MORPHOLOGY, GEOGRAPHY, AND ECOLOGY OF INCISED-LEAF VARIANTS OF *SYMPHYOTRICHUM LOWRIEANUM* (ASTERACEAE)

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ABSTRACT

Specimens identified as *Symphyotrichum cordifolium* and *S. lowrieanum* with incised and pinnatifid leaves have been noted since the mid-1800s. A search of herbarium records uncovered 31 unique collections and 53 herbarium sheets of plants whose leaf incisions and lobes ranged from 4–18 mm in length. In most specimens, at least half the cauline leaves had incised leaves. Basal leaves tended to be cordate, truncate, or rounded at the base and long rhizomes were often associated with the incised-leaf form. Incised-leaved specimens occurred in eight states, ranging from Maine to Tennessee, with concentrations in Pennsylvania and Tennessee. Most collection sites were associated with shale or limestone/dolomite in the Ridge and Valley and Appalachian Plateaus physiographic provinces at elevations of 200–800 m. Repeat collections of incised-leaved specimens from several populations showed spatial and temporal persistence of the variant phenotype. Although variants comprised the majority form in some populations, typical *S. lowrieanum* was usually also present. Circumstantial evidence suggested the incised-leaf phenotype has a genetic basis. The geographic, ecological, and temporal associations are best acknowledged by use of the rank of variety as; **Symphyotrichum lowrieanum** (L.) G.L. Nesom var. **incisum** (Porter ex Britton) F. Levy, **comb. nov.**

RESUMEN

Desde mediados del siglo XIX se han observado especímenes identificados como *Symphyotrichum cordifolium* y *S. lowrieanum* con hojas incisas y pinnatifidas. Una búsqueda en los registros de herbario descubrió 31 colecciones únicas y 53 pliegos de herbario de plantas cuyas incisiones y lóbulos foliares oscilaban entre 4 y 18 mm de longitud. En la mayoría de los especímenes, al menos la mitad de las hojas caulinares presentaban incisiones. Las hojas basales tendían a ser cordiformes, truncadas o redondeadas en la base y los rizomas largos se asociaban a menudo con la forma de hoja incisa. Los especímenes con hojas incisas se encontraban en ocho estados, desde Maine hasta Tennessee, con concentraciones en Pensilvania y Tennessee. La mayoría de los lugares de recolección estaban asociados con esquisto o piedra caliza/dolomita en las provincias fisiográficas de Ridge and Valley y las mesetas de los Apalaches a elevaciones de 200–800 m. Las recolecciones repetidas de especímenes con hojas incisas de varias poblaciones mostraron la persistencia espacial y temporal del fenotipo variante. Aunque las variantes constituían la forma mayoritaria en algunas poblaciones, normalmente también estaba presente el *S. lowrieanum* típico. Pruebas circunstanciales sugieren que el fenotipo de hoja incisa tiene una base genética. Las asociaciones geográficas, ecológicas y temporales se reconocen mejor mediante el uso del rango de variedad como; **Symphyotrichum lowrieanum** (L.) G.L. Nesom var. **incisum** (Porter ex Britton) F. Levy, **comb. nov.**

Key Words: cluster analysis, leaf development, lobed leaves, Ridge and Valley, teratology

INTRODUCTION

Plants with anomalous morphological forms are often transient curiosities caused by improper development, exposure to chemical mutagens, or in extreme instances, genetic variants historically referred to by the controversial term, “hopeful monsters” (Theissen 2006). Less extreme variants offer challenges to uncovering their genetic basis, evolutionary history, and placement in a taxonomic hierarchy (Jabbour et al. 2016). Among the myriad growth form variants, leaf architectural variants are readily observable and often of horticultural interest. An example of such a variant is found in *Betula pendula* where molecular studies have shown genes related to auxin transport pathways were associated with an incised-leaved form (Mu et al. 2013; Qu et al. 2020). A more simple genetic basis may underlie an incised-leaved form of the entire-leaved fern, *Asplenium scolopendrium* L., in which the incised leaf form segregated as a trait based on a single recessive gene (Lang 1923).

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In the *Symphyotrichum cordifolium* (L.) G.L. Nesom species complex of eastern and central North America, a group that includes two subspecies and several varieties as well as *S. lowrieanum* (Porter) G.L. Nesom, plants with incised and pinnatifid leaves (hereafter referred to as an incised-leaved form) were noted as early as 1832 (Gray 1884). In the late 19th and early 20th centuries, the incised form was recognized as a taxonomic variety but since then it has been treated as a curiosity, ecotype, or ignored. The purpose of this study was to examine the prevalence, and geographical and temporal distribution of incised-leaved forms in this species complex.

Taxonomic History of Incised-leaved Variants.—Gray (1884) provided the first literature mention of incised-leaved specimens of *Aster cordifolius* L. (= *Symphyotrichum cordifolium*), stating, "A singular abnormal state, collected by Moser on the Pocono in Pennsylvania, has some of the lower cauline leaves lanceolate and laciniate; others oblong-ovate, simply serrate, largely subcordate contracted into a winged petiole: perhaps a hybrid with *A. diffusa*." The first taxonomic recognition of incised-leaved asters in North America was Britton's (1892) succinct description of *Aster cordifolius* (L.) var. *incisus* Britton which specified, "leaves sharply serrate, or the lower incised, none of them cordate at the base." One of the specimens cited in the description has incised leaves (Pennsylvania: Poconos, *Moser s.n.*, Aug 1832, MO2967409 [isotype]) but four others (Pennsylvania: Poconos, *Moser s.n.*, Aug 1832, NY00158757 [holotype], P00711852 [isotype], P00711853 [isotype]; New York: Westchester Co., *Bicknell s.n.*, 1891, NY001158758 [paratype]) have sharply serrate, but not incised leaves, and none includes basal or lower cauline leaves. Bicknell subsequently collected specimens with incised leaves (New York: Westchester Co., 22 Sep 1895, NY 01850007; 2 Oct 1898, NY01859965) which he labeled with new names, *A. lowrieanus* Porter var. *bicknellii* or *A. bicknellii*; both names are *nomen nudums* as they lacked descriptions. However, some of his "bicknellii" specimens lack incised leaves (New York: New York Co., 16 Oct 1898, NY01849959; Orange Co., 3 Oct 1897, NY01849963; Westchester Co., 27 Sep 1896, NY01849985) so his concept of "bicknellii" is unclear.

