STUDIES IN THE VASCULAR FLORA OF THE SOUTHEASTERN UNITED STATES. VIII

Alan S. Weakley, Derick B. Poindexter, Bruce A. Sorrie, Eric A. Ungberg, Scott G. Ward

Southeastern Flora Project, UNC-CH Herbarium (NCU), North Carolina Botanical Garden University of North Carolina at Chapel Hill, C.B. 3280, Chapel Hill, North Carolina 27599-3280, U.S.A. weakley@unc.edu, dpoindex@live.unc.edu, basorrie@gmail.com, ungberg@gmail.com, sgward@ad.unc.edu

James W. Horn

Department of Biological Sciences, Florida Gulf Coast University 10501 FGCU Boulevard South, Fort Myers, Florida 33965-6565, U.S.A. jhorn@fgcu.edu

Wesley M. Knapp

NatureServe, 2550 South Clark Street, Suite 930, Arlington, Virginia 22202, U.S.A. & Southeastern Flora Project, UNC-CH Herbarium (NCU), North Carolina Botanical Garden University of North Carolina at Chapel Hill, C.B. 3280, Chapel Hill, North Carolina 27599-3280, U.S.A. Wesley_Knapp@NatureServe.org

Steven P. Grund

Western Pennsylvania Conservancy 800 Waterfront Drive, Pittsburgh, Pennsylvania 15222, U.S.A. sgrund@paconserve.org

ABSTRACT

As part of ongoing efforts to understand, document, and conserve the flora of the southeastern United States, we make new combinations to accord with our generic taxonomy, name a new hybrid, re-recognize a species relegated to synonymy in recent decades, lectotypify and generally clarify nomenclatural issues in several genera, clarify taxonomy and distributions of species, and report important new and current distribution records. In Doellingeria (Asteraceae), we clarify the taxonomy and distribution of D. sericocarpoides and D. umbellata in the region. In Trilisa, we summarize and clarify the taxonomy of the genus Trilisa (Asteraceae), name a new hybrid in the genus, and present a new key to the taxa in the genus. Species delimitation in Stillingia (Euphorbiaceae) has been controversial and unsettled in the region, and we examine the confused taxonomy and nomenclature of the genus Stillingia (Euphorbiaceae) in the southeastern United States, re-recognizing a species used by J.K. Small, but with an expanded circumscription and a clarification of various nomenclatural issues. We examine typification of Desmodium dillenii (Fabaceae) and its application to our modern understanding of the circumscription of taxa, recommending it be considered a junior synonym of Desmodium glabellum. In Juncus, we assign a lectotype for Juncus anthelatus, clarifying its application. In Primulaceae, we discuss the delineation of genera in Lysimachieae, and take a middle path regarding lumping/splitting, supporting the recognition of traditional and monophyletic segregates Trientalis, Steironema, Anagallis, Centunculus, while treating Lysimachia in a moderately broad sense, including Glaux and multiple subclades; in order to implement this taxonomy in the southeastern United states, we make a single new combination in Steironema. We also discuss generic circumscription in Selaginellaceae, and argue for the recognition at genus rank of six major clades, monophyletic, ancient, and morphologically recognizable; in order to apply this taxonomy in the southeastern United States, we make five new combinations in Bryodesma, Gymnogynum, and Stachygynandrum. Finally, we report important new records of locally, regionally, or globally rare species in North Carolina: Helanthium tenellum, Chenopodium berlandieri var. macrocalycium, Carex barrattii, Carex vestita, Eleocharis compressa var. compressa, Rhynchospora compressa, Rhynchospora sulcata, and Croton willdenowii.

RESUMEN

Como parte de los esfuerzos en curso para comprender, documentar y conservar la flora del sureste de los Estados Unidos, hacemos nuevas combinaciones acordes con nuestra propuesta taxonóomica, nombramos un nuevo híbrido, reconocemos una especie relegada a la sinonimia en las últimas décadas, lectotipificamos y, en general, aclaramos cuestiones nomenclaturales en varios géneros, la taxonomía y la distribución de las especies, e informamos importantes registros de distribución nuevos y actuales. En *Doellingeria* (Asteraceae), aclaramos la taxonomía y distribución de *D. sericocarpoides* y *D. umbellata* en la región. En *Trilisa*, resumimos y aclaramos la taxonomía del género *Trilisa* (Asteraceae), nombramos un nuevo híbrido en el género y presentamos una nueva clave para los taxones que incluye. La

