ANOTHER REVIEW OF THE *SYMPHYOTRICHUM PATENS* COMPLEX (ASTERACEAE), INCLUDING A NEW VARIETY OF *S. PATENS* FROM THE SOUTHERN BLACKLANDS, NEW RECORDS OF *S. GEORGIANUM* AND NOTES ON *GEORGIANUM*-LIKE PLANTS OUTSIDE ITS KNOWN RANGE

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ABSTRACT

Taxonomy of the *Symphyotrichum patens* complex is reviewed, and a new variety is described: **S. patens var. terranigrum** J.J.N. Campbell & Seymour. This variety is known mostly from the Black Belt grasslands of Alabama and Mississippi, but it extends east to calcareous soils on the Piedmont of North Carolina. Also, there are a few records of similar plants from the southern Interior Low Plateaus and the Ridge-and-Valley region as far north as Pennsylvania. Var. *terranigrum* is distinct in the minute stipitate glands that cover surfaces of stems and leaves, with non-glandular hairs dense or sparse or absent. In most variants of *S. patens*, glands are largely restricted to involucres and non-glandular hairs are dense, although glands are widespread in some plants of more typical *S. patens* that are concentrated in Appalachian regions. Leaves of the new variety tend to have a bluish-waxy sheen, usually darkening when dried; mid-stem leaves tend to be relatively short and clustered; and bracteal leaves tend to be abuptly reduced above the peduncle base. However, several collections appear transitional to var. *gracile* or var. *patens*. It is suggested that the presence of glands on stems and leaves is ancestral within the complex, and that var. *terranigrum* partly corresponds to the diploid population mapped by previous authors in the Black Belt. The polyploid *S. georgianum* is a largely allopatric species concentrated in less base-rich grasslands and thin woodlands on or near the Piedmont, but there is significant variation in glandularity and habit within this species plus similar plants from Texas to Pennsylvania. New county records are provided for *S. georgianum*, including the first from Tennessee. A largely eglandular variant of *georgianum* is concentrated on the Atlantic Coastal Plain. An undescribed *georgianum*-like taxon could be based on distinct collections concentrated in Texas but ranging from Oklahoma to Georgia.
KEY WORDS: *Symphyotrichum*, *S. patens*, *S. patens* var. *terranigrum*, *S. georgianum*, Asteraceae, blacklands, Black Belt, Piedmont, Mississippi, Alabama, Tennessee.

INTRODUCTION

Like violets in spring, the North American asters now known as species of *Symphyotrichum* sometimes seem designed to provoke exasperation and discord amongst systematic botanists during autumn, whilst the general public admires them from a more relaxed aesthetic perspective. Subgenus *Virgulus* (Raf.) Nesom is a relatively distinct and showy division within the genus; with rays usually blue to purple; phyllaries usually stipitate-glandular; cauline leaves 3-nerved, rounded to auriculate or amplexicaul at sessile bases; and with a basic chromosome number of x = 5. But appropriate sections within *Virgulus* remain unresolved, from A. Jones (1980) to Brouillet et al. (2006). Moreover, among plants known as sect. *Patentes* (Torr. & Gray) Nesom the circumscription of some taxa and their relationships remain uncertain.

Based on Brouillet et al. (2006), the core of sect. *Patentes* comprises *S. patens* (Ait.) Nesom, *S. phlogifolium* (Muhl. ex Willd.) Nesom and *S. georgianum* (Alex.) Nesom. In addition, *S. adnatum* (Nutt.) Nesom and *S. walteri* (Alex.) Nesom could be included, but those species of southeastern sandhills and pine flatwoods are highly distinctive in their somewhat scandent habit, and in their adnate viscid distal leaves (*adnatum*) or succulent (*walteri*) leaves. Two additional species also appear relatively close.
(1) *S. novae-angliae* (L.) Nesom is a widespread robust weedy species of relatively fertile soils in eastern states: diploid (2n = 10) or rarely tetraploid (A. Jones 1980, Semple 1984), with unusually large heads that have somewhat foliaceous, densely glandular phyllaries, and relatively narrow leaves (length/width ca. 5-10 versus 2.5-5) that are unusually dense up into

lower parts of the somewhat corymbiform inflorescence. It has been considered the sole member of sect. *Polyliguli* but it could be grouped with the following.
(2) *S. grandiflorum* (L.) Nesom is restricted to the Carolinas and Virginia, especially on sandy soils: dodecaploid (2n = 60) or occasionally hexaploid (Brouillet et al. 2006), with spreading rhizomes, more cuneate distal leaves and scabrous phyllaries. It has been grouped in sect. *Grandiflori* with some widely scattered diploid species that have less auriculate-clasping leaves: *campeste, pygmaeum, yukonense, fendleri* and *oblongifolium*.
It is likely that all of these species (listed in this paragraph) form a largely monopyletic group, distinguished from sect. *Virgulus* plus sect. *Ericoidi* by the presence of stipitate glands, at least in the inflorescence. However, there has probably been some reticulate evolution, as illustrated by *S.* × *amethystinum*, a common hybrid of *S. novae-angliae* and *S. ericoides* (Chmielewski & Semple 2003).

Symphyotrichum patens, *S. phlogifolium* and *S. georgianum* are species of southeastern states (Figure 1) that have been the focus of studies by R. Jones (1980, 1983, 1992). *S. phlogifolium* is a tetraploid (2n = 20) centered in Appalachian regions and typical of relatively mesic, shady habitats. It has often been confused with *S. patens*, which is a widespread southeastern species that occurs mostly in dry open habitats. *S. georgianum* is a generally distinctive decaploid (2n = 50) of dry woodlands and grasslands in a restricted southeastern range (Brouillet et al. 2006). These three species share phyllaries that are unequal and non-foliaceous, pubescent at least on margins, their apices green and usually somewhat glandular but not densely so (less than *novae-angliae*). Both proximal and distal cauline leaves generally have somewhat auriculate or amplexicaul bases, although this character is often less obvious along inflorescence branches, where leaves are usually much reduced.

Nesom (2006) reviewed the mapping of chromosome numbers in *Symphyotrichum patens* by Jones (1980, 1983), Semple (1984) and others. He confirmed that tetraploids are widespread across southeastern states, but that diploids (2n = 10) are concentrated on the Gulf Coastal Plain. Although diploids have generally not been recognized as distinct taxa, initial crossing experiments indicated that significant barriers to pollination exist between diploids and tetraploids (Jones 1983). One cluster of recorded diploids occurs in or near the Black Belt of Mississippi and Alabama. R. Jones (1980) had previously noted somewhat distinctive plants in the Black Belt, especially among diploids: with "...strongly adnate-ascending leaves and peduncular bracts, heavy glandular pubescence, and larger involucres..." However, he found that these characters also occurred to some extent within tetraploids from that region, and decided not to describe a new taxon. Some diploids west of the Mississippi River have been assigned to var. *gracile* (Hook.) Nesom by Jones (1983) and Brouillet et al. (2006). But Nesom (2006) reassessed var. *gracile* and could not discern a "geographic zone of morphological discontinuity that would enable or justify the recognition of two taxa." He concluded that only one additional variety is clearly distinguishable from typical *S. patens*: var. *patentissimum* (Lindl.) Nesom, which comprises tetraploids centered in the Ozarkian region.

The initial impetus for this paper was the observation of distinctive *patens*-like plants during 2009 at the Pulliam Prairie (Chickasaw County, Mississippi), which is one of the best known remnants of native grassland in the Black Belt (Campbell and Seymour 2011a, 2011b, 2012). These plants appeared to match Jones' (1980) description of diploids in the Black Belt. Subsequently, the first author reviewed collections filed under *Symphyotrichum patens* at several herbaria across southeastern states, in order to clarify if a new taxon was worth recognizing, how distinctive it might be, and where it occurs. During this review, many collections in the *patens-phlogifolium-georgianum* group were examined, and deeper complexity was discovered among *georgianum*-like plants than has been previously described. These observations are summarized below in the form of a provisional key, plus notes on individual taxa and selected maps.

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Figure 1. Distribution of *Symphyotrichum patens* and allies according to Kartesz (2014).

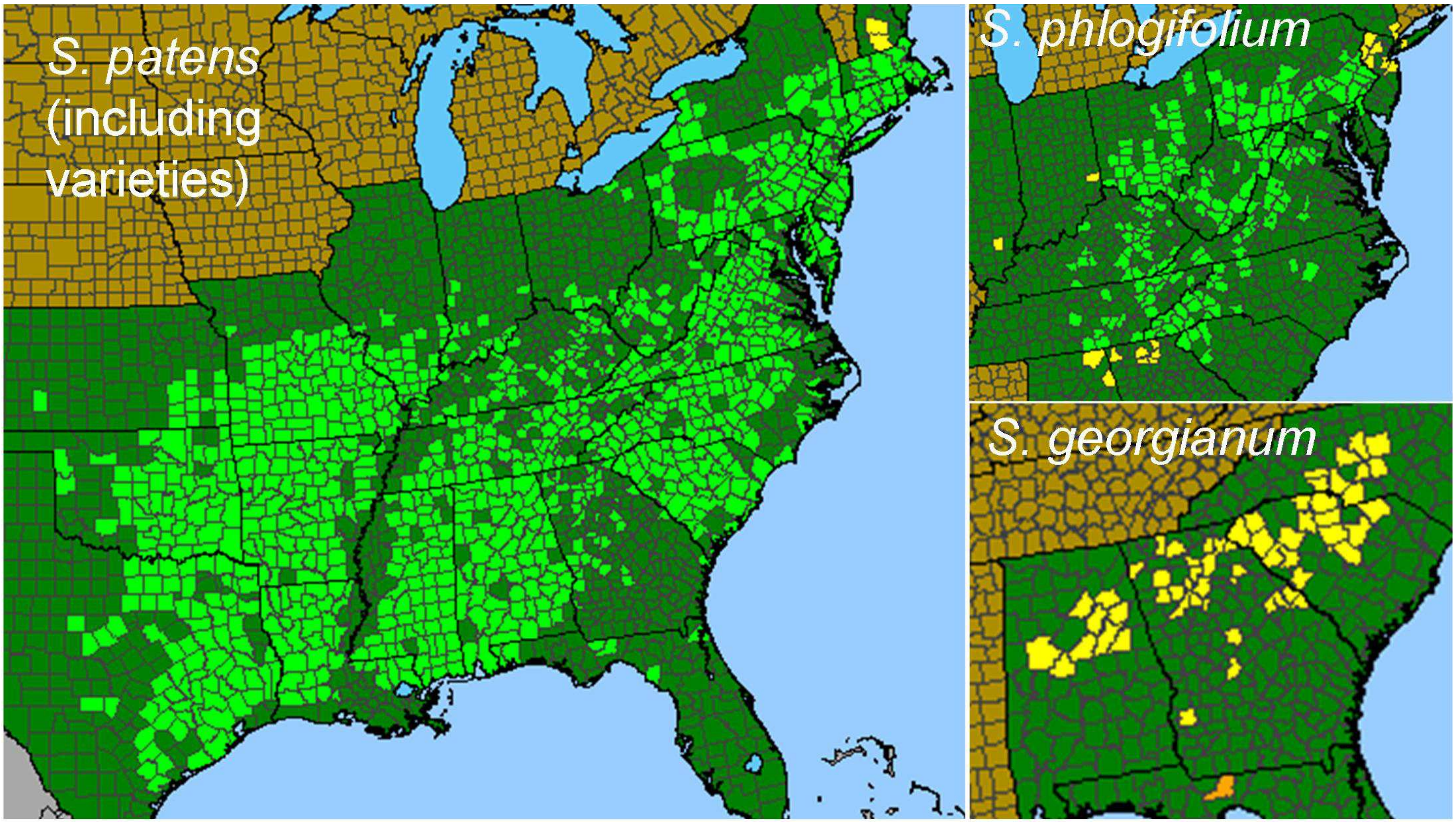
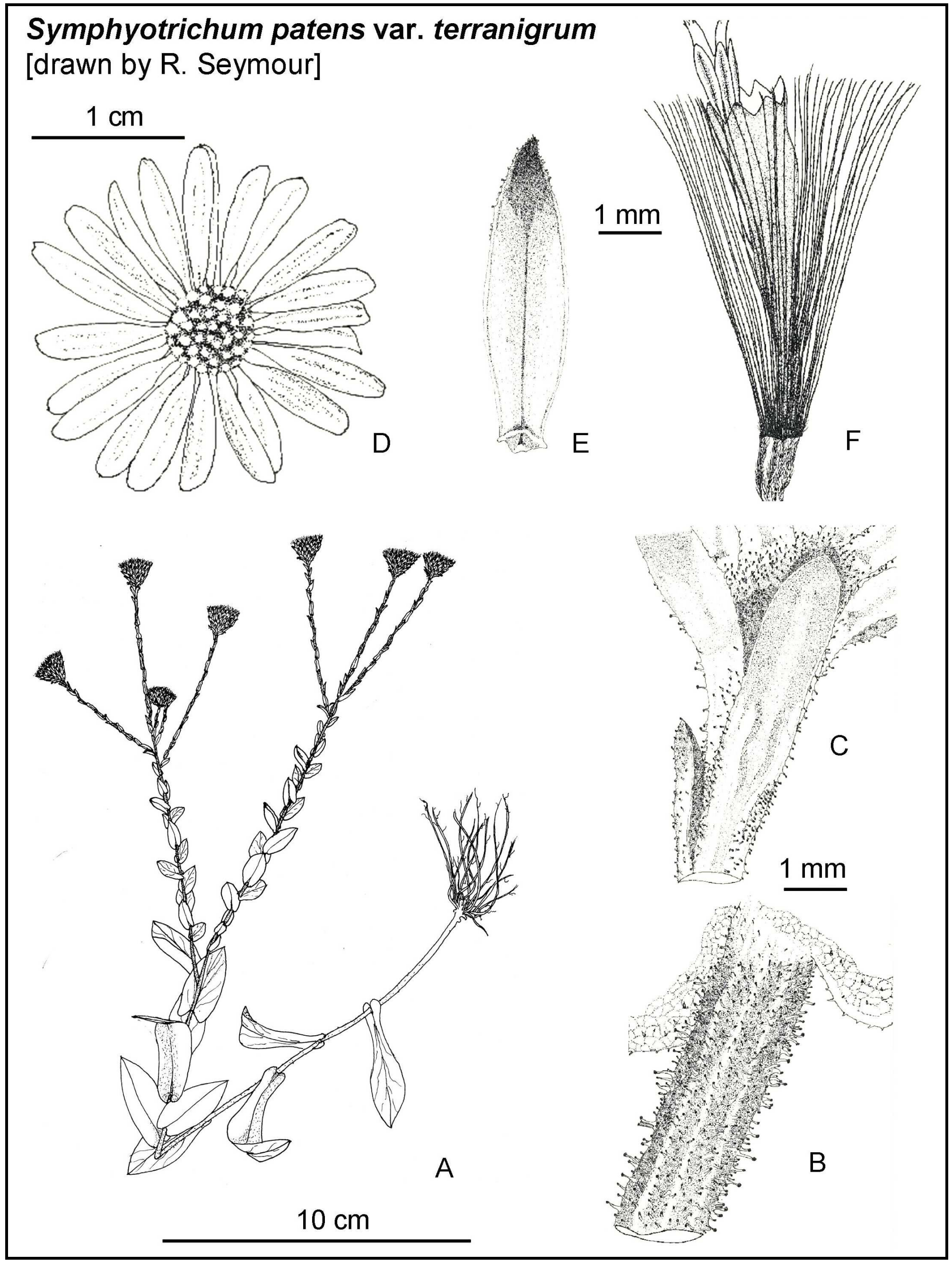