Prior to Britton's work, Porter (1889) described two varieties of *Aster cordifolius*: var. *laevigatus* Porter with thickish, appressed serrate, abaxially glaucous leaves and winged petioles; and var. *lanceolatus* Porter with thin, lanceolate, long acuminate cauline leaves that lack a cordate sinus. Porter (1893) elevated *Aster cordifolius* var. *laevigatus* to *A. leiophyllus* Porter, comprised of *A. leiophyllus* var. *lanceolatus* Porter and *A. leiophyllus* var. *incisus* (Britton) Porter. He included a Lackawanna Co., PA. locality for var. *incisus* but leaves of that specimen are neither incised nor sharply serrate (Pennsylvania: Lackawanna Co , *Porter s.n.*, 25 Aug 1884, PH00246390). A year later, Porter (1894) changed the specific epithet, naming *A. lowrieanus* Porter and its two varieties as above and decades later in 1946, an incised-leaved specimen was collected from Lackawanna Co., PA. (Pennsylvania: Lackawanna Co., *Glowenke 8479*, 14 Aug. 1946, PH00246608). Porter's *Aster lowrieanus* and its two varieties, var. *lanceolatus* and var. *incisus* (listed as a synonym of *Aster Lowrieanus Bicknellii* Porter), was included in the List of Pteridophyta and Spermatophyta Growing without Cultivation in Northeastern North America (Committee of the Botanical Club 1893).

In summarizing extensive cytological, morphological, and taxonomic investigations in *Aster*, Jones (1980a,b) reduced *A. lowrieanus* to *A. cordifolius* ssp. *laevigatus* A.G. Jones citing a "completely glabrous and usually somewhat glaucous" phenotype. Jones (1980b) speculated that hybridization and introgression from *A. laevis* contributed to the diagnostic traits of narrow-leaved forms. In the 1970s, Jones annotated many specimens identified as *A. lowrieanus*, *A. lowrieanus* var. *incisus*, and *A. bicknellii* to "*Aster cordifolium* L. ssp. *laevigatum* A.G. Jones stat. nov., ined. var. *lanceolatum*." Jones considered deeply incised and pinnatifid leaves to represent common developmental abnormalities as evidenced by several annotations that included comments such as, "aberrant form", "teratological form", and "not uncommon."

Nesom (1994) transferred *Aster cordifolius* and five of the named varieties to *Symphyotrichum* but without comment, he subsumed var. *incisus* into *S. cordifolium* var. *lanceolatum* (Porter) G.L. Nesom. In Flora of North America, Brouillet et al. (2006) included all *S. lowrieanum* and subspecific taxa of *S. cordifolium* in *S. cordifolium*. Citing Legault's (1986) comparison of field and greenhouse-grown plants, they stated the varieties of *S. cordifolium* "are not distinct and mostly represent phenotypic variants caused by growing conditions."

The morphology component of Legault's work included only material from Canada and neither leaf serration nor *S. lowrieanum* (including var. *incisus*) were included in the study. Moreover, diploid and tetraploid cytotypes were not morphologically distinguishable. More recently, Weakley and Southeastern Flora Team (2024) retained *S. lowrieanum* but recognized no subspecific taxa in that species or in *S. cordifolium* (var. *incisum* was not listed in the synonymy). Similarly, var. *incisum* is not in synonymy in Fernald (1950) or Weakley et al. (2013).

Morphological descriptions and identification keys in Fernald (1950), Cronquist (1980), and Weakley et al. 2013) use cordate basal and lower leaves as a diagnostic character for *Heterophylli* (Nees) Semple asters. Within the *Heterophylli* group, anthocyanic phyllary tips are diagnostic of *Symphyotrichum cordifolium* compared to green tips in *S. lowrieanum*. These floras do not mention *S. lowrieanum* var. *incisus* as a synonym but in the description of *Aster lowrieanus*, Britton and Brown (1923) state, "Races differ in leaf form and serration." Depending on the treatment consulted, specimens with cordate basal leaves could be assigned to *S. cordifolium*, specimens with shallowly cordate or tapered leaves to *S. lowrieanum*, and glabrous, tapered leaf specimens with long rhizomes to *S. shistosum* Porter. However, in modern floras and treatments, incised-leaved specimens with tapered basal leaves and those lacking basal leaves would both challenge and defy accurate identification via keys.

MATERIALS AND METHODS

Incised Leaves.—The criterion of at least one pinnatifid or deeply incised (incisions ≥ 4mm) leaf was used to compile a list of incised-leaved specimens. These leaf incisions ranged from 4–18 mm long on the short side (Fig. 1). A search of the SERNEC database of imaged specimens of *Symphyotrichum cordifolium*, including synonyms, was conducted to identify specimens with incised leaves. The search returned 7782 specimens (Fig. 2). For each specimen with incised leaves, the base of the basal leaves, if present, was categorized as cordate, rounded/truncate, or tapered as was the base of cauline leaves, the number and stem position of incised cauline leaves was tallied, and the root system, if present, was categorized as a caudex, short rhizome, long thick rhizome (>4 cm length, >3 mm diameter), or long thin rhizome (>4 cm length, ≤3 mm diameter; Fig. 1).

To compare the frequency of long rhizomes in incised and non-incised specimens, all images of *Symphyotrichum lowrieanum* in the SERNEC image database were examined. The majority of specimens had insufficient root systems to discern a caudex from a rhizome so these were not included in the analysis. The numbers of long rhizomatous and non-long rhizomatous specimens were tallied (duplicates were excluded) and the frequencies were compared between incised and non-incised-leaved specimens using Fisher's exact test of a 2 × 2 contingency table.