J. Bot. Res. Inst. Texas 16(2): 377-418. 2022 https://doi.org/10.17348/jbrit.v16.i2.1257 OPEN CACCESS This article has been licensed as Open Access by the author(s) and publisher. This version supersedes any other version with conflicting usage rights. delimitación de especies en *Stillingia* (Euphorbiaceae) ha sido controvertida e inestable en la región, y examinamos la confusa taxonomía y nomenclatura del género *Stillingia* (Euphorbiaceae) en el sureste de los Estados Unidos, reconociendo una especie utilizada por J.K. Small, pero con una circunscripción ampliada y una aclaración de varios problemas nomenclaturales. Examinamos la tipificación de *Desmodium dillenii* (Fabaceae) y su aplicación asegun nuestra comprensión moderna de la circunscripción de taxones, recomendando que se considere un sinónimo menor de *Desmodium glabellum*. En *Juncus*, seleccionamos un lectotipo para *Juncus anthelatus*, fijando su aplicación. En Primulaceae, discutimos la delineación de géneros en Lysimachieae, y tomamos un camino intermedio con respecto a la agrupación / división, apoyando el reconocimiento de segregaciones tradicionales y monofiléticas *Trientalis, Steironema, Anagallis, Centunculus*, mientras tratamos *Lysimachia* en un sentido moderadamente amplio, incluyendo *Glaux* y múltiples subclados. Para implementar esta taxonomía en el sureste de los Estados Unidos, hacemos una sola combinación nueva en *Steironema*. También discutimos la circunscripción genérica en Selaginellaceae, y argumentamos a favor del reconocimiento en el rango de género de seis clados principales, monofiléticos, antiguos y morfológicamente reconocibles; para aplicar esta taxonomía: En el sureste de los Estados Unidos, hacemos combinaciones en *Bryodesma, Gymnogynum y Stachygynandrum*. Finalmente, reportamos nuevos registros importantes de especies raras a nivel local, regional o global en Carolina del Norte: *Helanthium tenellum, Chenopodium berlandieri var. macrocalycium, Carex barrattii, Carex vestita, Eleocharis compressa var. compressa, Rhynchospora compressa, Rhynchospora sulcata y Croton willdenowii.*

INTRODUCTION

As part of ongoing work on the *Flora of the Southeastern United States* (Weakley & Southeastern Flora Team 2022) and related projects, as well as for general floristic, conservation, and scientific work in eastern North America, it is necessary or desirable to document taxonomic and nomenclatural changes and significant distributional records. In some cases, new combinations are needed to accurately reflect current taxonomic understanding. Some of these are changes in rank, whereas others are generic transfers to apply new (or old) generic concepts to taxa that do not have corresponding available names at specific or infraspecific levels. We have also addressed various nomenclatural issues and clarified characters and identification of difficult groups in the regional flora.

We here present an eighth volume of such changes, contributed by eight authors. It follows similar conventions and philosophical approaches as the earlier volumes in the series (Weakley et al. 2011, 2017, 2018a, 2018b, 2019, 2020, 2021). Primary authorship of the sections in this paper is as follows (and is also indicated at the beginning of each section): *Doellingeria* (BAS), *Trilisa* (SGW), *Stillingia* (JWH), *Desmodium* (SPG), *Juncus* (WPG & DBP), *Steironema* (ASW & DBP), *Bryodesma*, *Gymnogynum*, and *Stachygynandrum* (ASW), and *Helanthium*, *Chenopodium*, *Carex*, *Eleocharis*, *Rhynchospora*, and *Croton* (EAU).

ASTERACEAE

DOELLINGERIA: Doellingeria sericocarpoides (Asteraceae) revisited

Primary author: Bruce A. Sorrie

Discrepancies exist between the distribution of *Doellingeria sericocarpoides* Small as depicted in the latest version of Kartesz (2020) and in Semple et al. (1991). A revised map (Fig. 1), depicts the species as occurring strictly on the Coastal Plain from south-central North Carolina to northern Florida, central Alabama, central Mississippi, and southeastern Louisiana; thence west of the Mississippi River in central and northern Louisiana, eastern Texas, southeastern Oklahoma, and southern and central Arkansas.

In contrast with Fig. 1, Kartesz (2020) and Semple et al. (1991) show records of *D. sericocarpoides* from southern New York, New Jersey, the District of Columbia, southeastern Virginia, northern Alabama, northern Mississippi, and northeastern Arkansas—areas that lie within the Piedmont or Coastal Plain. The records from New Jersey, D.C., and Virginia are apparently based on specimens assigned by Fernald (1940) and Semple et al. (1991) to *Aster umbellatus* var. *brevisquamus* Fernald. The records from northern portions of Alabama, Mississippi, and Arkansas may represent *D. umbellata* (Mill.) Nees var. *umbellata*, based on visual inspection of specimen images at SERNEC (2021) and in-hand specimens at NCU. In this paper I review the identity of these specimens and assess the taxonomic status of *D. sericocarpoides* vis-a-vis *D. umbellata*. The status of *A. umbellatus* var. *brevisquamus* is also assessed, based on the relatively few specimens available for review.