Figure 2. Illustrations of type material for *Symphyotrichum patens* var. *terranigrum* J.J.N. Campbell & Seymour.

A. Plant in flower.
B. Stem, middle section.
C. Stem, summit below involucre.
D. Flowering head from above.
E. Involucral bract.
F. Seed (cypsela), floret and pappus.



A NEW VARIETY OF PATENS FROM THE SOUTHERN BLACKLANDS

SYMPHYOTRICHUM PATENS (Ait.) Nesom VAR. TERRANIGRUM J.J.N. Campbell & Seymour, **var. nov. Figures 2 & 3. TYPE: U.S.A., Mississippi. Chickasaw Co.,** Pulliam Prairie, locally common in dry grassland on chalk, 24 Sep 2009, *W.R. Seymour & J.J.N. Campbell *483* (holotype at MISS; isotype at APSC). Paratypes from same population, 23 Aug 2009, *W.R. Seymour & J.J.N. Campbell *482a* [few hairs] & *482b* [denser hairs] (MISS, APSC).

Additional collections examined are as follows; acronyms for herbaria follow Thiers (2014). In most plants, stipitate glands and regular non-glandular hairs are both more or less densely scattered over leaves and stems, but these characters often vary within populations. Collections with asterisks (* before herbarium acronyms) have stipitate glands but much sparser regular hairs. Collections with question marks (? before herbarium acronyms) have few glands and appear somewhat transitional from var. *terranigrum* to var. *gracile* or to var. *patens*. **U.S.A. Alabama.** Autauga Co.: in fairly moist prairie clay in full sun, Jones Bluff, W shore of Alabama River ca. 4 mi N of Jones Bluff Dam, SSE of Statesville, T16N R13E Sec. 8, 18 Aug 1982, *S.C. Gunn 1090* (?VDB). Bibb Co.: ca. 5.5 mi S of Centreville/Brent, powerline and roadside ketona dolomite glade at junction Highways 5 and 219, T24N R6W Sec. 26 SE/4, 2 Nov 1996, *J.R. MacDonald 9984* (IBE, MISS, MMNS); ca. 9.2 mi NE of Centreville, ca. 0.8 mi W of Bulldog Bend Bridge, "Goat Glade South," Ketona Dolomite outcrop above right (W) bank of Little Cahaba River, 8 Oct 2000, *J.R. Allison 12566* (UNA). Colbert Co.: dry calcareous glady place ca. 1 miles SW of Littleville, 30 Sep 1952, *R.N. Harper 4218* (?MO, ?NCU, ?UNA, US, "*Aster tenuicaulis*"). Crenshaw Co.: Ala. Hwy. 95 ca. 1 mi S of County Hwy. 19, blackbelt roadside, full sun, dry chalk soil, 29 Oct 1995, *A.R. Diamond 10087*

(BRIT); dirt roadside 0.3 mi N of Briar Branch, sandy clay soil, full sun, common, T10N R17E Sec. 8, 14 Oct 2001, *A.R. Diamond 12784* (*BRIT). Hale Co.: prairie edge by county [road] 61 ca 9.5 mi N of Uniontown; 6 Oct 1972, *R. Kral 48849* (?BRIT, MO, TENN, "*Aster patens* Ait. var."). Lawrence Co.: sandy clay of oak-pine hills by Ala 33 8.8 mi S of Moulton, 23 Sep 1970, *R. Kral 41252* (MO). Madison Co.: "monte near Huntsville, northern district," 27 Oct 1887, *C. Mohr s.n.* (UNA). Marengo Co.: ca. 3 mi S of Demopolis along US 43, outcrop of Demopolis Chalk, 7 Oct 1967, *R. Kral 29633A* (BRIT, VDB); chalk glades on W side of Demopolis by US 80, 6 Oct 1972, *R. Kral 48872* (MO, TENN, ?VDB, glands not dense, leaves relatively large). Shelby Co.: Oak Mountain Park, ridge near Peavine Falls, sunny, sandy-loam, dry area, infrequent, 23 Nov 1962, *R. Deramus 239* (UNA). Sumter Co.: 1 mile N of Epes, soft chalk outcrop, strongly caespitose, infrequent, 12 Sep 1967, *J.L. Thomas 1211* (*NCU, *UNA); chalk prairie edge above Tombigbee River just north of Epes, 5 Oct 1972, *R. Kral 48759* (*MO, *TENN, VDB, "*Aster patens* Ait. var. ?"); chalk barrens between Gainesville and Geiger by Ala. 116, 19 Sep 1975, *R. Kral 56580* (VDB); Rte. 116 2.6 mi W of jct. with Ala. 39, chalk outcrops, 7 Nov 1977, *R.L. Jones 2123* (VDB); US 11 at Tombigbee River, chalk outcrops, 8 Nov 1977, *R.L. Jones 2141* (*VDB); chalky soil beside I-59 and I-20 about 0.7 miles S of the Epes Exit on Ala. 21, S of Tombigbee River, 31 Oct 1993, *R.D. Thomas & S.D. Thomas 138,487* (*TENN); 0.3 air mi NW Old Bluffport, chalk outcrop, 32-35-37 N, 88-03-39W, 24 Oct 2006, *B.R. Keener 3260* (?UNA).

Georgia. Bibb Co.: growing in a pine-hardwood site 1-1.2 miles S of junction of Montpelier Station Rd and Hwy 74 W on the Payne Property, 30 Sep 1991, *J. & R. Payne s.n.* (GA). Catoosa Co.: in a grassy road edge on Lovingood Road, *H.R. DeSelm*, 3 Oct 1987 (EKY). Floyd Co.: Coosa Prairie, 20 Jun 2010, *M. Medley et al. s.n.* (in prep.).

Louisiana. St. Tammany Pa.: Covington, 31 Oct 1919, *Fr. Paul 1223* (?BRIT, scattered glands, leaves not much reduced, dark or crowded; collector was perhaps Abbot Paul Schauble, head of the Benedictine Order in Louisiana ca. 1910).
Mississippi. Lauderdale Co.: sandy cut-over wooded hill 0.4 miles W of Alabama line and E of Lauderdale, 24 Sep 1966, *S.B. Jones 10624* (*MISS). Neshoba Co.: open field and edge of ditch, State Highway 15, 9.5 miles S of Williamsville, 30 Sep 1967, *L.C. Temple 7492* (BRIT, GA, MISS); open field and edge of ditch on St Hwy 15 2.1 miles S of Lynwood, 12 Oct 1968, *L.C. Temple 10924*. Oktibbeha Co.: Rock Hill, steep N-facing bluff and associated chalk barrens ca 6 mi N of Starkville along Trim Cane Creek, 20 Oct 1930, *K.L. Gordon & B. Jones 3040* (?MMNS, perhaps closer to var. *gracile*); T19N R15E Sec. 16 on Old West Point Rd just east of railroad tracks, chalk outcrops on south side of road, 11 Sep 1994, *A. Leidolf 0932* (VDB, IBE); T19N R15E Sec. 16 SW/4, Osbourne Prairie, 0.25 miles N of Old West Point Rd and 16th Sect Rd, on 16th Section Rd; E of 16th Section Church cemetary and transmission lines, open chalk barrens bordered by Black Belt prairie, 14 Oct 2003, *H. Sullivan et al. 03-299* (*MMNS, depauperate); 16th Section Prairie, 26 Sep 2004, *M. Fishbein 5463* (?MISSA, perhaps closer to var. *gracile*). Walhall Co.: dry upland R/W State Highway 48 just W of Walthall-Marion Co. line, 4 Sep 1970, *L.C. Temple 12654* (?MISS).
New York. Nassau Co.: Hemstead Plains, Long Island,16 Sep 1893, "*The Jos. Schrenk Herb. presented 1902*" (?MO, see notes in Discussion).
North Carolina. Graham Co.: edge of woods along Yellow Creek, near Lake Fontana, 30 Sep 1995, *V.E. McNeilus 95-579* (MISSA-Entomology, TENN, "*Aster patens* var. *georgianus,*" depauperate or poorly preserved). Onslow Co.: flat pine-oak woods 0.6 miles NNW of Silverdale on road to Belgrade, 4 Oct 1957, *H.E. Ahles 36015* (NCU). Orange Co.: roadside

near upper bridge, Morgan Creek, 3 Oct 1909, *W.C. Coker s.n.* (NCU); dry soil in open woods Duke Forest, 25 Sep 1932, *L.R.Blomquist 5084* (WVU).
Pennsylvania. Lehigh Co.: open grassy place beside road at crest of wooded slope along stream, ca. 1.75 miles NNW of Emaus Post Office, 14 Oct 1917, *H.W. Pretz 9204* (NCU).
South Carolina. Aiken Co.: “Aiken”, 28 Sep 1866, *H.A. Ravenel s.n.* (MO). Chester Co.: clay margin of cutover pine woods near Armenia Church ca. 10 miles SSW of Chester, 18 Sep 1957, *C.R. Bell 10083* (?NCU). Lexington Co.: infrequent at edge of dry woods on crest, powerline row next to subdivision on N side Six Mile Creek, E of US 321, Cayce, 29 Sep 1988, *J.B. Nelson 7064* (USCH). York Co.: scattered with *Sporobolus clandestinus* on hard thin soil (Iredell) over gabbro, S side of Locust Hill Rd (= S-63) near junction with S-75, W of York, 27 Oct 1988, *J.B. Nelson 7181* (USCH).
Tennessee. Maury Co.: glade area SE of Columbia between highways 50 and 50A, 3 Oct 1979, *J.L. Collins 4582* (VDB, unusually narrow leaves); Rutherford Co.: rise in limestone prairie by US 41, SE side of Luverne, 24 Sep 1979, *R. Kral 64381* (?VDB); glades and barrens along Chaney Rd just off jct. with San Ridley Parkway at I-24, 16 Oct. 1984, *L.E. McKinney 01605* (VDB, primary branches with oblong leaves); Flat Rock State Natural Area, inside firelines ca. 0.5 trail-miles from Factory Road, 20 Sep 2007, *R. McCoy & T. Crabtree s.n.* (?APSC). Sullivan Co.: rocky roadside bank on Mt. City-Bristol Rd., 13 Oct 1940, *R.E. Shanks 1131* (MISS) and *A.J. Sharp 1133* (TENN).
Texas. Brazos Co.: 1 mi W of College Station, ungrazed field with *Andropogon scoparius*, 7 Oct 1949, *W.G. Swank s.n.* (?WVU). Harris Co.: dry prairie near Houston, middle of June 1843, *Ferd. Lindheimer s.n.* (?BRIT, “*Aster patens* var.”, glands few and mostly on small bracts of infl. branches, but leaves dark and crowded); Houston, prairies, 18 Sep 1917, *E.J. Palmer 12785a* (MO, “*Aster tenuicaulis*”).

West Virginia. Jackson Co.: common, dry roadbank on ridgetop, Co Rt 19 at Hickory Chapel, 2.25 mi E Rt I-77 and W of Kentuck; 11 Oct 2000, *A. Cusick 35693* (MU). Pendleton Co.: US-220 3.1 mi N of Franklin on US-33, 9 Oct 1981, *J. Semple & J. Chmelewski 5893* (MO, "*Aster phlogifolius*... 2n = 20 from rootstocks").