Cluster Analysis.—Visual inspection of the incised-leaved specimen occurrence map suggested locality aggregations in Pennsylvania and Tennessee. To test the aggregation hypothesis, an analysis for spatial clustering was conducted using SaTScan™ v10.1 software (Kulldorff & Information Management Services, Inc. 2022). The Bernoulli model in the software calculates the number of cases and controls in circular spatial windows and uses maximum likelihood to estimate the probability of exceeding an expected number of cases per window. Likelihoods and the associated probabilities were based on 9999 replications. This type of analysis is often used to test for disease clusters (Ingram et al 2018; Levin-Rector et al. 2024) and has had numerous applications in other disciplines (SaTScan™ Bibliography: https://www.satscan.org/references.html). In this application, unique occurrences of incised-leaved specimens are analogous to disease cases while typical specimens can be considered controls. Two analyses were conducted; one in which the control group was comprised of all imaged individuals of *Symphyotrichum cordifolium* (senso lato, including *S. lowrieanum*) in the part of the geographic range defined by the range of *S. lowrieanum*, yielding a sample of 1606 specimens. *Symphyotrichum cordifolium* was the appropriate control group because this was the identification on many incised specimens, many specimens originally identified as *S. lowrieanum* were later annotated to *S. cordifolium* due to the fluctuating nature of recognition of *S. lowrieanum*, and the *S. cordifolium* database was the one used to identify incised specimens. In the second analysis, *S. lowrieanum* was the control group, comprising a sample of 206 imaged specimens.

Fig. 1. Image of an incised-leaved specimen of *Symphyotrichum lowrieanum* (*Cusick 24854*) with a truncate proximal leaf, pinnatifid and deeply incised cauline leaves, and a long, narrow diameter rhizome.

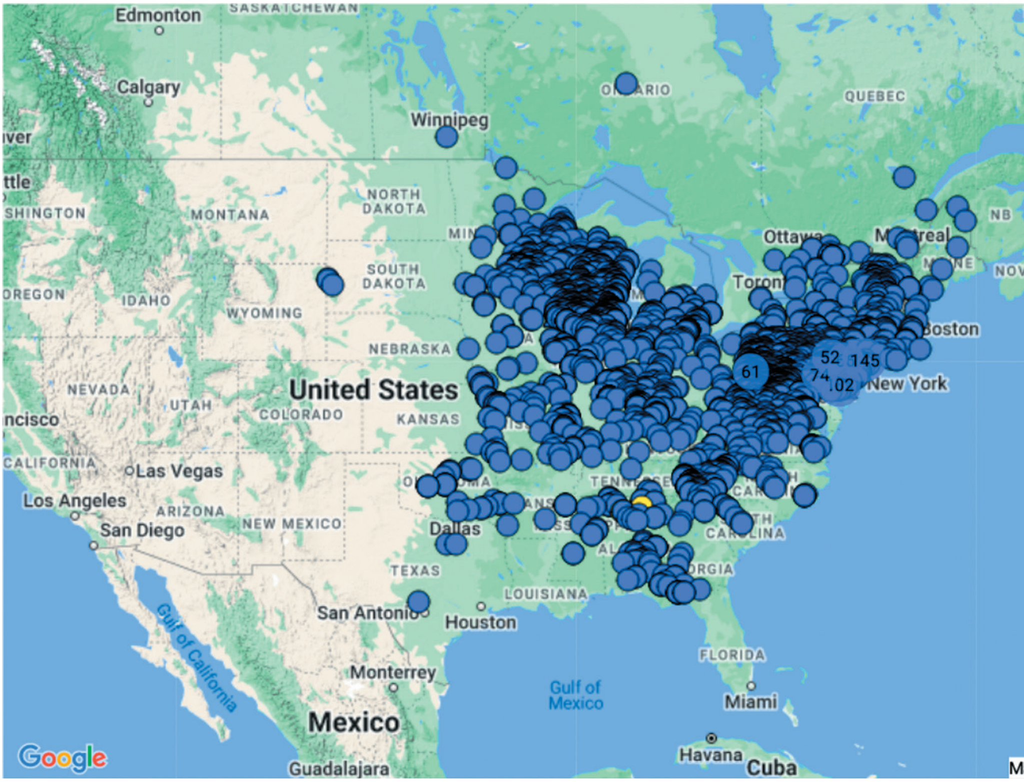

Fig. 2. Map showing collection locations of the 7782 imaged specimen of *Symphyotrichum cordifolium* (sensu lato, including *S. lowrienaum*) in the SERNEC database. Base map from Google Maps.

The geographic range of inquiry was delineated by counties with at least one *Symphyotrichum lowrieanum* specimen or one incised-leaved specimen identified as *S. cordifolium*. For each of the counties meeting these criteria, the number of non-incised specimens cataloged as either *S. cordifolium* or *S. lowrieanum* was tallied to serve as the county control group. Many specimens lack detailed location data but nearly all include the state and county. Therefore counties were used as the unit of area for cluster detection. Geographic coordinates for each county were based on the coordinates of the county seat. While the geographical range of incised specimens largely coincided with the range of *S. lowrieanum*, restricting the analysis to counties delineated in this way likely underestimates the geographic range of *S. lowrieanum* (Digital Atlas of the Virginia Flora 2024; Kentucky Plant Atlas 2024; Vascular Plants of North Carolina 2024). However, this is a more conservative approach than one that would include specimens of *S. cordifolium* from the entire geographic range of the species, an area that would add only additional counties and controls, but not cases, effectively exaggerating a cluster effect.

RESULTS

A total of 53 plants on 52 herbarium sheets had incised leaves representing 31 unique collections (specimens that differ in collection location or collection date; Table 1). The total includes 23 sheets by Levy & Walker; 20 of these were from six recently located sites in northeastern Tennessee (Table 1). Less than half (6/20) of the incised specimens had cordate basal leaves; 12 had a rounded or truncate base, and two had a tapered base. On many of the incised-leaved specimens, all cauline leaves were tapered to the petiole but some specimens had a few proximal leaves with rounded bases followed by more distal tapered leaves. Incised leaves was a characteristic of entire plants rather than single leaves. Plants meeting the criterion for incised leaves tended to have all (23/53 plants) or half or more (16/53 plants) of their leaves incised (Fig. 1). Long rhizomes were present in 18.0% (20/111) of non-incised specimens of *Symphyotrichum lowrieanum* and 77.8% (14/18) of incised specimens, a highly significant difference in frequencies (Fisher's exact P <0.0001). Plants with long rhizomes had a geographic range from northern Pennsylvania to northeastern Tennessee (Fig. 3). Narrow diameter rhizomes were present in five of the non-Tennessee and 10 of 11 of the Tennessee specimens that included rhizomes. Three specimens had thick rhizomes and three had a caudex.