Specimens of *D. sericocarpoides*, *D. umbellata*, and *A. umbellatus* var. *brevisquamus* from sixteen states were examined in hand at NCU. Additional specimens from Arkansas (at UARK) were measured by Theo Witsell. Measurements were made of several characters reported to be informative by previous investigators,



Fis. 1. Documented county distributions of *Doellingeria sericocarpoides* and *D. umbellata* south of and including the states of Delaware, Maryland, West Virginia, Kentucky, Arkansas, and Texas.

notably Semple et al. (1991, their Table 2): leaf length, leaf width, number of ray florets, involucre length, phyllary pubescence, and achene pubescence. Selected online specimens (SERNEC 2021) that were originally determined as *A. umbellatus* var. *brevisquamus* were measured for leaf length and width and number of ray florets. Phyllary and achene pubescence was assessed via three character states: glabrate, sparse, and moderate. Glabrate examples of achenes possessed some hairs on ribs but none on achene faces. Involucre length was measured from the base of the lowest bract to the summit of the longest bract. Whenever possible, at least two leaves were measured for length and width, including the petiole. Only leaves from the middle portion of the stem were selected, in all cases below inflorescence branches. Ray florets were counted only when obvious on specimen sheets; no counts were made when ray lamina were not clearly visible. Specimens assessed in this paper are cited below.

Informative Characters—Historical

Small (1898) provided the original description of *D. sericocarpoides*, which states that the leaves are "elliptic to lance-elliptic," leaves "narrowed into short petioles or nearly sessile," "involucres about 4 mm high," "bracts

sparingly pubescent," and "achenes almost glabrous." Curiously, he restricted his name and description to trans-Mississippi River plants.

Fernald (1940) used the name *Aster umbellatus* var. *latifolius* A. Gray for the plants that grow "on the Coastal Plain, from Florida to Texas, north to North Carolina and Arkansas." He stated that these plants had short and broad leaves relative to var. *umbellatus*, and longer involucres. In the same paper, he describes as new *A. umbellatus* var. *brevisquamus* for plants collected in the District of Columbia and southeastern Virginia. These plants had leaves lanceolate-elliptic to narrowly ovate, and very short involucres (2.5–4 mm).

Cronquist (1947) was apparently the first to call attention to the smaller number of ray and disc florets in *D. sericocarpoides* versus *D. umbellata*. Coupled with the former's "usually broader leaves" and "larger and firmer involuces," he recommended treating the two as full species. Another useful character mentioned by Cronquist was achene pubescence, which he rated as intermediate between the glabrous achenes of *D. infirma* (Michx.) Greene and the hairy achenes of *D. umbellata*.

Cronquist (1980) recognized *D. umbellata* and *D. sericocarpoides* and relied on floret number and achene pubescence in his key to these taxa. Cronquist's synonymy suggests that *Aster umbellatus* var. *brevisquamus* is a misapplied synonym of *D. sericocarpoides*. He therefore appears to agree with Fernald (1940, 1950) that plants found north of North Carolina are all members of nominate *D. umbellata* and that none belong to the southern *D. sericocarpoides*.

Semple et al. (1991) published a multivariate analysis of the *Aster umbellatus* complex, based on data gathered from 11 morphological characters (their Table 2). Their key emphasizes achene published a multivariate analysis of the *Aster umbellatus* complex, based on data gathered from 11 morphological characters (their Table 2). Their key emphasizes achene published a multivariate of ray florets, and midvein of phyllaries swollen or not. Their mapped distribution of *A. sericocarpoides* includes localities in New Jersey, the District of Columbia, and southeastern Virginia (including the holotype of *A. umbellatus* var. *brevisquamus*, which they treat as a synonym of *A. sericocarpoides*), northwestern Alabama, and northeastern Arkansas (their Fig. 15). This represents a much-expanded range for *A. sericocarpoides*. Interestingly, a second cited specimen from southeastern Virginia, originally determined as var. *brevisquamus*, was deemed by Semple at al. to be var. *umbellatus*. [Note that the authors state that the range of *A. sericocarpoides* includes the "outer edge of the Piedmont" in Augusta, Georgia, and in South Carolina and North Carolina; the area in question is the Sandhills Physiographic Region, which actually is the *inner edge of the Coastal Plain*.]