Perennial herbs usually 40–80 cm tall, cespitose, with short, thick, woody caudices and no rhizomes. Stems 1–5+, ascending to erect, with minute stipitate glands densely to sparsely scattered from peduncle to base, longer non-glandular hairs dense, sparse or largely absent. Leaves usually with bluish-waxy sheen and blackening when dried, relatively thick and stiff, with minute stipitate glands dense (especially on petioles and midribs) to sparse, otherwise glabrous to scabrid-puberulent with non-glandular hairs. Lower leaves early deciduous, subpetiolate with distinct constriction above flared base, blades spatulate to obovate, mostly 3–6 × 1.2–2.6 cm, bases cuneate, margins entire or subentire, apices acute to rounded. Mid-stem leaves usually clustered with internodes of 4–10 mm at their densest, sessile, blades ovate to lanceolate, (2–)3–5(–7) × (0.8–)1.1–2.3(–2.5) cm, with length/width = (1.5–)2–2.5(–3), their bases strongly cordate-clasping to slightly auriculate, apices acute to rounded. Distal leaves (below peduncles) distinctly reduced up each branch order, sessile, blades broadly to narrowly ovate, mostly 1–3 × 0.5–2 cm, bases strongly cordate-clasping to auriculate-amplexicaul, apices usually acute. Heads mostly 2.5–3 cm wide, in paniculiform arrays with divaricate branches. Peduncles stiffly ascending, slender, the longest ones 3–9 cm, the bracts appressed to spreading, linear, the lowest ones mostly 7–9 × 2–3 mm, then abruptly reduced above peduncle base to mostly 0.3–2 mm wide and grading into phyllaries. Involucres campanulate, ca. 6–9 mm. Phyllaries in 5–7 unequal series, appressed to slightly squarrose, lanceolate to linear, ca. 4.5–6.5 × 1–1.5 mm, bases ± indurate in proximal third, margins hyaline, erose to ciliolate distally, green zones diamond-shaped in distal third, outer apices obtuse to acuminate, inner apices often purplish red, faces strigillose to puberulent abaxially and near tip adaxially, stipitate-glandular distally. Ray florets ca. 15–20; corollas light violet, laminae ca. 6–12 × 1–2 mm. Disc florets ca. 30–60; corollas yellow, ca. 5–6 mm, tubes shorter than narrowly funnelform throats, lobes triangular, ca. 0.5 mm. Cypselae dull brown to purplish, oblong-obovoid, ca. 1-1.5 mm, faintly 5–8-nerved, faces white-sericeous, especially on nerves; pappi tawny, ca. 4-5 mm.

Flowering in September to October. Blackland prairies, calcareous glades, associated roadsides and woodland edges. U.S.A., Alabama, Georgia, Mississippi, New York, North Carolina, Pennsylvania, North Carolina, South Carolina, Tennessee, Texas, West Virginia (Figure 4). Most records of more distinctive plants are from the Black Belt on Cretaceous chalk in Alabama and Mississippi, but this taxon does extend east onto strips of calcareous soil along the Piedmont and Coastal Plain as far as North Carolina, and there is at least one distinctive collection from Texas (*E.J. Palmer 12785a*). There are also a few collections that appear at least transitional to this new variety from the southern Interior Low Plateaus in Alabama and Tennessee, and from the Ridge-and-Valley region as far north as Pennsylvania.

At the Pulliam Prairie, *Symphyotrichum patens* var. *terranigrum* grows in xeric to xerohydric grassland on gently sloping uplands with clayey vertisols derived mostly from Cretaceous chalk (Campbell & Seymour 2011b, 2012). The most common graminoids include *Aristida longespica*, *Sporobolus vaginiflorus***, *S. clandestinus**, *S. compositus* var. *drummondii**, *Schizachyrium scoparium*, *Panicum flexile**, *P. virgatum**, *Carex crawei***, *C. meadii*** and *Sisyrinchium albidum***. Locally frequent herbs include *Agalinis gattingeri*, A.*

*oligophylla***, *Asclepias viridiflora***, *Coreopsis lanceolata*, *Dalea candida**, D. purpurea***, *Erigeron strigosus var. calcicola***, *Eurybia hemispherica**, *Houstonia lanceolata*, H. nigricans***, *Hypericum sphaerocarpon***, *Liatris squarrosa* var. *glabrata***, *Linum sulcatum***, *Lobelia spicata* var. *leptostachya***, *Ruellia* cf. *humilis***, *Spiranthes magnicamporum***, *Solidago nemoralis* and *Symphyotricum laevis* var. *purpuratum**. Typical woody species in the intermixed thickets and woodland edges include *Berchemia scandens, Celtis tenuifolia**, Cercis canadensis*, Cornus drummondii**, Crataegus crus-gallii** [sensu lato], *Fraxinus americana** [sensu lato], *Juniperus virginiana*, Maclura pomifera**, Prunus angustifolia*, Sideroxyon lycioides*** and *Rhus glabra**. *Quercus stellata* and *Q. marilandica* are locally abundant in adjacent woodland on ridges and knolls at slightly higher elevation. [* Asterisks indicate species that are more common on base-rich soils; double asterisks indicate strong concentration; these allow easy comparison with other taxa below.]

Var. *terranigrum* varies considerably in the density of glands versus non-glandular hairs and in other characters, as noted above under the list of collections. At the Pulliam Prairie, plants more similar to var. *gracile* occur locally in the thin oak woods and edges on more acid clayey soils that overlie the characteristic chalk of the Black Belt. Some of the variation within this extensive remnant of the original vegetation, and at other sites, might be interpreted as intergradation between the varieties. Nevertheless, var. *terranigrum* is a generally distinctive, locally frequent plant in the Black Belt grasslands, and it deserves to be studied in more detail across southeastern states. Plants with dense glands but little or no pubescence on leaves and stems might be regarded as the ‘purest’ examples of var. *terranigrum*, and they are known only from a few sites in the Black Belt of Alabama (Crenshaw and Sumter Cos.) and Mississippi (Chickasaw, Lauderdale and Oktibbeha Cos.); see annotated list of collections above.

Symphyotrichum patens var. *terranigrum* is named after the 'blacklands' of southeastern states, which are concentrated on the Gulf Coastal Plain. The sticky 'xerohydric' vertisols of these regions form typical habitat for the plant (Campbell & Seymour 2011a). This taxon does not appear to have been recognized by earlier authors, but the history of varietal names within *S. patens* still needs clarification (Jones 1983, Nesom 2006). R.N. Harper in Alabama and E.J. Palmer in Texas both applied the name *Aster tenuicaulis* (Mohr) Burgess (in Small 1903) to their collections of var. *terranigrum*. However, Mohr (1901) had named "*Aster patens tenuicaulis*" for plants from sandy soils in southern Alabama (Washington and Mobile Cos.), in order to replace "*Aster patens gracilis*" of Hooker (1835), which was based on a type from Louisiana (Jacksonville Springs in Washington Parish)—not from Florida as assumed by Mohr. The appropriate treatment for "*Aster gracilis*"of Nuttall (1818) remains uncertain, since it was originally recognized "in the savannahs of Kentucky and Tennessee"—indicating typical *S. patens*—and Nuttall's description (with leaves "subamplexicaule") also suggests that he was referring at least in part to typical *S. patens*. Yet Asa Gray and others have identified a type collection for *A. gracilis* Nutt. as the plant now known as *Eurybia compacta* G.L. Nesom (Nesom 1995).

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Figures 3a-g. Photos of *Symphyotrichum patens* var. *terranigrum* at Pulliam Prairie in 2009. [See subsequent pages.]

PROVISIONAL KEY TO *SYMPHYOTRICHUM PATENS* COMPLEX

This synoptic key to *S. patens* and its allies is developed from keys of Jones (1983), Brouillet et al. (2006) and Nesom (2006), after considerable trial and error in herbaria. But because some of these taxa—or potential taxa—will probably become circumscribed in more detail and adjusted, the key must still be regarded as provisional. Notes on problems with individual taxa are provided below.

1a. Inflorescence elongated or broad, but not distinctly compact with ascending branches; heads mostly 2.5–4 cm across, the ray laminae 9–18 × 1–3 mm, usually pale blue/lavendar to pale violet/purplish, the phyllaries appressed or squarrose; mid-stem and distal leaves strongly cordate-clasping, their bases almost as wide as their middles; leaves waxy-thickened and deep bluish-green (especially more glandular plants) or thin and paler yellowish-green, their areolae mostly 0.5–1 mm across, their margins flat or slightly thickened, not undulate; rhizomes usually lacking or indistinct.

2a. Leaves thick, firm, usually short-hirsute to scabrous (sometimes almost glabrous), the veins not conspicuously raised; larger mid-stem leaves mostly 2–7 × 0.5–2.5 cm, narrowed in distal third to an acute or obtuse apex; stems and leaves with stipitate glands absent, scattered or dense; peduncles mostly 2–13 cm long, the inflorescence up to ca. 30–50 cm wide, usually wider than long; phyllaries in 4–7 strongly unequal series, appressed to squarrose, glandular to eglandular; rays usually pale blue to violet (sometimes lavendar to slightly purplish); disc corollas and pollen usually bright yellow [when fresh], including the ca. 0.5–1 mm lobes, or the lobes sometimes turning purple [especially in Appalachian plants]; cypselae ca. 2–3.5 mm, gray to brown, with long ascending hairs (ca. 0.4–0.6 mm) on ribs and between.

3a. Involucres campanulate or narrowly turbinate, mostly 5–7.5 mm long; phyllaries in 4–5(–6) series, often somewhat squarrose, acute to acuminate, middle ones 0.7–1.2 mm wide (linear-lanceolate), densely strigillose to almost glabrous; plants glandular (mostly stipitate-) or largely eglandular, with varied leaf size and branching.

4a. Mid-stem leaves mostly 3–5 cm long, separated by internodes of (0.5–) 1–2(–3) cm at their densest, often adnate-ascending; plants usually 0.4–0.8 m tall [to 1 m in cultivation]; heads mostly 7–11 mm wide.

5a. Stems and leaves with dense to sparse stipitate-glands, with or without eglandular hairs; plants somewhat bluish-waxy, often becoming blackish when dried; leaves abruptly reduced in size with each braching order; mid-stem leaves [directly below inflorescence] with length/width (1.5–)2–2.5(–3), overlapping along 10–20 cm; bracts on proximal thirds of peduncles mostly 1–2(–3) mm wide.
.... **S. patens var. terranigrum**

5b. Stems and leaves generally eglandular (except sometimes for scattered glands on distal branches), but with dense ascending eglandular hairs; plants usually dull greyish-green, not much darkening when dried; leaves usually with gradual or irregular reduction from base of stem to summit;

mid-stem leaves with length/width (2–)2.5–4(–4.5), not forming a distinct overlapping cluster; bracts on proximal thirds of peduncles mostly 2–3(–5) mm wide.
.... **S. patens var. gracile**
[This taxon may not be clearly separable from the "widespread typical variant" keyed out below under 6b.]

4b. Mid-stem leaves mostly 5–7 cm long, separated by internodes of (1–) 1.5–3(–4) cm at their densest, usually spreading; plants usually 0.8–1.6 m tall; heads mostly 9–12 mm wide.

6a. Leaves and stems with stipitate glands densely or sparsely scattered among longer glandular hairs; leaves usually somewhat bluish-green when dried; inflorescences usually less branched, ca. 10–30 cm wide, with peduncles mostly (1–)2–7(–9) cm long.
.... **S. patens:** largely Appalachian variant
[Some of these plants appear transitional to *S. phlogifolium*; see also "large-leaved plants from Mississippi and Tennessee" in notes below.]

6b. Leaves and stems without glands, usually dull greyish-green when dried; inflorescences usually much branched, ca. 30–50 cm wide, with peduncles mostly (4–)6–10(–13) cm long.
.... **S. patens:** widespread typical variant

3b. Involucres broadly turbinate, mostly 8–12 mm long; phyllaries in 4–7 series (grading into bracts), more or less appressed, obtuse to acute, middle ones 1.2–1.7 mm wide (ovate-lanceolate), densely strigillose or sericeous-strigose; plants largely eglandular (except for sparse sessile glands on phyllaries), usually with leaves only ca. 2–3 cm long at mid-stem, then developing many long stiff branches with abrupt further reduction in leaf size.
.... **S. patens var. patentissimum**

2b. Leaves thin, pliable (almost membranaceous), softly pubescent with long and short hairs, the secondary veins somewhat raised ("rugose, wrinkled"); larger mid-stem leaves ca. 8–13 × 2–3 cm, gradually narrowed in distal half to an acute apex; stems and leaves with dense stipitate glands in addition to hairs; peduncles mostly (0.5–)1–2(–3) cm long, the inflorescence usually no more than 20 cm wide and longer than wide; phyllaries in 3–4 unequal series, appressed, glandular; rays pale to dark purple (with slight reddish hue); disc corollas and pollen mostly white except for the ca. 1–1.5 mm lobes, which turn purple; cypselae ca. 2.5–4 mm, dark brown to black, with short hairs (ca. 0.2–0.3 mm) restricted to ribs.
.... **S. phlogifolium**

1b. Inflorescence usually somewhat compact (racemiform or corymbiform), at least in sections, with ascending branches; heads often up to 4–5 cm across, the ray laminae up to 14–24 × 1.5–3.5 mm, usually deep violet or purplish, the phyllaries mostly squarrose; mid-stem and distal leaves clasping to subclasping, usually widest near the middle; leaves usually somewhat waxy-thickened and deep bluish green, their areolae mostly 1–1.5 mm across, their margins often thickened, revolute and more or less undulate; rhizomes often produced.