On most incised-leaved specimens, basal and lower leaves had a narrow winged petiole with a slightly clasping base, a character consistent with *Symphyotrichum cordifolium* and *S. lowrieanum*. All cauline leaves below the inflorescence, except some of the most proximal on some specimens, were tapered to the base and many had acuminate tips. None of the Tennessee specimens had stem or leaf pubescence except for some specimens with sparse pubescence in the inflorescence. In the Tennessee specimens and in those viewable from images, phyllaries had narrow to wide green diamonds. Phyllary tips were often acute but some were more obtuse and others slightly acuminate but the green zone and tip characters were variable within plants and within heads. None of the Tennessee specimens had the diagnostic anthocyanic green zones of *S. cordifolium*. Ray flower color ranged from pale lilac to purple. Other than incised leaves with non-cordate leaf bases, and a tendency to long thin rhizomes, the morphology most closely fit *S. lowrieanum*. However, the tendency, especially in Tennessee populations, to long, thin rhizomes and a preference for steep shale slopes is reminiscent of the long, thin stolons and shale barren habitat of *S. schistosum* in Virginia.

Geographic Distribution and Physiography.—Asters with deeply incised or pinnatifid leaf margins were found in eight states, all in sites west of the Atlantic Coastal Plain, east of the Mississippi River, and east and south of the Ohio River (Table 1; Fig. 4). Of the 18 counties with incised-leaved specimens, 15 were located in Appalachian regions within those states except for one specimen from Maine and two specimens from New York (Appalachian Regional Commission, https://www.arc.gov/about-the-appalachian-region/). Twelve of the 18 counties in which specimens were found were located in Pennsylvania (seven counties) or Tennessee (five counties; Fig. 4)). States for which incised-leaved specimens were found represent 3299 of the total specimens and states lacking specimens had 4483 of the total specimens of *Symphyotrichum cordifolium* (sensu lato), a difference in frequency that was highly significant ($\chi^2 = 34.5$, df = 1, p <0.001).

All except the Maine and New York incised-leaved sites were located in two physiographic provinces, the Appalachian Plateaus (15 sites) and the Ridge and Valley (11 sites) and most (19/26) of these sites were from unglaciated areas. The Maine and New York specimens were from the New England physiographic province. No incised-leaved sites were from the Adirondack, Blue Ridge, Coastal Plain, or Piedmont physiographic provinces in the eastern U.S. or from physiographic provinces in more western parts of the geographic range of *Symphyotrichum cordifolium* (Central Lowland, Interior Low Plateau, Ozark Plateau, Superior Upland).

In the cluster analysis using either *Symphyotrichum cordifolium* or *S. lowrieanum* as the control group, two significant spatial clusters were detected; one comprised of the six sites in Greene, Hancock, and Hawkins counties in northeastern Tennessee (the Bays Mountain complex); the other was in a seven county region (Armstrong, Bedford, Centre, Indiana, Somerset, Warren, Washington) of the Allegheny Plateau of western Pennsylvania (Table 2).

Despite the wide geographical range of *Symphyotrichum cordifolium*, a distribution encompassing eastern Canada to the Gulf Coast and from the Atlantic Coast to the eastern edge of the Great Plains, there were instances in which unique sites for incised-leaved specimens were located in proximity to each other. In the Ridge and Valley physiographic province of northeastern Tennessee, five sites comprise the Bays Mountain complex, all associated with steep slopes underlain by shales and sandstones. Four sites, all within 3 km of each other and located within the Holston Army Ammunition Plant, are located on the north slope of Holston River Mountain (a side ridge of Bays Mountain); three of these sites are approximately 30–60 m of elevation below the ridge on steep convex lead slopes with thin soil, rock outcrops, and gnarly, old growth *Quercus*