In FNA, Semple and Chmielewski (2006) recognized *D. umbellata* and *D. sericocarpoides* as separate species, and treated *Aster umbellatus* var. *brevisquamus* as a synonym of the latter. They map *D. sericocarpoides* north to Virginia, Delaware, Maryland, and New Jersey.

Informative Characters—This Paper

Of the morphological characters that I assessed, leaf length versus width, number of ray florets, and achene pubescence (Table 1) were the most informative. Involucre length overlapped almost completely between *D. umbellata* and *D. sericocarpoides* and therefore was not considered further. Phyllary pubescence proved to be a weak discriminator, with the majority of specimens having glabrous or glabrate phyllaries regardless of taxon.

KEY TO DOELLINGERIA SERICOCARPOIDES AND D. UMBELLATA

1. Ray florets 3–5 per head, mean 4; midstem leaves relatively short and broad, length 4.0–11.4 cm, width 1.4–3.6 cm, ratio mean 3.0; achene pubescence glabrate to sparse ______ D. sericocarpoides

 1. Ray florets 5–12 per head, mean 8; midstem leaves relatively long and narrow, length 5.0–15.0 cm, width 0.9–2.9 cm, ratio mean 5.1; achene pubescence sparse to moderate ______ D. umbellata

The key will identify correctly the vast majority of plants, provided that multiple characters are used. A small number of long- and narrow-leaved plants in Arkansas and elsewhere, but which possess only 3–5 ray florets, are considered to be aberrant *D. sericocarpoides*. Such plants are rare and local as far as is known. Similarly, certain short- and broad-leaved plants of the Northeastern states and from uplands west of the Appalachians, but which possess 6 or more ray florets, are considered to be aberrant *D. umbellata*.

Alleged Northern D. sericocarpoides

New York—Werier (2017) searched for specimens allegedly reported for this state, but failed to uncover any *D. sericocarpoides*. He placed it on the Excluded List.

Character	D. sericocarpoides	D. umbellata	Aster umbellatus var. brevisquamus	
leaf length	4.0–11.4 cm; n=51	5.0–15.0 cm; n=65	3.3-8.3 cm; n=11	
leaf width	1.4–3.6 cm; n=51	0.9–2.9 cm; n=65	1.0–2.5 cm; n=11	
mean leaf length/width	3.0	5.1	3.7	
number ray florets achene pubescence involucre length	3–5; mean 4.0; n=24 glabrate to sparse 3.0–5.5 mm; mean 4.6; n=32	5–12; mean 8.2; n=33 sparse to moderate 3.0–6.0 mm; mean 4.5; n=30	6–8; mean 7.1; n=8 no data 3.0–5.8 mm; mean 4.5; n=16	

TABLE 1. Characters used to separate Doellingeria sericocarpoides from D. umbellata.

New Jersey—I located specimens at NY from three counties that were annotated by Semple as *D. sericocarpoides*: Atlantic Co, *Pennell 8141*; Monmouth Co., *Mackenzie s.n*; Ocean Co., *MacElwee s.n.* Measurements of leaf length vs. width indicate that the first two are *D. umbellata*, while the third is equivocal vs. *D. sericocarpoides*. A fourth New Jersey specimen (Morris Co., *Griscom s.n.* CHRB) is in fact *D. umbellata* as determined by me.

Pennsylvania—Fernald (1940) stated that specimens of very locally distributed plants were *Aster humilis* Willd., a short-statured and "broad-leaved phase" of *A. umbellatus*. Cronquist's (1980) synonymy suggests that *Aster umbellatus* var. *humilis* is misapplied as a synonym of *D. sericocarpoides*. Finally, Semple and Chmielewski (2006) treated *Aster humilis* as a synonym of *Doellingeria infirma*.

Maryland—Specimens from Allegany and Prince George's counties, both at NY, are in fact *D. infirma* as confirmed by me.

Virginia—Fernald (1940) described *A. umbellatus* var. *brevisquamus* for plants collected in the District of Columbia and southeastern Virginia. Specimens of var. *brevisquamus* that I have examined from this region, including those determined by Fernald, show relatively long but relatively broad leaf blades and an intermediate number of ray florets (Table 1). These intermediate values suggest possible introgression, but the small number of specimens available for study make any taxonomic conclusions unclear at this time.