7a. Plants with distinct long rhizomes (usually >15 cm), usually 50–100 cm tall and often drying to relatively dark bluish-green; leaves with or without dense glands; leaves below mid-stem not especially large and generally withering before flowering; involucres mostly 8–12 mm high, the heads mostly 3–5 cm wide, up to to ca. 30(60) per stem in more or less racemiform to paniculate arrays.

8a. Stems and leaves glandular; heads mostly 4–5 cm wide
.... **S. georgianum**: glandular variant
8b. Stems and leaves eglandular; heads mostly 3–4 cm wide
.... **S. georgianum**: eglandular variant

7b. Plants with short spreading offsets or rhizomes (usually <15 cm), usually 20–60 cm tall and drying to relatively pale olive/grayish-green; leaves usually eglandular; some leaves below mid-stem often distinctly larger (with subpetiolar base) and persistent to flowering; involucres mostly 6–8 mm high, the heads mostly 2.5–4 cm wide, up to ca. 15(30) per stem in more or less corymbiform arrays.
.... **S. aff. georgianum**: possible new taxon
[These are the “short western plants” noted below from Alabama, Georgia, Louisiana, Mississippi, Oklahoma and Texas.]

Figure 4. Map of counties with records of *Symphyotrichum patens* var. *terranigrum* and apparent transitions to var. *gracile* or var. *patens*. See text for sources of data.

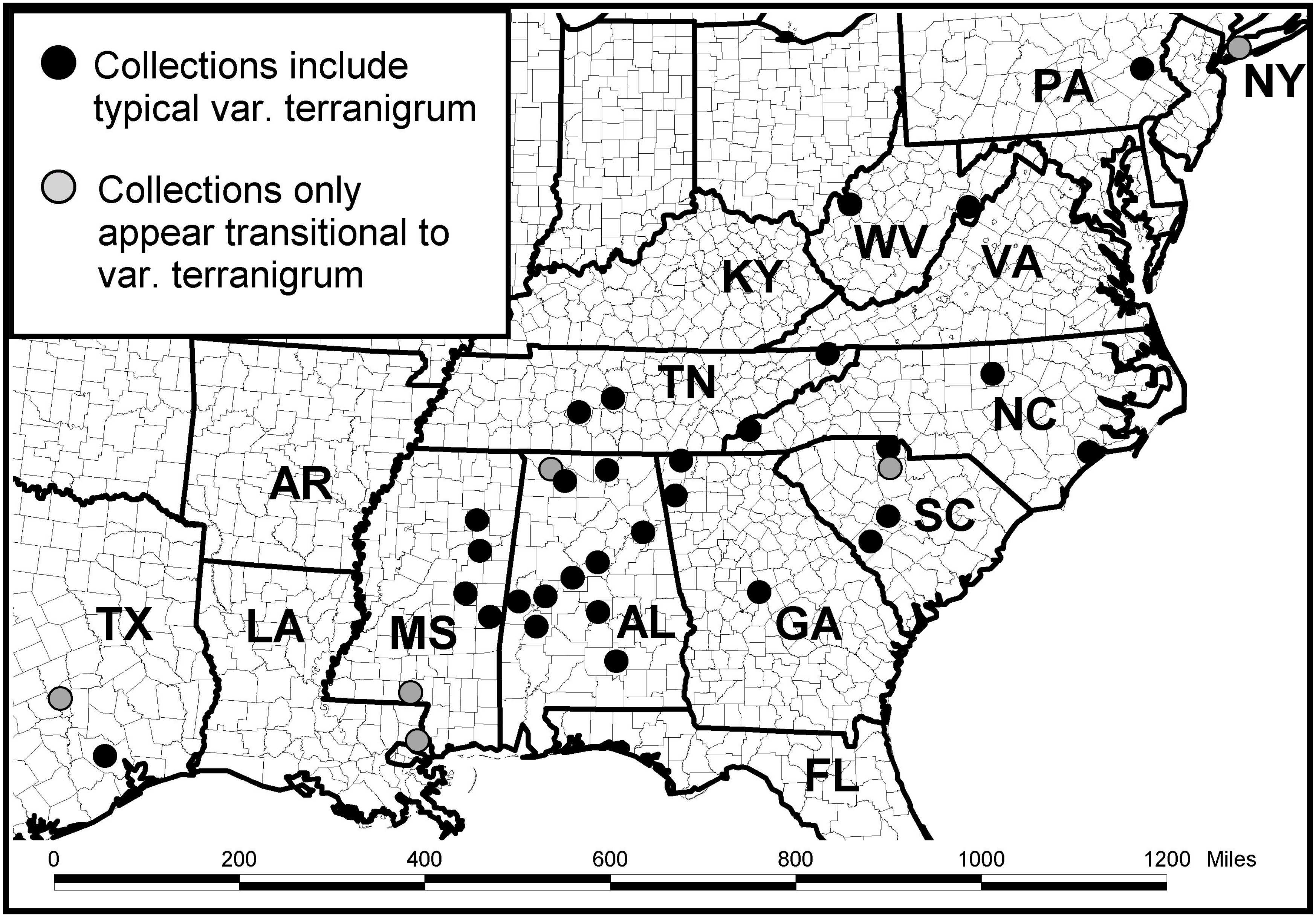
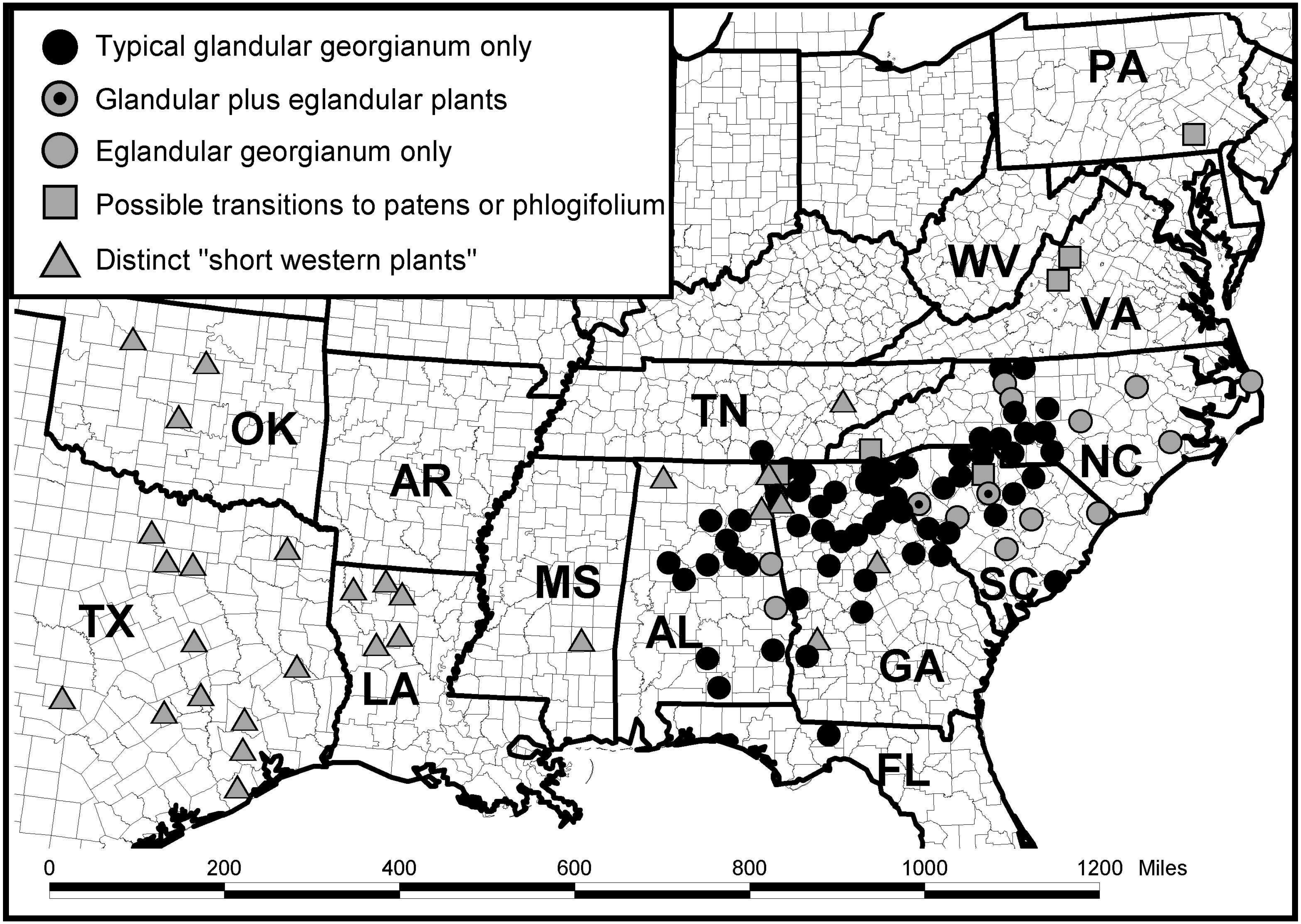


Figure 5. Map of counties with records of *Symphyotrichum georgianum* or *georgianum*-like plants. See text for explanation of taxa and sources of data.



NOTES ON TAXA (IN SAME ORDER AS KEY)

[* Asterisks below indicate associated species that are more common on base-rich soils; double asterisks indicate stronger concentration.]

Symphyotrichum patens. It has been difficult to maintain consistent segregates, and definitive molecular studies are still needed. But the following 5 or 6 entities can be tentatively outlined. This species is highly variable in glandularity, sizes and shapes of leaves, branching patterns of inflorescences and head sizes. Further clarification is needed regarding rhizomes. Brouillet et al. (2006) stated: "cespitose; with short, thick, woody caudices, tangled or sometimes cormoid, and long rhizomes." Jones (1983) stated: "Plants cespitose, with new stems arising in clusters at or near the old stem bases. Underground stem a caudex, or occasionally with short rhizomes." Based on our cultivation of several plants and examination of many herbarium specimens, distinct rhizomes are not formed, except perhaps rarely in a few plants referable to var. *gracile* or to the 'Appalachian variant' noted below. The only described taxon within the whole *S. patens* group that regularly has distinct rhizomes appears to be *S. georgianum*. Further clarification is also needed in chromosome numbers. It is suggested here that var. *terranigrum* and var. *gracile* largely correspond to the mapped concentrations of diploids within *S. patens* on the Coastal Plain (Nesom 2006), but there are probably exceptions (Jones 1980). For example, a collected plant from West Virginia assigned above to var. *terranigrum* was determined to be tetraploid: *J. Semple & J. Chmelewski 5893* (MO), under the name "*Aster phlogifolius.*" Also, a hexaploid has been recorded under var. *patens*; see below.

***S. patens* var. *terranigrum*.** See notes under description above.

S. patens* var. *gracile (Hook.) Nesom [= *Aster tenuicaulis* (C. Mohr) Burgess]. These plants are relatively slender, with long, minutely bracteate flowering branches and relatively small heads with little glandularity. In a few collections at BRIT from Texas (Comanche Co., Dallas Co., Denton Co.), rhizomes are present, suggesting transitions to the "short western plants" outlined below. Jones (1983) mapped var. *gracile* no further east than Alabama. Brouillet et al. (2006) stated that it "is most common in the southwestern part of the species range... It is mostly diploid, some tetraploids occurring in Texas and Louisiana." But, following Cronquist (1980), they also recorded it as far east as Maryland. Nesom (2006) could not discern any discontinuity from typical var. *patens*, noting typical var. *gracile*-like plants through "part of the range of var. *patens*... commonly northeastward at least into North Carolina." From general review of collections for this paper, plants referred to var. *gracile* using the key above are concentrated on the Gulf Coastal Plain, from Oklahoma and Texas to Georgia and Florida. Further work is needed to refine the morphological and cytological basis for distinction and to provide a more precise map.

Because ecologists have generally not recognized this variety, details of its habitat are not well documented. Nevertheless, it is likely that much of the "*Symphyotrichum patens*" recorded in *Pinus palustris* woodland can be referred to var. *gracile* (Mohr 1903, Penfound & Watkins 1937, Peet & Allard 1993, Kush et al. 2000, Maceina et al. 2000). Peet & Allard described three types of longleaf pine woodland with *S. patens*: Piedmont Upland, Southern Subxeric and Southern Mesic. The most common trees and shrubs in these types were *Pinus palustris* (usually dominant), *Diospyros virginiana*, *Quercus marilandica*, *Q. margarettiae* and *Q. incana* and *Vaccinium arboreum*; others included *Aronia arbutifolia*, *Gaylussacia dumosa*, *Hypericum hypericoides, Ilex glabra, I. vomitoria, Oxydendron arboreum, P. echinata, P.*

virginiana, Q. falcata, Q. laevis, Q. montana, Q. pumila [= *Q. elliottii*], *V. crassifolium, V. elliottii, V. fuscatum* and *V. tenellum*.

***S. patens*: Appalachian variant**. As outlined in the key above, these are plants with scattered glands on leaves and stems, relatively narrow, less branched inflorescences, and disc corollas that often turn purple at tips. These characters suggest a transition from *S. patens* var. *patens* to *S. phlogifolium*, which shares the same typical chromosome number (2n = 20); Jones (1983) was able to make hybrids in cultivation. But in a few collections, there appear to be distinct rhizomes, suggesting transitions to *S. georgianum* instead: for example, in old collections from Mass. (Andover) and Pa. (Delaware Water Gap) at MU. This 'Appalachian variant' was recorded from the following states: Ala., Conn., Ga., Ind., Ky., Mass., N.Car., N.H., N.J., N.Y., Ohio, Pa., S.Car., Tenn., Va., W.Va. Its range is about the same as that of *S. phlogifolium*.

