarrulosa*). Basal leaves mostly obovate-spatulate. Heads sessile to short-pedunculate in a spiciform capitulescence or usually pedunculate in a racemiform to corymbiform capitulescence. Phyllaries oblong-triangular, apically rounded to obtuse-rounded. Corolla tubes usually pilose within (glabrous in *L. ligulistylis* and *L. ohlingerae*).

*Species included (in three informal groups)*: **1**) southern range, linear basal leaves, large heads: *L. ohlingerae* (Blake) B.L. Rob.; **2**) southern range, smaller basal leaves, smaller heads: *Liatris gholsonii* L. Anderson, *L. gracilis* Pursh, *L. patens* Nesom & Kral; **3**) northern range, larger basal leaves, large heads: *Liatris aspera* Michx., *L. ligulistylis* (A. Nels.) K. Schum., *L. scariosa* (L.) Willd. (including *L. borealis*), *L. squarrulosa* Michx. (including *L. scabra* (Greene) K. Schum.)

Series *Scariosae* is separated here into three subgroups, generally differing in head size and in basal leaf morphology. Addition of *L. ohlingerae* and the apparently interrelated *L. gracilis*, *L. gholsonii*, and *L. patens* expands Gaiser's concept of ser. *Scariosae*. The latter three species range widely in head size (3–6[–9], 3–5[–6], and 7–12 florets, respectively). *Liatris ohlingerae* has 20–30 florets, glabrous corolla tubes, basal leaves hardly wider than the cauline, and may not belong with ser. *Scariosae*. Heads of *L. squarrulosa* also are markedly variable—11–26(–28) florets. *Liatris scariosa*, *L. ligulistylis*, and *L. aspera* are larger-headed—ca. 19–ca. 80, ca. 30–70, and (14–)18–24(–30) florets, respectively—and have more northern geographic distributions. *Liatris scariosa* and *L. ligulistylis* usually produce heads on long peduncles, as in *L. ohlingerae* and *L. patens*, and there is a tendency in the first three species for the corolla tubes to be glabrous.

*Liatris ohlingerae* is distinct in its relatively few, broadly campanulate heads in a cymiform arrangement. Small (1924, 1933) considered the species so remarkable that he treated it as the monotypic genus *Ammopursus*, emphasizing (1924, p. 393) the “succulent foliage, the open inflorescence, the somewhat zygomorphic corollas with inflated throats, and the short pappus.” Gaiser placed *L. ohlingerae* in “series *Cylindraceae*” (a group treated here within sect. *Liatris*) because of its similarity in habit (mostly the arrangement of heads) to *L. cymosa*, but the pappus bristles of *L. ohlingerae* are barbellate rather than plumose as in sect. *Liatris*. Blake's original description (1923) of the species apparently emphasized the campanulate heads, noting that the species was nearest *L. scariosa*. The puberulent vestiture and long-pedunculate heads of *L. ohlingerae* also are shared similarities with ser. *Scariosae*, but the internally glabrous corolla tubes are unusual for sect. *Graminifolium*.

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## ANNOUNCEMENT

### THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Vidal de Freitas Mansano, of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, and Benjamin M. Torke, currently a graduate student in the Department of Biology, Washington University, St. Louis, are the joint recipients of the Rupert Barneby Award for the year 2005. They will be studying the systematics and diversification of *Swartzia* (Leguminosae, Papilionoideae, Swartzieae), a prominent neotropical tree genus of approximately 140–180 species, with species diversity concentrated in lowland rainforests of the Guianas and Amazonia.

The New York Botanical Garden now invites applications for the Rupert Barneby Award for the year 2006. The award of US\$ 1,000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a detailed letter describing the project for which the award is sought, and the names of 2–3 referees. Travel to the NYBG should be planned for sometime in the year 2006. The application should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, 200th Street and Kazimiroff Blvd., Bronx, NY 10458-5126 USA, and received no later than December 1, 2005. Announcement of the recipient will be made by December 15.

Anyone interested in making a contribution to THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Luteyn.