Alabama—Semple et al. (1991) map both *D. sericocarpoides* and *D. umbellata* in Marion County. The only specimen at SERNEC is *Kral 36975* (VDB), which displays the narrow leaf blade and attenuate leaf tip of *D. umbellata*.

Alleged Southern D. umbellata

Alabama—The Alabama Plant Atlas (2021) and Kartesz (2020) map *D. umbellata* in a number of counties in the southern Coastal Plain portion of the state. My research indicates that *D. umbellata* occurs only in Cherokee, Clay, and Cleburne counties at the southern end of the Appalachian Mountains, plus Marion County in the upper Coastal Plain (6.7 miles E of Hamilton, *Kral 36975* VDB). Specimens from Bibb and Pickens counties and southward are *D. sericocarpoides*.

Arkansas—Semple et al. (1991) map it in Lawrence County, but I have not found a specimen to corroborate the record. Specimens at UARK from Drew, Jefferson, Hot Spring, and Miller counties exhibit relatively long and narrow leaves and are suggestive of *D. umbellata*; however, the small number of ray florets places them with *D. sericocarpoides*.

Florida, Georgia, and Mississippi—Kartesz (2020) maps it in a total of 5 counties in the East Gulf Coastal Plain; all are actually *D. sericocarpoides*.

Mississippi—Kartesz (2020) maps it in Marshall and Lee counties in the northern portion of the Coastal Plain. I have not seen specimens from either county. However, *Temple 3936* (NCU) from Prentiss Co.; *Ray, Jr.* 7448 (FSU) from Tishomingo Co.; and *McDaniel 33934* (FSU) from Winston Co. fall cleanly into *D. umbellata*. Thus, *D. umbellata* occurs in the northeastern corner of the state in the transition zone between the Coastal Plain and the Interior Plateau Region.

North and South Carolina—Kartesz (2020) maps *D. umbellata* in Moore, Chesterfield, and Richland counties in the Sandhills Region; all are actually *D. sericocarpoides*.

To summarize, Doellingeria sericocarpoides is restricted to the southern Coastal Plain Province, whereas

D. umbellata occurs northward and westward in the Piedmont, Mountains, and northern Coastal Plain (Fig. 1). The taxonomic status of "intermediate" plants named as *Aster umbellatus* var. *brevisquamus*, is unresolved and needs additional investigation, ideally with more material than appears to be available.

Specimens examined in this study:

Doellingeria sericocarpoides

ALABAMA. Baldwin Co.: Orzell & Bridges 12338 (NCU); Harper 4141 (NCU). Mobile Co.: Shinners 28973 (NCU); Lelong 4786.1 (NCU). ARKANSAS. Garland Co.: Demaree 52858 (NCU). Georgia. Thomas Co.: Faircloth 6264 (NCU); Godfrey 70110 (NCU). LOUISIANA. De Soto Par.: Thomas 73665 (NCU). Washington Par.: Allen & Vincent 2736 (NCU); Thieret 32654 (NCU). MISSISSIPPI. Forrest Co.: Rogers 4923-C (NCU). Prentiss Co.: Temple 3936 (NCU). Stone Co.: Temple 4483 (NCU). NORTH CAROLINA. Cumberland Co.: Sorrie & Carter 6002 (GH, NCU); Ahles 33527 (NCU). Harnett Co.: Radford 8768 (NCU). Hoke Co.: Ahles 33814 (NCU). Lee Co.: Stewart s.n. (NCU). Montgomery Co.: Radford 14661 (NCU). Richmond Co.: Gupton 2139 (NCU). Scotland Co.: Ahles 36918 (NCU). OKLAHOMA. McCurtain Co.: Waterfall 17033 (NCU). TEXAS. Anderson Co.: Orzell & Bridges 8636 (NCU).