***S. patens*: large-leaved plants from Mississippi and Tennessee** (not separated in key above). There are a few unusual collections of *S. patens* with little glandularity, exceptionally large primary leaves (mostly 15–25 mm wide) and relatively short peduncles (mostly 1–10 cm). These plants do not fit readily into any one of the four groups above. They occur mostly in more mesic situations: examples include *T.R. Simmons CL-689* (MMNS) from Clay Co., Miss.; *D. Morgan 1473* (MMNS, IBE) from Jones Co., Miss.; *H.M. Sullivan 05-111* (MMNS) from Lee Co., Miss.; *D. Meeks 363* (IBE) from Tippah Co., Miss.; *M.B. Brooks 555* (IBE) from Webster Co., Miss.; *V.E. McNeilus 89-991* (TENN) from Cumberland Co., Tenn.; and *R.K. Clements 570* (TENN) from Franklin Co., Tenn. Some of these plants have been confused with *S. phlogifolium.*

S. patens* var. *patens. This common variant of *S. patens* lacks glands on leaves and stems, and generally has robust, widely spreading inflorescences. Almost all chromosome counts have indicated tetraploid status, with 2n = 20 (Nesom 2006). However, Semple recorded 2n = 30 on the label for *J. Semple 10984* from Walker Co., Georgia (BRIT, WAT). In Figure 5, this collection is included with "possible transitions" to *S. georgianum*, which is the only taxon in the *patens*-complex with 2n known to be more than 20.

Var. *patens* is widespread across southeastern states, but uncommon to absent in some warmer sections of the Coastal Plain, in some cooler sections of the central Appalachian Mountains, and in the Ozark-Ouachita region. It is most common in thin dry woods and grassy openings on strongly to moderately acid soils. Typical woody plants in optimal habitat include *Pinus echinata, Quercus marilandica* and *Q. stellata* (locally dominant) plus *Carya ovata, C. glabra, C. tomentosa, Cornus florida, Nyssa sylvatica, P. virginiana, Q. alba, Q. coccinea, Q. falcata, Q. montana, Q. velutinum, Rhus copallina, Sassafras albidum, Vaccinium arboreum, V. pallidum* and *V. stamineum* (NatureServe 2014: associations CEGL 4756, 5018 and 7500).

S. patens* var. *patentissimum. This largely replaces typical var. *patens* in most of Arkansas and Missouri, plus minor parts of Oklahoma, Kansas and Illinois, but intermediate plants do occur in zones of overlap (Nesom 2006). There are also records from Texas, Louisiana, Mississippi and Kentucky, as reviewed by Nesom, but these have mostly been somewhat dubious or the plants appear intermediate. For Kentucky, there is a collection from Graves Co. that is referable to var. *patentissimum* (*R. Athey 466* at EKY). But other reported collections appear no more than intermediate: from Hickman Co. (*J.T. Grubbs 1214* at GA & MUR); and from McCracken Co. (*R. Athey 2143* at BRIT, MO & NCU).

Within the Ozark and Ouachita Mountains at the center of its range, optimal habitat appears to be in thin woods or full sun on rocky glades (often with basic sandstones and shales) and dry grasslands with moderate acidity. Typical woody associates include *Quercus stellata* (locally dominant) plus *Carya texana, Celtis tenuifolia**, Fraxinus americana** [sensu lato], *Juniperus virginiana**, *Pinus echinata*, *Prunus americana** [sensu lato], *Rhus copallina, Ulmus alata** and *Vaccinium arboreum* (NatureServe 2014: associations CEGL 7814 and 7824).

Symphyotrichum phlogifolium. This is largely Appalachian, but details of its western range need to be clarified (Figure 1). In Kentucky, there are a few scattered records west to the western Knobs or even Shawnee Hills (Jones 1983, 1992; J. Campbell and M. Medley, in prep.). It has also been reported from southern Indiana (Jones 1983) and perhaps southern Illinois (USDA 2014a). However, in Tennessee *S. phlogifolium* remains unknown west of Appalachian regions (Chester et al. 1997; D. Estes, pers. comm.), and the record from Mississippi (Cronquist 1980) remains dubious. Jones (1983) showed that this species can cross readily with *S. patens* in cultivation. Hybrids have not yet been proven to exist in the wild, but suggestive collections include the following: *R. Kral 70974* from Marshall Co., Alabama (VDB); *A. Cronquist 4798* from Walker Co., Georgia (BRIT); and *C.A. Hammer 173* from Gallia Co., Ohio (VDB). Also, collections noted above under the "Appalachian variant" of *S. patens* may be interpreted in terms of introgression from *S. phlogifolium*. And at least one collection from North Carolina suggests a transition to *S. georgianum* (see below).

Typical habitats for *S. phlogifolium* are thin woods and edges in partial shade on subxeric to submesic slopes with moderate to low soil acidity. Based on personal experience, collection data (especially at BRIT-VDB), and published surveys (e.g., Hardin 1988, Kauffman et al. 2004, Marx 2007, Thompson 2008, Larson 2011), *Quercus alba* may be the most common associated tree; other species include *Acer rubrum, A. saccharum*, Carya glabra, C. ovata*, Diospyros virginiana, Fraxinus americana** (sensu lato), *F. quadrangulata**, Juniperus virginiana*, Liriodendron tulipifera, Pinus strobus, Platanus occidentalis, Prunus serotina**, *Q. coccinea, Q. muhlenbergii**, Q. rubra, Q. shumardii**, Q. velutina, Sassafras albidum, Tsuga canadensis* and *Ulmus rubra**. At some localities, rocky glades or grasslands are intermixed with wooded habitats. The species is rare to absent within more mountainous sections of the Appalachians and where strongly acid soils predominate.

Symphyotrichum georgianum. The range of this species is centered on the Piedmont of Alabama (in a small disjunct section), Georgia, South Carolina, North Carolina and possibly (with atypical plants) Virginia to Pennsylvania (Figure 5). It also extends north into the adjacent Ridge-and-Valley and onto the southern Cumberland Plateau, especially in Alabama, and there are a few records from the central Coastal Plain south to Leon Co., Florida (Weakley 2012). Collections from the counties listed below were verified at the herbaria shown in parentheses. *S. georgianum* is reported here from Tennessee for the first time, based on a collection that had been filed under *S. patens*. In addition, there are a few old collections from Pennsylvania and Virginia that appear intermediate between *georgianum* and *patens*; see notes above under the 'Appalachian variant' of *patens*. Several other misidentifications or questionable identifications were discovered, and records of atypical 'eglandular plants' are provided in the subsequent section.

On the Piedmont, typical habitat is dry thin woodland and grassland on basic hardpan soils (formed from diabase, dolomite, kyanite, etc.), probably maintained by frequent fire before settlement (Weakley 2012). Typical woody associates, based on the literature plus collection data, include *Quercus stellata* and *Q. marilandica* (both locally dominant before settlement) plus *Cercis canadensis**, *Cornus florida, Hypericum prolificum*, Ilex longipes, Juniperus virginiana*, Pinus echinata, P. palustris, P. taeda, Quercus velutina, Symphoricarpos orbiculatus*, Vaccinium arboreum* and *Viburnum rafinesquianum** (Tompkins 2013, NatureServe 2014: association CEGL 3711). However, mostly different associates were reported on Cambrian (Ketona) dolomite of the disjunct Piedmont in Bibb Co., Alabama (Allison & Stephens 2001), and on Eocene chalk of the Coastal Plain in Houston Co., Georgia (Echols & Zomlefer 2010). At both localities, *S. georgianum* was rare but it occurred in grassland and brushy transitions similar to the Black Belt habitat of *S. patens* var. *terranigrum*; associates included a much higher proportion of calciphiles than for *S. georgianum* further east.

***S. georgianum*: typical glandular plants**. Following are recorded counties. Question marks (? before acronyms) indicate uncertain identifications, usually due to incomplete collections.
Alabama: Bibb (EKY), Barbour (VDB), Blount (BRIT, GA, VDB; *R. Kral 37826,* "rays deep violet, very lovely and perhaps the finest aster I have ever seen"), Butler (VDB), Calhoun (VDB), Clay (VDB), Covington (NCU), Etowah (GA, VDB), Shelby (VDB), St. Clair (EKY, VDB). Jones (1992), Allison and Stevens (2001) and USDA (2014a) add, for the species, Talladega and Tuscaloosa.
Georgia: Clarke (GA), Chatooga (GA), Dawson (BRIT, GA, NCU), Elbert (GA), Fulton (GA), Habersham (US), Harris (GA), Houston (GA), Jones (BRIT), Madison (EKY, GA, VDB), McDuffie (BRIT), Rabun (GA), Randolph (GA, US), Richmond (EKY), Rockdale (BRIT, GA,

US). Jones (1983) adds, for the species, Catoosa, Cherokee, Hart, Walton and Warren. USDA (2014a) adds Spalding for the species, while M. Medley and R. Ware (pers. comm.) have recorded it from Gordon, Murray and Paulding. An additional old collection that is probably from Fulton Co. may be transitional to the "short-western plants" outlined below: Atlanta, damp shady copses, 22 Oct 1888, "*Aster patens* var. *georgianus*" of C. Mohr s.n. (?US)
North Carolina: Gaston (EKY, NCU, US), Mecklenberg (EKY), Montgomery (NCU, VDB), Randolph (NCU), Richmond (NCU), Rowan (EKY), Stanly (NCU, VDB), Stokes (NCU), Surry (NCU) and Union (EKY, VDB). There is also an odd collection grown from Macon Co. that was initially identified as *S. phlogifolium*, but it suggests more similarity to *S. georgianum* (*J.C. Semple 10856* at NCU).
?**Pennsylvania**. Lancaster Co., "about the mouth of the Tucquan in Eozoic" [sic], 20 Sep 1901, *A.A. Heller s.n.* (?US). This incomplete collection appears to have a rhizome; it suggests *S. georgianum* or a transition to *S. patens*.
South Carolina: Abbeville (GA, USCH), Charleston (NCU), Cherokee (EKY, NCU, USCH, VDB), Chesterfield (GA), Edgefield (GA, NCU, USCH), Fairfield (EKY, USCH), Kershaw (NCU), Laurens (EKY), McCormick (BRIT, GA, NCU, US), Oconee (BRIT, GA), Pickens (US), Richland (GA, EKY, USCH), York (EKY, NCU, USCH). Jones (1983, 1992) adds Union for the species. There is also an odd collection from Chester Co. that suggests a transition to *S. patens* (*C.N. Horn 6241* at US).
Tennessee. Marion Co., steep limestone slope by US 41 ca. 4 miles SSE of Monteagle, 7 Oct 1969, *R. Kral 37623* (GA).
?**Virginia**. Augusta Co., vicinity of Fordwick and Craigsville in Allegheny Mts., alt. 480 m, 14 Sep 1913, *E.S. Steele 190* (?US); Rockbridge Co., vicinity of Goshen in the Alleghenies, 425 m alt., 11 Sep 1904, *E.S. Steele s.n.* (?US). Both of these colls lack sufficient plant base to show

rhizomes, but they have *georgianum*-like leaf texture, dense glands on leaves and stems, and relatively large heads on long ascending branches. It is possible they are intermediate in some way between *S. georgianum* and *S. patens*.

***S. georgianum*, largely eglandular plants**. At least some of the collections from the following counties have few or no glands, except at phyllary tips. Otherwise they are similar to typical *S. georgianum*. These plants have been recorded for certain only from the Carolinas, but it is likely that eglandular plants will be confirmed in Georgia and Alabama. Several of the older records of "typical glandular *georgianum*" (see above) may not have been double-checked for the presence of glands. Eglandular plants are concentrated further east than typical *S. georgianum*, extending onto the Atlantic Coastal Plain (Figure 5). Their range is similar to that of *S. grandiflorum*, which Jones (1983) suggested might be involved in the ancestry of *S. georgianum*.
?**Alabama**: Randolph (?VDB; lower parts missing), Lee (?VDB; rhizome not clear).
North Carolina: Dare (NCU), Davie (NCU), Jones (NCU), Lee (NCU), Nash (NCU), Yadkin (NCU).
South Carolina: Abbeville (NCU), Fairfield (NCU), Horry (USCH), Orangeburg (NCU), Saluda (NCU), Sumter (USCH).

Symphyotrichum* sp., aff. *georgianum: here informally named "short western plants." In searching through folders of *S. patens*, the following distinct but variable collections were discovered from scattered sites on the Gulf Coastal Plain and southern Cumberland Plateau, mostly on sandy soils; a selection is shown in Figure 6. Most of them resemble *S. georgianum* in having relatively large heads, more or less corymbiform inflorescences with ascending branches, distal leaves not strongly auriculate-amplexicaul, and in some cases they are clearly rhizomatous. Unlike typical *georgianum*, these plants are relatively short, several do not appear to have distinct rhizomes, and glands are often sparse to absent. The key above summarizes observations for this group of collections. Note that Jones (1980) initially mapped *S. georgianum* in Louisiana, but based on a "dubious, mixed collection" (Jones 1983) that needs to be compared with these plants. Collections that have rhizomes are indicated by "/ R" after herbarium acronyms; collections that are glandular below the inflorescence are indicated by "/ G" (lower case indicates character not clearly expressed).