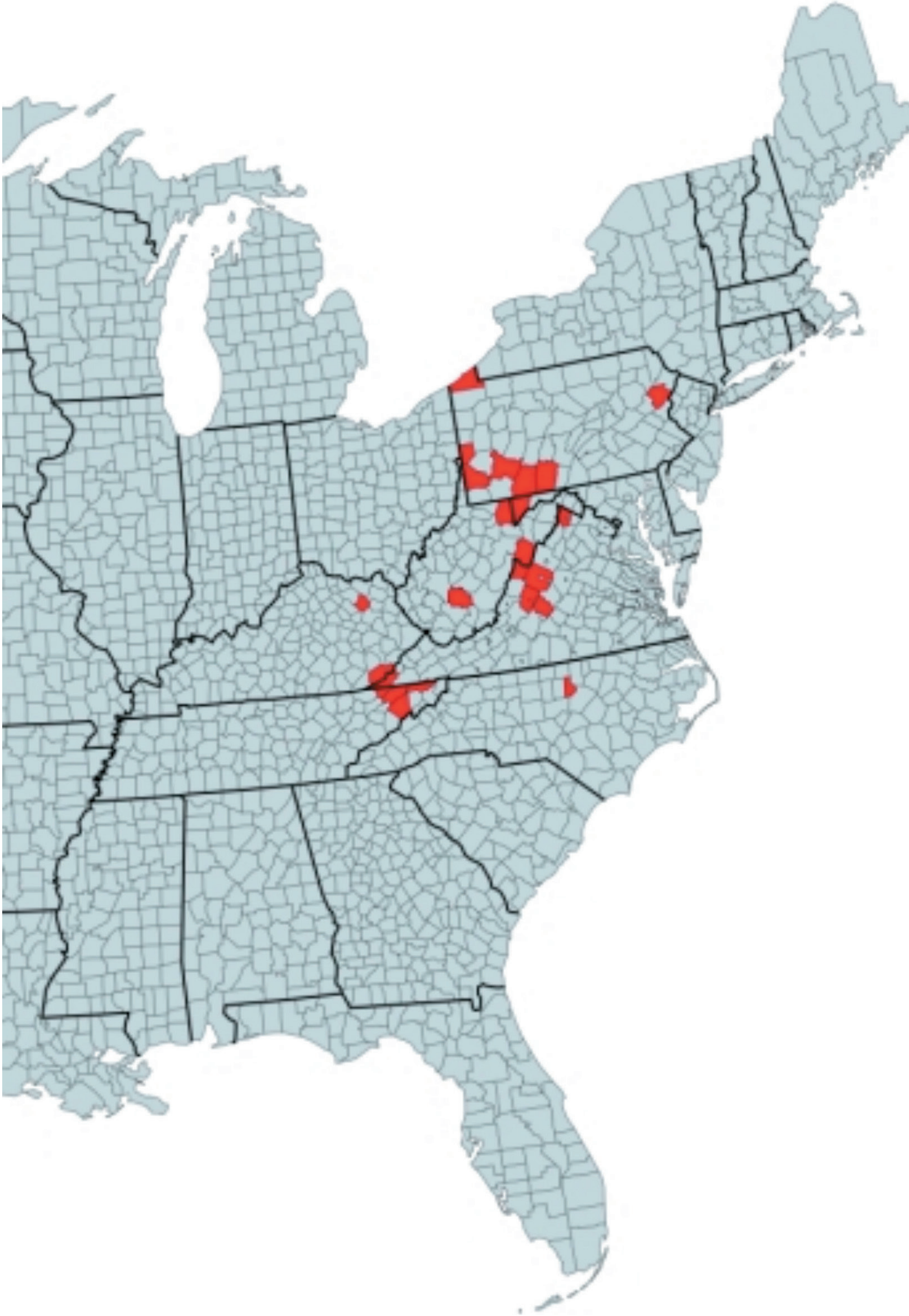

Fig. 3. Map showing counties (red) from which an imaged specimen of *Symphyotrichum lowrieanum* had long rhizomes (≥4 cm).

Table 1. List of aster specimens with incised leaves, arranged alphabetically by state and showing collection details. P.P. = physiographic province listed as; Appalachian Plateau (Allegheny or Cumberland Plateau; AP), New England (NE), or Ridge and Valley (RV).

ID	Collector(#)	Year	Catalog Number	County, State	P.P.	Habitat and Location
Symphyotrichum cordifolium						
1	DEA 7649	195?	APSU0125282	Breathitt, KY	AP	
2	Cusick 27126	1987	CM327325; NY1849888	Garrett, MD	AP	oak-maple woods; 2600 ft; SW Grantsville
3	Chamberlain & Knowlton, s.n.	1904	HUH00831646	Franklin, ME	NE	woods; 1400 ft; Stubbe Mtn.
4	Bicknell 8587a	1895	NY01850007	Westchester, NY	NE	Grassy Sprain Lake
5	Bicknell 8417	1898	NY01849965	Westchester, NY	NE	S. Bryn Mawr woods
6	Bright, s.n.	1926	CM079951	Armstrong, PA	AP	Mossgrove [*sic*]
7	Bright, s.n.	1926	CM079952	Armstrong, PA	AP	Mosgrove
8	Berkheimer 2303	1940	SLRO002449	Bedford, PA	AP	Road bank; alt. 2610 ft; 3 3/4 WNW Alum Bank
9	Berkheimer 3476	1943	CM079937	Bedford, PA	AP	wood road bank; 2600' 3 3/4 mi WNW Alum Bank
10	Berkheimer 8043, 8045	1946	CM079936;	Bedford, PA	AP	rich woods; 1140'; 1 3/4 mi NNW Breezewood
11	Berkheimer 21754	1962	PH00246609	Bedford, PA	AP	rich woods; 1300'; 2 3/8 mi SW Beans Cove Church
12	Bright, s.n.	1929	CM079889	Fayette, PA	AP	in thickets at Ohiopyle
13	Glowenke 8478	1946	PH00246608	Lackawanna, PA	RV	dry, open, oak wooded slope; 2 mi ESE Scranton
14	Britton, s.n.	1896	NY01849967	Monroe, PA	RV	Tannersville
15	Jennings & Boardman, s.n.	1942	CM079835	Somerset, PA	AP	moist slope; Pleasant Union
16	Wahl 12309	1951	PH00246604	Warren, PA	AP	along Conewango Creek, 1.5 mi SSW of Russell
17	Buker, s.n.	1959	CM079816	Warren, PA	AP	8.5 mi NE of Scandia
18	Carson, s.n.	1861	PH00246499	no county, PA		Wilmer's Woods
19	Moser, s.n.	1832	MO2967409	Poconos, PA	AP	
20	Levy & Walker 24110, 24111, 24157	2024	ETSU	Greene, TN	RV	Bear Hollow Rd., steep hill 1/4 mi NE of Rt. 70
21	Patrick, Phillipe & Wilson-Phillip 521	1977	TENN-V-0221363; TENN-V-0221363a	Grundy, TN	RV	two small clumps with variations of this tendency; Savage Gulf
22	DeSelm 02-313	2002	TENN-V-0221219	Hancock, TN	RV	Stony Fork Rd., north 1.8 mi
23	Levy & Walker 24119, 24168, 24170	2024	ETSU	Hancock, TN	RV	Stony Fork Rd., 1.75 mi N Rt 31, population near top of steep dolomite and marble knob
24	Levy & Walker 21650, 21656, 21665	2021	ETSU	Hawkins, TN	RV	Holston River Mtn., 0.5 mi E of fire tower
25	Levy & Walker 21662, 21663, 21664, 21668	2021	ETSU	Hawkins, TN	RV	Holston River Mtn., 0.1 mi W of jct of Indian Pipes Trail and River Mountain Rd.
26	Levy & Walker21537, 21541	2021	ETSU	Hawkins, TN	RV	Holston River Mtn., 30 m below western-most high point
27	Levy & Walker 23469	2023	ETSU	Hawkins, TN	RV	Holston River Mtn., steep mid-slope woods, ~0.5 mi N of Bunker 108
28	Levy & Walker 24162, 24164, 24165, 24176, 24181, 24183, 24186	2024	ETSU	Sullivan, TN	RV	Holston Mountain, mid-slope forest and roadbanks, N exposure, metapopulation of five sites, four along Big Creek Rd. between Holston Mountain Rd. and Flatwoods Rd. (11 km), one on spur ridge along Big Arm Wood Rd. of Cove Ridge
29	Wieboldt 3150	1977	VPI-V-0024953; WILLI47695	Lee, VA	RV	mesic hardwoods along Indian Creek 2 mile SW of Wheeler
30	Steele 135	1926	WVA-V-0081925	Preston, WV	AP	north of lake, vicinity of Boys Camp; 750 m
31	Cusick 24854	1985	NY1849949	Preston, WV	AP	NE Terra Alta