Doellingeria umbellata

GEORGIA. Towns Co.: Jones, Jr. 870 (NCU). KENTUCKY. Calloway Co.: Athey 2134 (NCU). Harlan Co.: Levy s.n. (NCU). MARYLAND. Allegany Co.: Downs 4896 (NCU). Garrett Co.: Reveal et al. 5037 (NCU); Downs 7363 (NCU). Prince George's Co.: Reed 27303 (NCU). MISSISSIPPI. Tishomingo Co.: Ray, Jr. 7448 (FSU). NORTH CAROLINA. Alleghany Co.: Poindexter 08-1256 (NCU); Radford 41017 (NCU). Ashe Co.: Jenkins 359 (NCU); Radford 41199 (NCU). Cherokee Co.: Radford 17498 (NCU). Clay Co.: Radford 16141 (NCU). Haywood Co.: Harbison s.n. (NCU). Henderson Co.: Freeman 57808 (NCU). Jackson Co.: Semple 11593 (NCU); Bozeman 7958 (NCU). Macon Co.: Biltmore 111b (NCU); Coker et al. s.n. (NCU). Madison Co.: Ahles 46321 (NCU). Mitchell Co.: Ahles 49830 (NCU). Swain Co.: Barksdale s.n. (NCU). Warren Co.: LeGrand s.n. (NCU). Yancey Co.: McLeod 1671 (NCU). TENNESSEE. Cumberland Co.: Rodgers & Brock 100 (NCU). Grundy Co.: Clark 1184 (NCU). Johnson Co.: Barclay s.n. (NCU). VIRGINIA. Botetourt Co.: Freer 12277 (NCU). Dinwiddie Co.: Harvill 21017 (NCU). Henrico Co.: Harvill 17624 (NCU). WEST VIRGINIA. Grant Co.: Downs 7253 (NCU). Mineral Co.: Downs 7474 (NCU). Randolph Co.: Clarkson 648 (NCU).

TRILISA: *Trilisa* ×*subpaniculata*, a rare new hybrid (Asteraceae: subtribe Liatrinae) from peninsular Florida, U.S.A., with a revised key and identification notes for *Trilisa* in the southeastern United States. Primary author: Scott G. Ward

A new, rare hybrid is described from Sarasota County, Florida, U.S.A. *Trilisa ×subpaniculata* hyb. nov. occurs in Florida dry prairie in close proximity to its two parents, *Trilisa paniculata* and *Trilisa subtropicana*. It is strongly intermediate in vegetative and reproductive morphologies, with a more compact, thinly corymbiform inflorescence than *T. subtropicana*, but lacking the villoso-hirsute stems of *T. paniculata*. Furthermore, *T. ×subpaniculata* has glandular peduncles (differing from the glabrous peduncles of *T. subtropicana*), and has thinner, glabrous stem leaves with rounded-acute apices (differing from the hirsute, deltoid leaves of *T. paniculata* with acute apices). It is unknown if hybrid individuals have been previously overlooked, although it seems probable that this hybrid is uncommon to rare across its range. Additional surveys are needed for this hybrid taxon across central and southern Florida, where wide overlap exists between its two parent species. Further discussion is made on *Trilisa* identification, with a revised dichotomous key and pictures provided for all four taxa in the southeastern United States.

Trilisa subtropicana (Delaney, N. Bissett, & Weidenh.) E.L. Bridges & Orzell was recently elevated to species status (Orzell & Bridges 2017) after years of taxonomic shifting. Initially recognized as distinct by J.K. Small as early as 1933 (Small 1933), this species went unnamed until more than 60 years later, when published as *Carphephorus subtropicanus* (Delaney et al. 1999). Since then, the species garnered support as a variety of the more widespread *Carphephorus odoratissimus* (J.F. Gmel.) H. Hebert (Wunderlin & Hansen 2001; Orzell & Bridges 2002), until its recent re-recognition at species level as *Trilisa subtropicana* within a more narrowly circumscribed genus (Orzell & Bridges 2017). Compared to *Carphephorus, Trilisa* and *Litrisa* have smaller heads (involucres 3.5–6 mm high), fewer phyllaries per head (5–12), lack recaptacular paleae, and have leaves either bearing punctate glands in *Litrisa* or without any shining resin dots in *Trilisa odoratissima* (J.F. Gmel.) Cass., as well as some overlap in morphological characters, *T. subtropicana* has been recognized at varietal level (Wunderlin & Hansen 2001), with a few intermediate specimens being cited in the initial varietal combination (Wunderlin & Hansen 2001). Despite a few intermediate specimens, numerous distinct *T. subtropicana* collections have been observed throughout central and south Florida, with other distinct specimens being

observed as far north as Citrus county (Chassahowitzka Wildlife Management Area, personal observation) and apparently far southern Levy County (*L.J. Majure 8478*, FLAS; specimen not observed). Additional supporting specimens have been observed as far north as Polk County (*Corogin SB215*, FLAS), and Sumter County (*Baltzell 2746*, FLAS). Specifically, *T. subtropicana* has been shown to be distinct from *T. odoratissima* based on a mostly defined geographic separation in central and southern Florida, an absence of coumarin or vanilla odor, shorter and thinner basal leaves (less than 15 cm long; less than 5 cm wide), stem leaves entire, more elliptic, and tightly clasping the stem, involucres more densely viscid, inflorescences broader than tall, and the primary inflorescence branches diverging at a wider, more arcuate angle (Delaney et al. 1999; Orzell & Bridges 2002; Orzell & Bridges 2017; Figs. 2, 3).