Alabama: Cherokee Co., ca. 2 miles W of Jamestown, SW4 S29, Lookout Mountain, cut-off and burned area, occasional, 11 Oct 1986, *S. McDaniel 29161* (IBE, VDB / G). Colbert Co., just S of Muscle Shoals and river by Ala. 17, sandy silt of oak flats, 21 Oct 1976, *R. Kral 59430* (VDB / G).

Georgia. Dade Co., roadbank of I-59 0.1 mile from Alabama line south of Rising Fawn, 15 Oct 1989, *R.D. Thomas & B.G. Thomas 113,837* (TENN / Gr). Floyd Co., common, cliffs of the Coosa, above Blacksbluff Road near Rome, S of quarry on Colbert very rocky silt loam over clay and Conasauga limestone, 20 Oct 1968, *L. Lipps et al. 4037* (BRIT, limited basal collection, but heads very compact on branches only ca. 1 cm long). ?Putnam Co., SW of Warfield US-129 SW of Little River, near Old Macon Crescent (MP-5), 6.3 km N of GA-212, disturbed area, full sun, red clay, 18 Oct 1999, *J.C. Semple 10874* (WAT, GA, BRIT, "2n = 20"; very few/no glands, and also mounted on sheet is piece with much smaller leaves).

Louisiana: Bosseir Pa., sandy soil near Haughton, 12 May 1925, *E.J. Palmer 27166* (MO / R? but depauperate collection). Claiborne Pa., drier portions, open sandy slough and seepage area, 18 mi SW of Junction City, 29 Oct 1964, *R. Kral 23238* (VDB). Lincoln Pa., Woodland Park off La Hwy 146, Ruston, open upland mixed forest, clay seepage area, N 92 deg 37 min W 32 deg 32 min, 4 Nov 1988, *T.L. Purifoy 75* (MU). Natchitoches Pa., 3 mi E Robeline, burned over sandy loblolly pine stand, 27 Oct 1962, *R. Kral 16138* (VDB). Webster Pa., [no location], 7 Nov 1971, *H. Thompson 6* [Southeastern State College] (BRIT, only 15 cm tall). Winn Pa., recently cleared and burned longleaf pine woods besides USFS Rd 554, 0.5 miles N of La 126 and La. 1233 in Kisatchie National Forest N of Pine Ridge, Sec. 8 T13N R5W, 16 Nov 1990, *R.D. Thomas 122829* (GA, MU / gr).

Mississippi. Jasper Co., Tallahala Wildlife Management Area; ca. 0.3 miles W of Randall Hill Cemetary; T4N R10E Sec. 13 NE4 NW4, common throughout area, 25 Oct 1988, *D.T. Carraway 467* (IBE / g).

Oklahoma. Cleveland Co.[?], dry hillsides 8 mi E of Norman, 10 Oct 1924, *W.E. Bruner s.n.* (BRIT / R?). Major Co., sandy soil 14 mi NE of Seiling, 25 Aug 1927, *R. Stratton 471* (MO). Payne Co., clay loam soil 5 mi E of Stillwater, 29 Sep 1932, *R.M. House 71* (MO). [These collections have relatively small heads, short leaves, no glands on stems or leaves, tight clumps only ca. 30–35 cm tall.]

Tennessee. Knox Co., Cherokee Bluffs, Knoxville, limestone under rich loamy soil, woods edge, 3 Oct 1965, *G.H. Morton 420* (BRIT / G). Roan Co., wasteground, Mt. Roosevelt State Forest, ca. 2 mi W of Rockwood along Hwy. 70, 21 Oct 1984, *L.E. McKinney 3415* (VDB; G).

Texas. Angelina Co., rolling sandy longleaf line area above lake at Boykin Springs, Angelina National Forest, 30 Nov 1962, *D.S. Correll 26863* (BRIT). Brazoria Co., Nash Ranch, 275 acre hay meadow W of CR 25 ca. 8.7 mi N of intersection with Hwy. 35 in West Columbia, infrequent in drier places with *Panicum* spp., *Muhlenbergia capillaris, Schizachyrium scoparium, Rhynchospora* sp. and *Paspalum plicatum*, 27 Oct 2005, D.J. Rosen 3597 (BRIT; R). Brazos Co., Minter Springs 11 miles SW of Millican, stems 6 dm high or more along a creek, 8 Nov 1945, *V.L. Cory 50591* (BRIT, US / R; leaves with thick margin like *georgianum* but relatively open diffuse inflorescence that suggests *S. patens* var. *gracile*); low moist area on sandy soil in partial shade, along White Creek, A&M College Swine Unit W of main campus, 16 Nov 1951, E.C. Conrad 385 (BRIT / R?). Dallas Co., "sandy woods" or "Dallas sands", 1880, *J. Reverchon 4360* (MO, US; "*Aster patens* var. *gracile*" or "*Aster subsessilis* Burgess"; no glands even on phyllaries, rather dense corymbiform inflorescence). Gillespie Co. [?], "Geb [?] Hollow, Gillespie"; "*from the coll of G. Jermy" s.n.* (MO, purchased 1897 / R?). Harris Co., prairies, Houston, Sep 1842, *G. Engelmann s.n.* (MO / gR); sandy loam, much leaves among grass, clearing in woods under *Pinus, Quercus, Vaccinium* and grasses, ca. 0.2 mi N of Buffalo Bayou and 250-300 yards E of Post Oak Rd., Houston Memorial Park, 25 Oct 1956, *A. Traverse 247* (BRIT / R). Lee Co., roadside adjacent to oak forest, deep sandy soil, 1.7 mi on 77 N of jct. 21 and 77, 28 Oct 1983, W.F. Mahler 9698 (BRIT / R). Limestone Co., post oak savannas, Hwy. 14 and park road 28, Fort Parker State Park, Aug 1993, *J. Singhurst et al. 1308* (BRIT / R). Montgomery Co., 2.25 mi S of Willie, freq. in sandy pineland, 10 Nov 1945, *V.L. Cory 50678* (BRIT / R). Tarrant Co., sandy soil, Lake Worth, 10 Sep 1924, *A. Ruth 421* (BRIT; R); post oak belt, Eagle Mountain Lake, E side near boat club, 12 Oct 1946, *E. Whitehouse 17334* (BRIT / R). Titus Co., blooming after mowing, 3 mi W Mt. Pleasant on Hwy. 67 near bridge over small creek, 2 Nov 1946, *E. Whitehouse 17750* (BRIT). Wise Co., CR 2445, sandy roadside at 253 m elevation, N33 20 13.48 W97 32 54.28, 26 Sep 2003, *R.J. O'Kennon & C. McLemore 19049* (BRIT / R)

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Figure 6 [next pages]. Examples of *Symphyotrichum* aff. *georgianum*, undescribed "short western plants": *D.T. Carraway 467* from MS (IBE); *R. Kral 23238* from Louisiana (BRIT); *G. Engelmann s.n.* from Texas (MO); *J. Reverchon 4360* from Texas (MO); *A. Traverse 247* from Texas (BRIT); *R.M. House 71* from Oklahoma (MO). See details of collection data in text.


INSTITUTE FOR BOTANICAL EXPLORATION (IBE)
HERBARIUM
COMPOSITAE
Aster patens Ait. var. patentissimus (Lindl) T. & G.
MISSISSIPPI. Jasper Co.: Tallahala Wildlife Mngmt area, ca 0.3 miles W of Randall Hill Cemetary, T4N R10E S13 NE4 NW4, rays blue, disks yellow. Common throughout area.
October 25, 1988
Daniel T. Carraway 467
Institute for Botanical Exploration (IBE)


Aster patens Ait. var. gracilis Hook.
Examined in a revision of Aster section Patentes (Asteraceae).
Ronald L. Jones 1979 Vanderbilt University
HERBARIUM
VANDERBILT UNIVERSITY
VDB
45316
PLANTS OF LOUISIANA
Claiborne Par. 29 Oct 1964 R.Kral 23238
Aster patens
Drier portions. Open, sandy slough and seepage area 18 mi. s.w. Junction City.
Det: R.Kral


Aster patens Ait. var. patens
Examined in a revision of Aster section Patentes (Asteraceae).
Ronald L. Jones 1979 Vanderbilt University
Missouri Botanical Garden
48180
Herbarium
S. pat (LB)
Aster patens Ait
Prairies, Houston
TEXAS
Collected by F. Lindheimer.
George Engelmann, M. D.
ST. LOUIS, Mo.
Sept. 1842
MISSOURI BOTANICAL GARDEN

Toward var patens! RLJ
Aster patens Ait. var. gracilis Hook.
Examined in a revision of Aster section Patentes (Asteraceae).
Ronald L. Jones 1979 Vanderbilt University
Missouri Botanical Garden
50016
Herbarium
TEXAS FLORA
No. 421
aster patens. var. gracilis
sandy wood.
J. REVERCHON.
sept.
MISSOURI BOTANICAL GARDEN


247
Botanical Research Institute of Texas
Determined by Lloyd H. Shinners
9 July, 1957
PLANTS OF TEXAS
Names Aster patens Ait.
Field number 247
Date 25 Oct., 1956
County Harris
Location ca. 1/5 mi. N of Buffalo Bayou*
Altitude 55'
Habitat clearing in woods, sandy**
Growth form and habit herb, annual, erect
Height
Diameter
Flower-blue-lavender rays
Associated Plants under Pinus sp., Quercus sp., w. Vaccinium sp., & grasses.
Miscellaneous notes
*& 250 -300 yds. E of Post Oak Rd., Houston Memorial Park.
**loam, much leaves among grass.
Collected by A. Traverse


Aster patens Ait. var. gracilis Hook.
Examined in a revision of Aster section Patentes (Asteraceae).
Ronald L. Jones 1979 Vanderbilt University
MISSOURI BOTANICAL GARDEN
1222947
HERBARIUM
71.
HERBARIUM OF THE OKLAHOMA AGRICULTURAL AND MECHANICAL COLLEGE
STILLWATER, OKLAHOMA
Aster patens Ait.
Clay loam soil, 5 mi. E. of Stillwater, Payne Co., Okla.
September 29, 1932
Coll.: R. M. House
Det. : Robert Stratton

DISCUSSION

ECOLOGY AND RANGE OF VAR. *TERRANIGRUM*

The Appendix below organizes information assembled above on typical habitats of taxa within the *Symphyotrichum patens* complex in terms of compositional gradients among woody associates. It illustrates the general segregation of taxa along habitat gradients except for *S. patens* var. *patentissimum* versus *S. georgianum*, which have ranges that do not overlap at all.

Across most of its range, *S. patens* is typical of medium to strongly acid soils. Var. *patens* is infrequent to absent on calcareous soils, but often occurs in calcareous glades where more acid material has slumped or washed in from above. Var. *gracile* is typical of acid sandy soils on the Coastal Plain; see also, Mohr (1901). Var. *patentissimum* is typical of moderately acid soils in the Ozark-Ouachita region; see also Yatskievytch (1999). These observations are supported by descriptions of varied grassland and woodland types, as summarized by NatureServe (2011) and detailed in numerous regional or local studies. For example, Campbell et al. (1989, 1991) listed typical *S. patens* as a frequent species in remnants of ‘sandy barrens’ (open grassy woodland) on acid soils of the Cumberland Plateau, but Lawless et al. (2006a,b) did not report it at all from the ‘xeric limestone prairies’ of Kentucky or elsewhere in east-central states. In contrast, var. *terranigrum* appears largely restricted to xeric calcareous soils, mostly on or near the Coastal Plain of southeastern states. Its fragmented known range reflects the limited occurrence of such habitats in this region. To the north of its clustered records in the Black Belt of Alabama and Mississippi, it is virtually unknown on limestones of the Interior Low Plateaus, but its ecological place there is taken by other asters, including *S. oblongifolium* (Nutt.) Nesom and *S. pratense* (Raf.) Nesom, both in subgenus *Virgulus*.

Disjunct records of plants resembling *S. patens* var. *terranigrum* to the northeast of the Black Belt, as far as LeHigh County, Pennsylvania, and Nassau County (Long Island), New York, are provocative. Pretz's 1917 collection from Pennsylvania does not appear to have been part of a published flora, although he did start a series (Pretz 1911). Laughlin and Uhl (2003) reported that there are still remnants of 'xeric limestone prairies' in this Ridge-and-Valley section of the state, although none are currently known in the Great Valley of LeHigh County. Ten of the 12 state-listed rare species that Laughlin and Uhl noted as associated with such prairies in Pennsylvania also occur in the Black Belt, often growing with *S. patens* var. *terranigrum* or nearby in Mississippi: *Bouteloua curtipendula* (Michx.) Torr., *Dichanthelium oligosanthes* (Schult.) Gould, *Linum sulcatum* Riddell, *Lithospermum canescens* (Michx.) Lehm., *Onosmodium hispidissimum* Mack., *Ophioglossum engelmannii* Prantl, *Ranunculus fascicularis* Muhl. ex J.M. Bigelow, *Ruellia humilis* Nutt., *Senna marilandica* (L.) Link and *Solidago rigida* L. Despite the virtual eradication of their original vegetation, these species remain clustered in southeastern counties of Pennsylvania. It is likely that further inventory of old roadsides, rough unimproved pastures and other grassland remnants on calcareous soils throughout the Ridge-and-Valley will provide additional records of var. *terranigrum*.