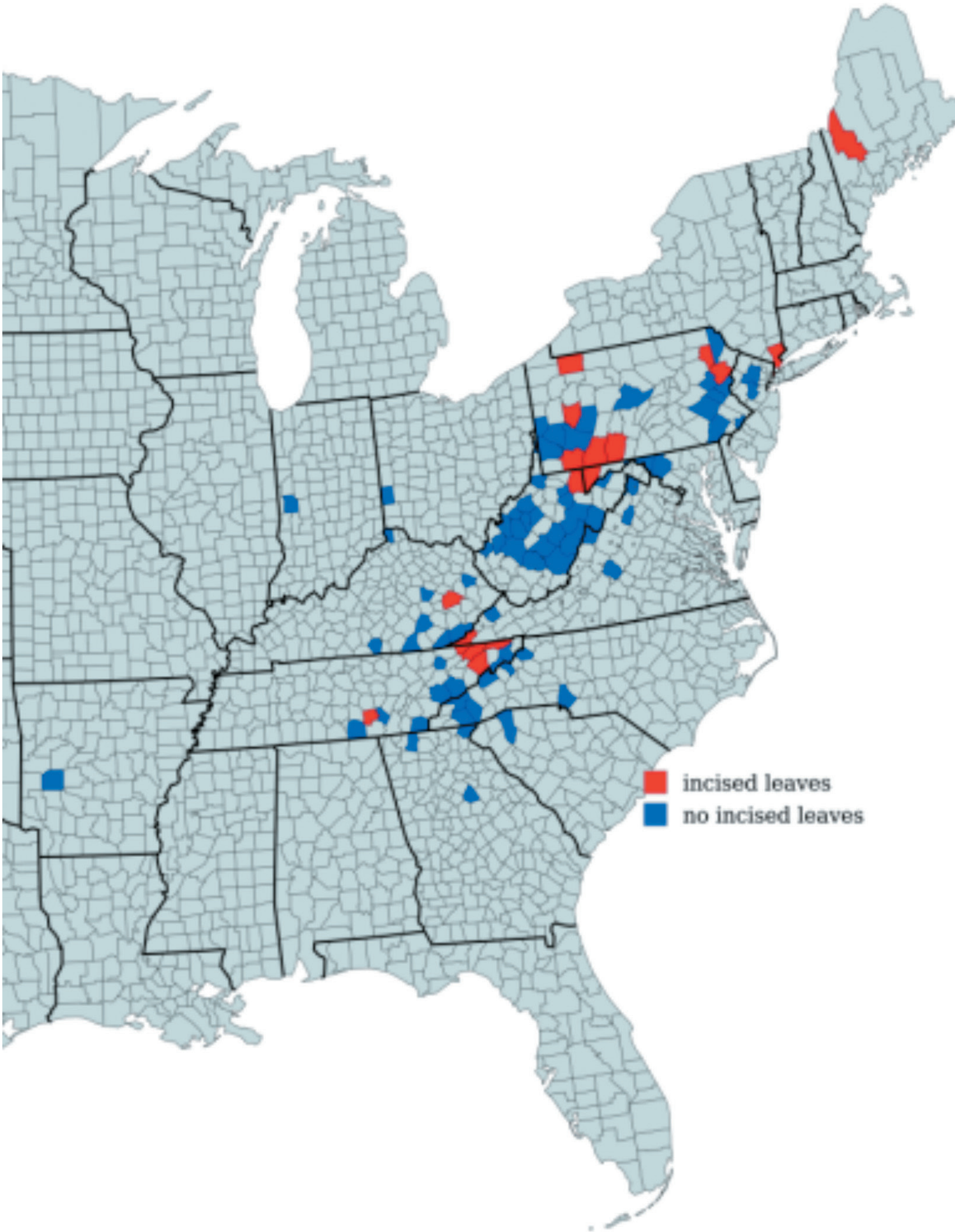

Fig. 4. Map showing counties from which an imaged specimen of *Symphyotrichum lowrieanum* was collected (blue) and counties from which an incised-leaved specimen was collected (red).

Table 2. Spatial clusters of incised-leaved *Symphyotrichum* identified as either *S. cordifolium* (*S.c.*, senso lato) or *S. lowrieanum* (*S.l.*). Control refers to the species of typical plants, N = number of specimens, Exp. = Expected, L.L. = log likelihood

Control	Cluster ID	Location	$N_{control}$	$N_{incised}$	Exp. $N_{incised}$	L.L.	p
S.c.	1	ne. TN	25	6	0.38	12.3	<0.0001
	2	w. PA	163	9	1.93	8.7	0.006
S.l.	1	ne. TN	12	6	0.88	8.8	0.009
	2	w. PA	15	9	1.62	12.1	<0.0001

Fig. 5. Leaves of *Symphyotrichum lowrieanum* showing variation from the typical form to incised-leaf forms, all from a single population on Holston Mountain, Sullivan County, Tennessee. Each leaf is from the lower to middle stem of a different plant; all were collected within 0.2 km of each other and photographed 8 November 2024.

montana Willd. that forms a partly open canopy at 600–700 m elevation (Levy et al. 2024). A fourth site occurs at mid-slope (elevation 520 m). The fifth site is near the southwest end of Bays Mountain, 33 km to the southwest where a population occurs on a steep knob at 450 m elevation. Several plants with pinnatifid leaves were found at each site as were plants with incised leaves and plants more typical of *S. lowrieanum* (Fig. 5). Typical *S. cordifolium* with broad, cordate basal leaves is common throughout the region but it is usually in more mesic concave draw slopes. Two additional sites, both over limestone and dolomite are located in this region of the Ridge and Valley; one 55 km southwest in Hancock County, TN., the other 82 km west in Lee County, VA. The site in Greene County, Tennessee, encompassing an area of ca. 0.5 km^2, supports a population of hundreds of incised-leaved plants on a steep upper north-facing slope of a shale knob (Fig. 6). At the Tennessee sites, associated species included *Solidago caesia* L. and *S. sphacelata* Raf. The Holston River Mountain sites had *Avenella*