Despite the attention to *T. odoratissima* and *T. subtropicana*, little has been paid to the third species of *Trilisa*, *T. paniculata*, which differs greatly from its congeners. On 4 September 2021, a small population of *Trilisa* was discovered growing in dry prairie habitat in Sarasota County, FL which exhibited intermediate characteristics between *Trilisa paniculata* and *Trilisa subtropicana* (Figs. 4, 5, 6). Distinguishing between these two taxa is generally straight-forward, given the highly reduced upper stem leaves and widely spreading corymbiform inflorescences of *T. subtropicana* (Fig. 7) compared to the conspicuously villoso-hirsute stems, densely arranged upper stem leaves, and paniculate inflorescences of *T. paniculata* (Fig. 8). Although the potential hybrids were in early flower, they clearly showed characteristics of both parents. A return visit one month later was made to locate more hybrid plants at anthesis. Flowering plants were collected from both parents and their hybrid, with hybrids showing strong similarities in stem, leaf, and involucre vestiture with *Trilisa subtropicana* and an intermediate thyrsoid/paniculate inflorescence and stem leaf shape somewhat similar to *Trilisa paniculata*. Some individuals observed also appeared to represent possible back-crossed individuals of F1 hybrids with *T. subtropicana*, although no genetic analyses were performed for this study.

After examining digital voucher specimens of both parent taxa, it appears that this hybrid has not been documented prior to its discovery in Sarasota County, Florida. Both parental species were listed as common to occasional in Myakka River State Park in Huffman (1998), but no evidence was suggested for possible introgression between the two taxa. Despite considerable efforts on the *Trilisa subtropicana/T. odoratissima* complex in Florida (Delaney et al. 1999; Orzell & Bridges 2002; Orzell & Bridges 2017), and research into hybrid genera in the Liatrinae (Schilling 2011), no mention has been made of hybrids between *Trilisa species*. Additional surveys are needed to search for hybrids across the sympatric range of *T. subtropicana* and *T. paniculata*, and further surveys for potential hybrids between the much more widespread and overlapping *Trilisa odoratissima* and *Trilisa paniculata* would probably increase our overall knowledge of hybridization within *Trilisa* in the Southeastern Coastal Plain. Descriptions below are based upon limited numbers of plants from the only observed population.

Trilisa ×subpaniculata S.G. Ward, hyb. nov. TYPE: U.S.A. FLORIDA. [Sarasota Co.]: Myakka River State Park, N of Pine Level Gate, growing along *Serenoa repens* patches in dry prairie north of SR72 (Pine Level Gate) with *Andropogon cabanisii*, *Quercus minima, Lyonia lucida, Hypericum tenuifolium, Vaccinium darrowii*, and *Aristida beyrichiana*. 27.220615, -82.282145. 04 Oct 2021, S.G. Ward 1417 [HOLOTYPE: NCU, Fig. 6].

Diagnosis.—Plants (40–)60–100 cm. Stems glabrous proximally, viscid/stipitate-glandular distally (within inflorescence). Basal leaves 1–10 per culm, 4.5–12.5 cm long, 0.5–3.0 cm wide, oblanceolate, spatulate, elliptic, margins subentire to minutely crenate. Proximal stem leaves (immediately above basal rosette) thinly oblanceolate, medial and distal leaves gradually reduced in length. Distal stem leaves elliptic to thinly deltoid, tapering apically, minutely clasping stem, stem leaf apices subacute to rounded-acute. Mid to upper stem leaves entire to minutely crenate. Heads arranged in compact corymbiform cymes. Inflorescence subpaniculate to nearly thyrsiform, typically longer than wide, columnar to narrowly spreading. Inflorescence axis, peduncles and involucres moderately to densely viscid or stipitate glandular (inflorescence branches more glandular distally). Phyllaries acute, subacute, or rounded apically. Pappus of numerous capillary bristles. *Comparisons.*—*Trilisa* ×*subpaniculata* differs from *T. paniculata* by the absence of villoso-hirsute stems, the

presence of a subpaniculate, subthyrsiform inflorescence, and more rounded-acute stem leaf apices. It differs

383



Fi6. 2. *Trilisa odoratissima* (basionym *Carphephorus odoratissimus*) [M.T. Strong 2836, USF]. This taxon differs from *Trilisa subtropicana* in having longer (>15 cm) and wider (>5 cm) basal leaves, wider stem leaves that are conspicuously toothed along the margins, inflorescences with a greater length-width ratio, and secondary branches of the inflorescence that extend from the main axis at a lesser (more ascending) angle (10–20°)



Fig. 3. Comparison of *Trilisa subtropicana* and *Trilisa odoratissima*. Pictures of *T. subtropicana* were taken in Sarasota County, FL on 04 October 2021; pictures of *T. odoratissima* were taken in Brevard County, FL on 22 August 2021. **A.** Stem leaves of *T. odoratissima*. **B.** Stem leaves of *T. subtropicana*. **C.** Inflorescence of *T. odoratissima*. **D.** Inflorescence of *T. subtropicana* (often more widely divergent). Photos by Scott G. Ward.