The 1893 collection by Joseph Schrenk from Hempstead Plains on Long Island, New York, is more difficult to interpret. It does match *S. patens* var. *terranigrum* in its dense glands and dark crowded leaves, but the habitat is not typical. Original soils of these plains appear to have been formed mostly in a silty mantle on strongly acid sand and gravel outwash deposits. Further investigation of soils in this region could be useful; the original A horizon of the Hempstead soil series was a "black silt loam" with moderate acidity that has probably been reduced by erosion after settlement (USDA 2014b). The previously documented flora does not include any *S. patens*, and there are virtually no calciphiles listed (Stalter & Seyfert 1989). Faunistic evidence supports the concept of a periglacial origin for this ecosystem, with little connection to southeastern grasslands (Hamilton 2012).

A fundamental question arises. Do real biogeographic connections exist among these cited collections of *S. patens* var. *terranigrum*, through dispersal from a common ancestor?—Or did some of these plants have independant origins from a broader gene-pool of the whole species? In addition to more molecular analysis, deeper understanding of relationships with herbivores could eventually help with this question. It is likely that glands in these plants, like other Asteraceae, have some function in deterring herbivores, and that their frequency in populations is influenced by genotypic selection as well as by environmental effects on plant development (e.g., Levin 1973, Kelsey et al. 1984, Guillet et al. 1997). Moreover, larger herbivores could have promoted long-distance dispersal of seed in fur or gut (e.g., Myers et al. 1997, Rosas et al. 2008). Dispersal by bison and other large animals, now extinct, may well have been concentrated along calcareous "barrens" and fertile lowlands of the Ridge-and-Valley region (DeSelm 1994, Brown 2000, McDonald 2000, DeSantis & Wallace 2008), and along base-rich "prairies" of the Atlantic Piedmont (Schmidt & Barnwell 2002, Tompkins et al. 2010).

TAXONOMIC TREATMENT OF *PATENS* COMPLEX IN GENERAL

Taxonomy of the *Symphyotrichum patens* group remains somewhat unsettled for several reasons. As in several other large genera of Asteraceae, the gross morphology of individual species is often plastic, defying description of consistent differences in branching pattern, leaf-shape or pubescence. Even with flowering heads, careful observation and precise descriptive language is sometimes inadequate to distinguish taxa based on single characters. Moreover, it seems likely that the divergence of taxa has been relatively recent and reticulate—resulting in occasional intermediate forms, hybrids or otherwise atypical plants, especially among polyploids.

The primary division here—couplet 1 of the key above—remains tentative in its language. For previous treatments, *Symphyotrichum georgianum* has been distinguished using several characters: rhizomatous habit; leaf texture thick, with revolute margins; leaves less clasping, at least distally; and larger heads, mostly notably in the rays (Jones 1983, Brouillet et al. 2006). After examination of much typical *georgianum*, plus other affiliated plants, it is reasonable to add emphasis of the relatively compact inflorescences, with ascending branches, that are usually evident in collections. However, with inclusion of the anomalous "short western plants" under 1b, one has to loosen up the ray size and rhizome characters in this couplet. When those western plants are better understood, the key can probably become more definitive.

A more thorough survey of chromosome numbers is still needed within the whole *patens* complex, together with further taxonomic assessment of collections vouching for previous counts. As noted above, it is likely that var. *terranigrum* and var. *gracile* partly correspond to the two clusters of diploids (2n = 10) previously mapped east and west of the Mississippi River, respectively. These two groups of plants tend to be associated with seasonally xeric open habitats on calcareous (var. *terranigrum*) or non-calcareous (var. *gracile*) soils, mostly on or near the Coastal Plain. Tetraploids (2n = 20) have become more widespread across southeastern states (typical var. *patens*), or largely Ozarkian (var. *patentissimum*), or largely Appalachian (*S. phlogifolium*), and they tend to occur in more densely wooded landscapes, especially the relatively large-leaved *phlogifolium*.

Typical plants of the decaploid (2n = 50) *S. georgianum* deserve deeper analysis in relation to the additional variants suggested above, and in relation to Jones' (1983) hypothesis that this species originated from hybridization of *S. patens* var. *patens* (2n = 20) and *S. grandiflorum* (2n = 30, 60). Its robust growth form is presumably well-suited to the oak savannas and glades that are its native habitats. Rhizomes in grassland may have some general value related to moderate disturbance from browsing or burning on locally more fertile soils, following the rationale of Craine et al. (2001), N'Guessan (2007) and others. Unfortunately, this species has become generally imperiled within its small range (NatureServe 2014), and its original ecology remains somewhat obscure.

The phylogenetic and functional significance of stipitate glands deserves further attention. This character is central to distinction of *S. patens* var. *terranigrum* and of several other taxa within subgenus *Virgulus*, at various taxonomic levels. Morphological patterns suggest that it is an ancestral character within sect. *Grandiflori* (sensu lato), where it is retained in all taxa, and within sect. *Patentes*, where it is lost in several taxa (Brouillet et al. 2006). Table 1 summarizes the occurrence of glands within these sections, and suggests a potential relationship with the base-status of typical soils for each taxon. There is an association between "sparse to dense" or "dense" glands (coded at least "2 or 3") and base-rich soils ("BASIC" or "basic"): $P < 0.01$ with Fisher's exact test. However, a more rigorous analysis is needed.

Distinctly stipitate (= "stalked") glands or glandular hairs are relatively uncommon on stems or leaves below the inflorescence among Angiosperms of eastern North America. These include a few additional Asteraceae, mostly with short stalks (in *Artemisia*, *Heterotheca, Pseudognaphalium*). Other examples include some *Cannabis sativa* (Cannabaceae), *Cuphea* *viscosissima* (Lythraceae), both species of *Juglans* (Juglandaceae), several species of Caryophyllaceae (in *Cerastium*, *Holosteum, Silene*), Onagraceae (in *Circaea*, *Oenothera*), Solanaceae (in *Nicotiniana, Physalis, Solanum*), and Lamiaceae (in *Scutellaria, Trichostema*). General knowledge of these species suggests a broader association between stipitate glands and base-rich soils, with correlated variation among closely related taxa in some cases (e.g., loss from *T. brachiatum* to *T. dichotomum* to *T. setaceum*). As noted above, such patterns may involve deterrence of hervibores by the glands before the foliage itself is eaten. And there is increasing evidence for the global principle that pressure from herbivory tends to increase on more fertile soils (e.g., Scholes 1990, Edwards et al. 2000, Eskelinen 2008, Smit et al. 2009).

There are obvious priorities for further research.
(1) More chromosome counts; differences in ploidy may be critical for understanding species concepts.
(2) Establishment of living collections; differences in vegetative growth need better description, and there can also be experiments with growth on varied types of soil. Also, potential hybridization can be investigated.
(3) More detailed genetic and molecular investigation; the taxonomy presented here can then be tested.
(4) General synthesis of data for a thorough revision; in addition to phylogeny, some aspects of nomenclature will deserve deeper consideration, e.g., should the subspecies concept be applied to *patens* and its closest allies versus *georgianum* and its closest allies?
(5) Experimental comparisons of glandular versus non-glandular plants when subjected to herbivory in varied ecological contexts.

Table 1 [see next page]. Potential relationship of glandularity to typical soil base-status among taxa of *Symphyotrichum* Subgenus *Virgulus* sect. *Patentes* plus sect. *Grandiflori** (sensu lato, indicated by asterisks in first column). This is a provisional exploration, pending more precise descriptions of typical habitats. The probable clade that comprises sect. *Virgulus* plus sect. *Ericoidi* is excluded because those plants have a complete lack of glands, even within the inflorescence; their typical habitats span a wide range of soil base-status. Taxonomy and data come primarily from Brouillet et al. (2006) plus information presented in this paper.

<u>Glandularity is coded as follows</u>.
1 = glands largely restricted to inflorescence.
2 = glands sparse or rarely dense on some leaves and upper stem.
3 = glands sparse to dense on all leaves and most stem.
4 = glands usually dense on all leaves and most stem.

<u>Typical soil for each taxon is based on limited information in several cases</u>.
ACID: concentrated (>80%) to sandy or boggy soils, especially on southeastern Coastal Plain.
acid: common on soils as above, but also frequent to a lesser degree on clays and silts.
ab: poorly known habitats or mixed or intermediate, based on available information.
basic: common on base-rich soils, but also frequent to a lesser degree on more acid soils.
BASIC: concentrated (>80%) on relatively base-rich clays/silts or calcareous soils.

<u>Range is coded as follows, indicating at least the central concentration for each taxon</u>.
AC = Atlantic Coastal Plain; AM = Appalachian Mountains and adjacent regions; GC = Gulf Coastal Plain; GP = Great Plains; NE = New England and adjacent Canada; OZ = Ozark and Ouachita region; PM = Piedmont; RM = Rocky Mountains; SE = southeastern U.S.A (more or less widely scattered); abbreviations for states are added in some cases for detail.

Table 1. [See caption on previous page.]

SPECIES OR VARIETY	GLANDULARITY	TYPICAL SOIL	RANGE
S. patens var. *gracile*	1	ACID	GC (TX-FL)
S. patens var. *patentissimum*	1	ab	OZ
*S. × amethystinum**	1	ab	GP-NE
S. patens var. *patens*	1 or 2	acid	SE
S. georgianum-eglandular	1 or 2	acid	PM-AC
S. walteri	1 or 2	acid	AC (FL-NC)
S. aff. *georgianum*-short western	1, 2 or 3	acid	GC+ (OK-GA)
S. fontinale	2	ACID	GC (FL)
*S. grandiflorum**	2	ACID	AC (SC-VA)
*S. pygmaeum**	2	ab	Arctic
*S. fendleri**	2	ab	GP (central)
S. adnatum	2 or 3	ab	GC (LA-FL)
*S. campestre**	2 or 3	acid	RM-CA
*S. yukonense**	2 or 3	basic	Arctic
S. phlogifolium	3	basic	AM
*S. novae-angliae**	3	BASIC	NE-wide
S. georgianum-typical	3 or 4	basic	PM
S. patens var. *terranigrum*	4	BASIC	SE (MS-AL+)
*S. oblongifolium**	4	BASIC	GP-wide

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APPENDIX: Typical Habitats of *Symphyotrichum* sect. *Patentes* Taxa in Relation to Major Ecological Gradients across Southeastern U.S.A.

A. Hydrological gradients in terms of modal positions for tree species.

A1. Simplified summary of gradients in warm- to mid-temperate woods (broadly defined). Mesic conditions (= M) are at center-left; more open, stressed or disturbed conditions increase to upper right (xeric extreme = X), to lower right (hydric extreme = H), or to lower left (riparian or rheophytic with active scouring = R).
Six-letter codes indicate approximate modal positions of species, using first three letters of genus and species; if more than one mode, the average is usually shown.
Red letters = codes for species associated with strongly acid soils (low pH ca. 4-5); green = medium acid (pH ca. 5-6); blue = circumneutral (high pH ca. 6-7); used for index below.
Dark grey fill = generally continuous forest; medium grey = more open woods, often mixed with shrubland or grassland; pale grey = zones usually dominated by shrubs or graminoids.
Parentheses indicate species with relatively northern ranges, which are replaced by other species to the south within this region.
** Ring-porous wood; * semi-ring-porous.

A2 to A7. Distribution of taxa along these gradients, based on general review of common woody associates; see text for references. Underlining indicates most abundant associates; parentheses ( ) indicate minor or peripheral associates; brackets [ ] indicate shrubs, added in some cases to the species listed in A1. Shadings indicate concentrations. “Index of basiphily” is a 10-point scale calculated as mean from associates: low pH = 1; medium = 5; high = 10.

A1. Hydrological gradients among trees of southeastern states.

		CLIFFS	CLIFFS	CLIFFS	PINVIR JUNVIR ULMSER**	PINRIG QUEPRI** ULMALA**	QUELAE** QUEILI** CELTEN**	XERIC EXTREME
MESIC SLOPES (below)	CLIFFS	QUECOC** QUEVEL** QUESCH**	QUEMON** CARGLA** FRAQUA**	VACARB QUEFAL** (ULMTHO)**	PINECH (POPGRA) FRABIL**	QUEMAR** MALCOR* GLETRI**	QUEMRG** MALANG* RHUGLA**	GRASS-LAND
TSUCAR HALTET CLAKEN	MAGMAC QUERUB** TILAME	CASDEN** CAROVA** ULMRUB**	OXYARB QUEALB** QUEMUE**	CARPAL** CARTOM** CARCAR**	PINTAE SASALB* PRUSER*	PINPAL QUESTE** GYMDIO**	QUEINC** (QUEIMB)** (QUEMAC)**	GRASS-LAND
TSUCAN FAGGRA ACESAC	BETLEN LIRTUL AESFLA	MAGACU ACERUB CARCOR*	ILEOPA NYSSYL FRAAME**	(PINSTR) (JUGCIN)* JUGNIG*	QUENIG** ROBPSE** MORRUB*	QUEHEM** DIOVIR* MACPOM**	PINSER QUEPHE** QUESIN**	GRASS-LAND
PLAOCC	HALCAR BETNIG ACENEG	MAGTRI LIQSTY ULMAME**	MAGGRA QUESHU** CARLAC**	PERBOR QUEPAG** CELSPP**	QUELAU** ILEDEC FRAPEN**	(QUEPAL)** CHATHY CARMYR*	PINELL TAXASC QUELYR**	BOG or MARSH or FEN
POPDEL	ACESNM CATSPE**	ACETRI CARILL*	QUEMIC** FRASUB**	NYSBIF FRAPRO**	MAGVIR FRACAR** POPHET	PERPAL TAXDIS CARAQU*	CYRRAC NYSAQU GLEAQU**	STAGNANT WATER
RHEIC EXTREME	SALSER SALCAR SALINT	ALNSER SALNIG	CORSTR PLAAQU	CEPOCC FORACU	DECVER HIBSPP	STAGNANT WATER	STAGNANT WATER	HYDRIC EXTREME

A2. *Aster patens* var. *terranigrum*: index of basiphily = 8.5 (1 low/4 medium/15 high).