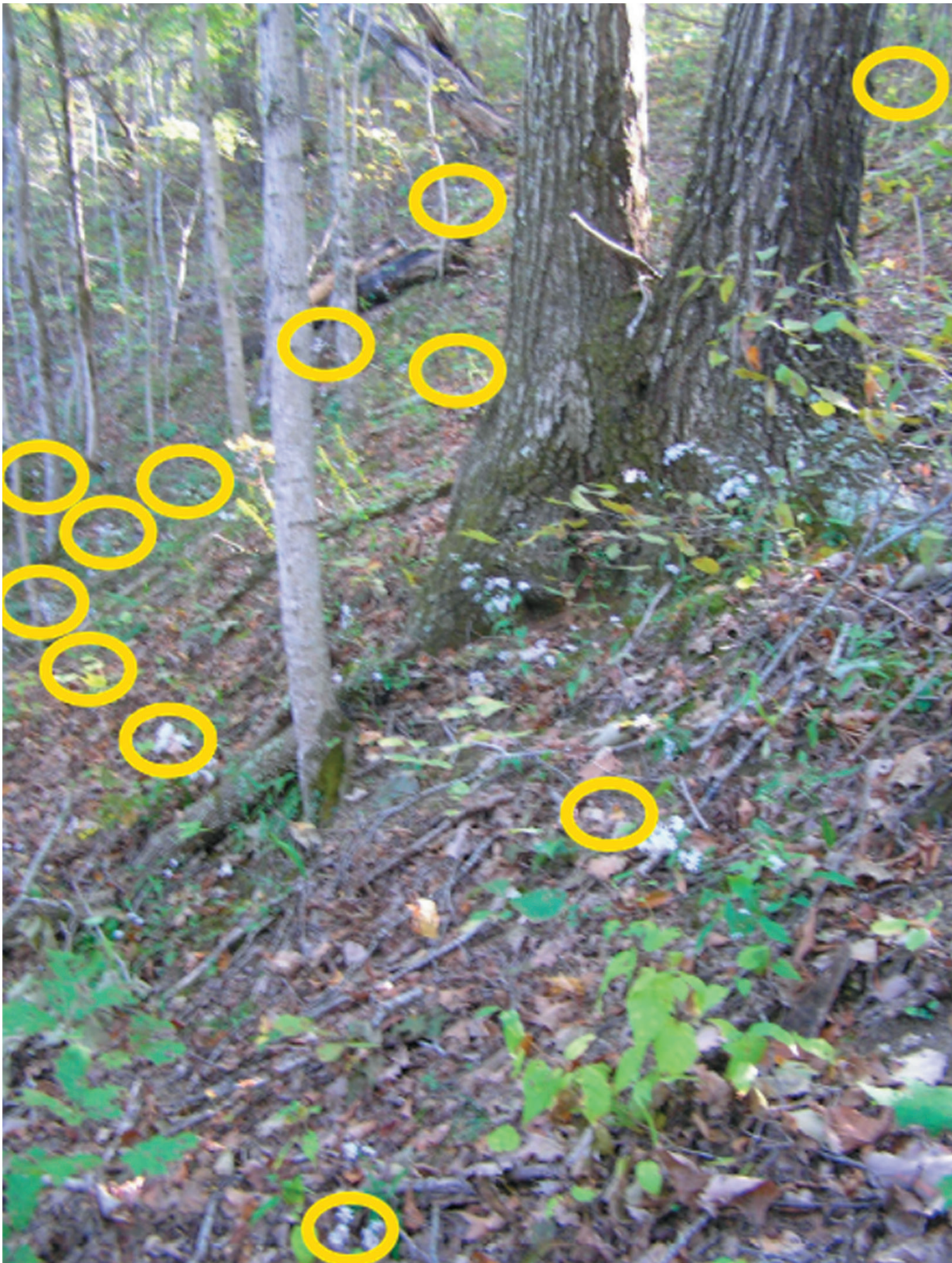

Fig. 6. Photograph of a population of *Symphyotrichum lowrieanum* dominated by incised-leaved plants in Greene County, Tennessee. In addition to plants near the large oak tree, yellow circles show locations of other patches of flowering incised-leaved plants.

flexuosa (L.) Drejer and *Penstemon brevisepalis* Pennell, two species typical of thin soils. Also in northeastern Tennessee, a metapopulation comprised of five sub-populations, each with ca. 10–40 incised-leaved individuals, occurs on the north slope of Holston Mountain, Sullivan County, Tennessee, at 670–730 m (mid-slope) elevation. The closest pair of sub-populations are <0.5 km apart and the most distant pair are ca. 11 km apart. The Bays Mountain complex and the Holston Mountain metapopulation are separated by 42 km. Other examples of sites in proximity to each other include; the two New York specimens, collected within 2 km of each other, the four sites in Bedford Co., PA located within 43 km of each other, and the two specimens each from Mosgrove, Armstrong Co , PA and Preston Co., WV (for the latter, label data is insufficient to ascertain precise locations).

Herbarium records can provide insight into temporal population persistence of the incised leaf phenotype. For example, in Bedford County, PA, in the Appalachian Plateau physiographic province, three sites occur within 35–43 km of each other at elevations of 342–792 m. Collections from these sites occurred from 1943–1962 and while not repeated from the same populations, they suggest the phenotype persists over decades. Similarly, specimens from three sites within 22 km of each other in Warren County, PA, also in the Appalachian Plateau, were collected over an eight-year span. More noteworthy from a temporal perspective are two specimens from the same vicinity in Preston County, WV collected 49 years apart. Strong direct evidence that populations are not transient was noted at the Hancock County, TN site where the population has persisted from DeSelm's collection in 2002 until a Levy & Walker collection in 2024 from the same locality. Because individual plants have not been tracked across years, the temporal stability of the incised-leaved phenotype within plants is unknown but rootstocks and seeds have been collected to address this question. However, multiple stems from a common rootstock were invariably similar in; shape of the leaf base, leaf width, degree of leaf incision, and the proportion of incised cauline leaves.

DISCUSSION

Taxonomic Implications.—Subsuming incised-leaved specimens into *Symphyotrichum cordifolium* (s.l.) or *S. lowrieanum* creates taxon ambiguity because cordate basal leaves is a key diagnostic character of *Aster* subsect. *Heterophylli* (Gray 1884; Semple & Brouillet 1980). Porter's description of *A. cordifolius* var. *lanceolatus* Porter does not refer to basal leaves but states the cauline leaves are "lance-ovate to narrowly lanceolate … the cordate sinus almost or quite filled up. …" Among the incised-leaved specimens examined, some, including many of those from Tennessee, had basal leaves with a rounded, truncate, or tapered base. A more practical difficulty is associated with species identification because cordate basal and lower cauline leaves are typically a primary diagnostic character in keys to asters. In addition to cordate basal leaves, in many typical specimens of *S. cordifolium*, the lower and middle cauline leaves are also cordate and therefore the loss of basal leaves by flowering time is usually not problematic. However, a comparable loss in incised-leaved specimens can further complicate identification. A similar problem with identification caused by unusual leaf dissection was found in *Glandularia gooddingii* (Briq.) Solbrig and as in the incised-leaved *Symphyotrichum*, those variants were found in only a subset of the geographic range (Nesom 2010). Perhaps of greater scientific importance, subsuming variants that have been observed over nearly two centuries, are temporally stable within populations, and that have physiographic and ecological associations hinders future research into the genetic basis and evolutionary trajectory of the trait, the developmental pathway leading to basally tapered, marginally incised leaves, and the underlying cause of the correlation of those two leaf characters and their association with long, thin rhizomes.

Factors Militating Against Taxonomic Recognition.—Plants with the incised leaf phenotype usually occur in mixed populations with typical plants. In northeastern Tennessee, the area with a cluster of populations and the most recent and detailed observations, incised-leaved plants may be common and can constitute a majority of the population. But invariably, typical *Symphyotrichum lowrieanum* is also present as are intermediate forms. The degree of lobing varies among plants within populations, ranging from plants with incised leaves to plants with deeply lobed leaves, and varies within and among plants, from plants with all leaves incised or lobed to plants with only a lower leaf incised or lobed. Assuming the leaf trait has a genetic component, the extreme variability among plants may reflect hybridization between differentiated taxonomic entities, hybridization among variant forms within a taxon, or an intraspecific variant with incomplete penetrance. Experimental crosses showed interspecific hybridization among several *Heterophylli* asters is possible but *S. lowrieanum* was not included in those experiments (Avers 1953a). Nevertheless, after examining morphological variation in natural populations, Avers concluded that natural hybrids were uncommon, largely because of ecological separation, and where hybrids occurred, they were most likely to backcross with parental species (Avers 1953a,b). Variability in the degree of leaf incisions within and among plants may also represent a more extreme form of the proximal to distal pattern of cauline leaf development, which in several *Heterophylli* species is accompanied by a transition from more pronounced serrations to weaker serratations or to entire leaf margins. Lastly, some specimens show asymmetry of the incision pattern which may be an indicator of developmental instability (Leamy & Klingenberg 2005).

Alternative Explanations for the Incised Phenotype.—On some specimens annotated to *Aster cordifolius* ssp. *laevigatus* var. *lanceolatus*, Jones' annotation label states the incised phenotype may be a teratological form, that is, a developmental abnormality. Dissected leaf variants presumed to be tetatologies are well known in various taxa. For example, in a compendium of teratologic forms in plants, Masters (1869) listed dozens of species with variants showing "leaf fission" in which simple leaves are replaced by dissected or laciniate leaves. Historically, teratological forms were considered non-heritable but some may also be caused by genes influencing development. Leaf dissection variants have been useful in uncovering leaf developmental pathways that can modulate leaf margins and dissection (Blein 2013; Conklin et al. 2019). For example, experimental evidence has shown that the simple leaves of *Arabidopsis thaliana* (L.) Heynh. can be converted into dissected leaves by over-expression of the *RCO* gene whose action inhibits tissue growth at leaf margin serrations. However, other ontogenic pathways can also lead to dissected leaves (Conklin et al. 2019). Alternatively, the incised phenotype may arise in different populations via recurrent mutation. Such a process should be ecologically and geographically random in which case variants would be observed sporadically throughout the range. Unless these variants are subject to environment-dependent differential selection, this explanation is unlikely because occurrences have both ecologic and geographic correlates (James et al. 2021). A final explanation to account for the occurrence pattern within and among populations posits that the incised phenotype represents a differentiated taxon that is currently experiencing secondary contact, hybridization, and introgression with related taxa. Unfortunately, a lack of fine scale resolution in molecular studies of *Symphyotrichum* renders phylogenetic evidence unattainable with current methods (E. Schilling, pers. comm.).

Factors Favoring Taxonomic Recognition.—The incised-leaved specimens share ecologic and physiographic characteristics. Ecologically, incised-leaved plants and populations are found at mid-elevations, generally from 200–800 m, in mesic to xeric oak-dominated forests. Although sometimes found on road banks, these occurrences may represent remnants of previously forested sites rather than recent colonizations. Although incised-leaved populations occur exclusively in uplands, with only a few exceptions, they are restricted to the sedimentary bedrocks of the Appalachian Plateau and Ridge and Valley physiographic provinces and are absent from the Blue Ridge. Populations comprised of many or few incised-leaved plants are not transient but can persist for decades or possibly centuries.

The lack of taxonomic recognition for an obvious morphological variant, one that most likely has a genetic basis and whose populations can persist over long periods of time in mixed assemblages with related taxa, would inhibit future research. In the absence of taxonomic recognition, locating herbarium specimens with the variant phenotype requires examination of thousands of herbarium specimens from taxa with complex taxonomic histories. Recognition may also engender species descriptions and identification keys accounting for the novel features of incised-leaved plants. If taxonomic recognition is afforded, the question of taxonomic rank for a variant most often found in mixture with typical forms is more difficult. These variants may represent an ecotype but in current practice, the rank of forma is rarely applied or used. Therefore, to avoid obscurity for a variant prior to more in-depth study, the most prudent approach may be to resurrect Porter's variety and refer to these plants as:

Symphyotrichum lowrieanum (L.) G.L. Nesom var. **incisum** (Porter ex Britton) F. Levy, **comb. nov.** ≡ *Aster cordifolius* L. var. *incisus* Britton, Bull. Torrey Bot. Club 19(7):224. 1892. *Aster leiophyllus* Porter var. *incisus* (Britton) Porter, Bull. Torrey Bot. Club 20(6): 255. 1893. *Aster lowrieanus* Porter var. *incisus* (Britton) Porter, Bull. Torrey Bot. Club 21(3):121. 1894. Type: U.S.A. Pennsylvania: mons Pocono, Aug 1832, *C.J. Moser, s.n.* (holotype: NY00158757; isotypes: MO2967409, P00711852, P00711853).

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