					JUNVIR CERCAN	ULMALA	CELTEN	**X**
					FRABIL	(QUEMAR) SIDLYC	PRUANG (RHUGLA)	
M			(QUEMUE)	(CARMYR)	(PRUSER)	(QUESTE) (GLETRI)	CRACRU	
				(JUGNIG)	(MORRUB)	(DIOVIR) MACPOM		
				(CELLAE)				
R								**H**

A3. *Aster patens* var. *gracile*: index of basiphily = 1.1 (11 low/3 medium/0 high)

					PINVIR		QUELAE	**X**
			QUEMON	VACARB QUEFAL	PINECH	QUEMAR	QUEMRG	
M			OXYARB			PINPAL	QUEINC	
			NYSSYL	ILEVOM		DIOVIR		
R								**H**

A4. *Aster patens* var. *patens*: index of basiphily = 2.5 (12 low/12 medium/0 high)

					PINVIR			**X**
		QUECOC QUEVEL	QUEMON CARGLA	VACARB QUEFAL	<u>PINECH</u>	<u>QUEMAR</u>	RHUCOP?	
M		(CASDEN) CAROVA	(OXYARB) QUEALB	(CARPAL) CARTOM	(PINTAE) SASALB*	(PINPAL) <u>QUESTE</u>		
		(ACERUB)	NYSSYL	[CORFLO]		(DIOVIR)		
R								**H**

A5. *Aster patens* var. *patentissimum*: index of basiphily = 4.6 (4 low/7 medium/3 high)

					JUNVIR	ULMALA	CELTEN	X
				VACARB QUEFAL?	PINECH FRABIL	QUEMAR? PRUAME	RHUCOP	
M				CARTEX	SASALB?	QUESTE		
						DIOVIR?		
R								H

A6. *Aster georgianum*: index of basiphily = 4.4 (5 low/8 medium/3 high)

					JUNVIR [CERCAN]			**X**
		QUEVEL	[CORFLO]	VACARB QUEFAL? [VIBRAF]	PINECH [HYPPRO]	QUEMAR	[RHUCOP]	
M					PINTAE [ILELON] [SYMORB]	PINPAL QUESTE		
R								**H**

A7. *Aster phlogifolium*: index of basiphily = 6.4 (2 low/11 medium/8 high)

					JUNVIR			X
		QUECOC QUEVEL QUESCH	CARGLA FRAQUA		FRABIL			
M	QUERUB	CAROVA ULMRUB	QUEALB QUEMUE		SASALB PRUSER			
TSUCAN ACESAC	LIRTUL	ACERUB	FRAAME	PINSTR		DIOVIR		
PLAOCC								
R								H

B. Soil pH-related (left-right) and mesic-xeric/disturbance (lower-upper) gradients.

B1. This soil pH-related gradient is a more detailed expansion of the color-coded gradient illustrated above in A1. The mesic-xeric/disturbance gradient combines the somewhat parallel mesic-subxeric-xeric and mesic-submesic-grassland sequences of A (where they are left-to-right). It excludes species of largely rheic (scoured riparian) and hydric habitats. Several smaller species are added, but some related pairs are combined in the same box if they are segregated mostly along the hydric-xeric gradient (lower-to-upper in A).
Colors indicate the following taxonomic concentrations.
Pink (lower left): mostly *Tsuga, Magnolia, Betula, Rhododendron*.
Orange (center left): mostly *Quercus, Carya, Ilex, Nyssa, Acer rubrum*.
Yellow (upper left): mostly *Pinus, Quercus*, Ericaceae.
Brown (lower right): *Fagus, Acer saccharum* (s.l.), *Tilia, Halesia, Liriodendron, Liquidambar*.
Green (center right): mostly *Aesculus, Juglans, Fraxinus*, Ulmaceae, some *Quercus* and *Carya*.
Blue (upper right): mostly Rosaceae, Fabaceae, *Rhus, Juniperus*, some Ulmaceae, *Quercus*; includes all thorny trees (and note several other ecomorphological trends among species groups).

B2 to B7. Distribution of taxa along these gradients, based on general review of common woody associates; see notes above on each taxon for references. Underlining indicates most abundant associates; parentheses ( ) indicate minor or peripheral associates; brackets [ ] indicate shrubs, added in some cases to the species listed in A1. Shadings indicate concentrations. “Index of basiphily” is more refined than in A, and is calculated as mean of associate positions along the five gradient classes: 0 (low pH), 0.25, 0.5, 0.75, 1 (high pH).

B1. Soil pH-related and mesic-xeric/disturbed upland gradients.

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND	*Quercus myrtifolia* *Quercus laevis* *Kalmia* spp.	*Pinus palustris* *Pinus virgin./clausa* *Vaccinium* spp. *Quercus prinoides*	*Rhus copallina* *Malus* spp. *Corylus americana* *Chionanthus virgin.*	*Juniperus virginiana* *Crataegus* spp. *Prunus* spp. (plums) *Cercis canadensis*	*Sideroxylon* spp. *Crataegus* spp. *Celtis tenuifolia* *Frangula caroliniana*
TRANSITIONAL OPEN WOODS OR THICKETS	*Quercus ilicifolia* *Quercus georgiana* *Pinus rigida/serotina*	*Quercus incana* *Quercus margaretta* *Quercus marilandica* *Pinus echinata/elliottii*	*Diospyros virginiana* *Quercus stellata* *Carya tomentosa* *Sassafras albidum*	*Rhus glabra* *Robinia pseudoacacia* *Ulmus alata/crassifolia* *Q. imbricaria/phellos*	*Cornus drummondii* *Gleditsia triacanthos* *Maclura pomifera* *Q. macrocarpa/sinuata*
MORE OPEN SUBMESIC OR SUBXERIC	*Quercus arkansana* *Quercus coccinea* *Quercus montana* *Oxydendrum arboreum*	*Pinus taeda/strobus* *Ilex vomitoria* *Q. hemispae./laurifolia* *Carya pallida*	*Q. falcata/pagoda* *Quercus alba* *Quercus velutina* *Carya glabra/texana* *Cornus florida*	*Prunus serotina* *Fraxinus bilt./profun.* *Carya carolin./myrist.* *Ostrya virginiana* *<Cladrastis kentukea*	*Gymnocladus dioica* *Juglans nigra* *Quercus shumardii* *Q. muehlenbergii* *<Ulmus serotina/thom.*
SUBMESIC OR TRANSITION TO SUBXERIC	*Magnolia macro./ashei* *Rhododendron maxim.* *Tsuga caroliniana*	*Castanea dentata* *Nyssa sylvatica* *Ilex opaca* *Quercus nigra*	*Acer rubrum* *Quercus rubra* *Hamamelis virginiana* *Ilex decidua/longipes*	*Carya ovata/laciniosa* *Juglans cinerea* *Morus rubra* *Asimina triloba*	*Celtis occident./laevig.* *Aesculus glabra* *Fraxinus quadrangul.*
MESIC TO SUB-MESIC WOODS	*Betula lenta/alleghen.* *Magnolia fras./pyram.*	*Magnolia acuminata* *Magnolia grandiflora* *Persea borbonia*	*Liriodendron tulipifera* *Liquidambar styracifl.* *Halesia diptera*	*Fraxinus amer./penns.* *Aesculus flava/sylvat.* *Carpinus caroliniana*	*Carya cordiformus* *Ulmus rubra*
MESIC WOODS	*Tsuga canadensis*	*Magnolia tripetala* *Halesia carolina*	*Fagus grandifolia* *<Halesia tetraptera*	*Acer saccharum/florid.* *Tilia heterophylla/car.*	*Acer nigrum/leucod.* *Tilia americana*

Aster patens var. *terranigrae*: index of basiphily = 7.8 (0/1/2/6/6)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND				***Juniperus virginiana*** ***Crataegus engelmanii*** ***Prunus angustifolia*** ***Cercis canadensis***	***Sideroxylon lycioides*** ***Crataegus crus-galli*** ***Celtis tenuifolia***
TRANSITIONAL OPEN WOODS OR THICKETS		**(*Quercus marilandica*)**	**(*Diospyros virginiana*)** **(*Quercus stellata*)**	***Rhus glabra*** **(*Ulmus alata*)**	***Cornus drummondii*** ***Maclura pomifera***
MORE OPEN SUBMESIC OR SUBXERIC				***Fraxinus biltmoreana***	
SUBMESIC OR TRANSITION TO SUBXERIC					
MESIC TO SUB-MESIC WOODS					
MESIC WOODS					

Aster patens var. *gracile*: index of basiphily = 2.7 (1/9/2/0/0)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND		***Pinus palustris*** ***Pinus virginata*** ***Vaccinium* spp.** ***Quercus elliottii***			
TRANSITIONAL OPEN WOODS OR THICKETS		***Quercus incana*** ***Quercus margaretta*** ***Quercus marilandica*** ***Pinus echinata***	***Diospyros virginiana***		
MORE OPEN SUBMESIC OR SUBXERIC	***Quercus montana***	***Ilex vomitoria***	***Quercus falcata***		
SUBMESIC OR TRANSITION TO SUBXERIC					
MESIC TO SUB-MESIC WOODS					
MESIC WOODS					

Aster patens var. *patens*: index of basiphily = 3.5 (3/9/11/1/0)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND		***Pinus palustris*?** ***Pinus virginiana*** ***Vaccinium arboreum***	***Rhus copallina***		
TRANSITIONAL OPEN WOODS OR THICKETS		***Quercus marilandica*** ***Pinus echinata***	***Diospyros virginiana*?** ***Quercus stellata*** ***Carya tomentosa*** ***Sassafras albidum***		
MORE OPEN SUBMESIC OR SUBXERIC	***Quercus coccinea*** ***Quercus montana*** ***Oxydendron arbor.*?**	***Pinus taeda*** ***Carya pallida*?**	***Quercus falcata*** ***Quercus alba*** ***Quercus velutina*** ***Carya glabra*** ***Cornus florida***		
SUBMESIC OR TRANSITION TO SUBXERIC		***Castanea dentata*?** ***Nyssa sylvatica***	***Acer rubrum*?**	***Carya ovata***	
MESIC TO SUB-MESIC WOODS					
MESIC WOODS					

Aster patens var. *patentissimum*: index of basiphily = 5.4 (0/4/5/4/1)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND		***Vaccinium arboreum***	***Rhus copallina***	***Juniperus virginiana*** ***Prunus american***	***Celtis tenuifolia***
TRANSITIONAL OPEN WOODS OR THICKETS		***Quercus marilandica*?** ***Pinus echinata***	***Diospyros virginiana*?** **<u>*Quercus stellata*</u>** ***Sassafras albidum*?**	***Ulmus alata***	
MORE OPEN SUBMESIC OR SUBXERIC		***Carya texana***	***Quercus falcata*?**	***Fraxinus biltmoreana***	
SUBMESIC OR TRANSITION TO SUBXERIC					
MESIC TO SUB-MESIC WOODS					
MESIC WOODS					

Aster georgianum: index of basiphily = 5.0 (0/5/6/5/0)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND		***Pinus palustris*** ***Vaccinium arboreum***	**(*Rhus copallina*)**	***Juniperus virginiana*** ***Cercis canadensis*** **[*Hyperocum prolific.*]**	
TRANSITIONAL OPEN WOODS OR THICKETS		<u>***Quercus marilandica***</u> ***Pinus echinata***	<u>***Quercus stellata***</u>	**[*Viburnum rafinesqu.*]**	
MORE OPEN SUBMESIC OR SUBXERIC		***Pinus taeda***	***Quercus falcata?*** ***Quercus velutina*** ***Cornus florida***	**[*Symphoricarpos orb.*]**	
SUBMESIC OR TRANSITION TO SUBXERIC			**[*Ilex longipes*]**		
MESIC TO SUB-MESIC WOODS					
MESIC WOODS					

Aster phlogifolium: index of basiphily = 6.1 (2/1/8/6/4)

BROAD CLASSES OF VEGETATION	POOR ACID SOILS (pH ca 4-5) ultisols or dystrochrepts	INTERMEDIATE POOR ACID TO AVERAGE SOILS	AVERAGE SOILS (pH ca. 5-6) mixtures/tansitions among soil classes	INTERMEDIATE AVERAGE TO BASE-RICH SOILS	BASE-RICH SOILS (pH ca. 6-7) alfisols, eutro-chrepts or mollisols
DISTURBED OR XERIC SCRUB OR GRASSLAND				***Juniperus virginiana***	
TRANSITIONAL OPEN WOODS OR THICKETS			***Diospyros virginiana*** ***Sassafras albida***		
MORE OPEN SUBMESIC OR SUBXERIC	***Quercus coccinea***	***Pinus strobus***	***Quercus alba*** ***Quercus velutina*** ***Carya glabra***	***Prunus serotina*** ***Fraxinus biltmoreana***	***Q. shumardii*** ***Q. muehlenbergii***
SUBMESIC OR TRANSITION TO SUBXERIC			***Acer rubrum*** ***Quercus rubra***	***Carya ovata***	***Fraxinus quadrangul.***
MESIC TO SUB-MESIC WOODS			***Liriodendron tulipifera***	***Fraxinus americana***	***Ulmus rubra***
MESIC WOODS	***Tsuga canadensis***			***Acer saccharum***	