Fig. 4. **A.-C.** Inflorescence and flowering heads of *Trilisa ×subpaniculata* (*Trilisa subtropicana x Trilisa paniculata*). Note the more tightly ascending secondary inflorescence branching (A, B) and viscid inflorescence axis and pedicels (B, C). **D.** Terminal portion of *Trilisa subtropicana* cyme. Note lack of viscid glands below phyllaries. Photos taken on 04 October 2021 by Scott G. Ward.



FIG. 5. Side-by-side comparison of *Trilisa paniculata* (TP), *Trilisa subtropicana* (TS), and their hybrid, *Trilisa ×subpaniculata* (TH). **A.** Proximal to medial stem leaves. **B.** Cyme development, note central flowering heads developing prior to lateral flowering heads (most evident here in *T. subtropicana*). **C.** Flowering heads and pedicels. **D.** Corymbiform (TS), subpaniculiform (TH), and paniculiform (TP) cyme (inflorescence) structure in *Trilisa*. Photos taken on 04 October 2021 by Scott G. Ward.



Fig. 6. Trilisa xsubpaniculata hyb. nov. holotype, collected 04 October 2021 in Florida dry prairie in Sarasota County, FL. Photo by Shanna Oberreiter.



of North Caroling

UNIVERSITY OF NORTH CAROLINA HERBARIUM

ASTERACEAE

Trilisa subtropicana (J.F. Gmelin) Cassini

Myakka River State Park. North of Pine Level Gate. Growing along Serenoa patches in dry prairie north of SR72 with Andropogon cabanisii, Quercus minima, Lyonia lucida, Hypericimu tenufolium, Vaccinium darrowii, Aristida beyrichiana.

27.220615, -82.282145

Sarasota County, FL

mm/dd/yyyy: 10/4/2021

Scott G. Ward 1418

Fig. 7. Trilisa subtropicana (Delaney, N. Bissett, & Weidenh.) E.L. Bridges & Orzell [S.G. Ward 1418] from Sarasota County, FL. Photo by Shanna Oberreiter.



from its other parent, *T. subtropicana*, by the presence of viscid inflorescence branches and peduncles, and having a more thinly diverging, more subthyrsiform inflorescence. Plants are glabrous vegetatively like *T. subtropicana*, with an inflorescence similar to *T. paniculata*. Basal leaves are similar to both parents, with mostly entire margins and occasional minor toothing. Stem leaves of *T. subpaniculata* are similar in shape to *T. paniculata*, but they have a greater l:w ratio, are completely glabrous, and are less densely arranged (although proximal stem leaves can still be densely arranged; Fig. 5a). Conversely, mid-upper stem leaves are slightly more densely arranged than *T. subtropicana*, and are generally less oblanceolate. The stem leaves and inflorescence bracts of *T. subtropicana* and *T. ×subpaniculata* are both more noticeably reduced compared to the only moderately reduced upper leaves and bracts of *T. paniculata*. All descriptions of the peduncles of *Trilisa subtropicana* and *Trilisa odoratissima* (basionym *Carphephorus odoratissimus*) are specified as glabrous (Delaney et al. 1999; Orzell & Bridges 2002; Nesom 2006; Orzell & Bridges 2017), which differs from the viscid/stipitate-glandular peduncles of *T. ×subpaniculata* and *T. paniculata*.

Ecology.—Trilisa × subpaniculata occurs in Florida dry prairie in Sarasota County, Florida, a treeless, hyperseasonal habitat, dominated by Aristida beyrichiana Trin. & Rupr, Serenoa repens (W. Bartram) Small, Quercus minima (Sarg.) Small, and Ilex glabra (L.) A. Gray in addition to numerous Ericaceae, Cyperaceae, Poaceae, Asteraceae, and Fabaceae. Historically, this habitat experienced frequent fire-return-intervals (1-3 years), with relatively high levels of micro-scale vascular plant diversity (upwards of 40+ taxa per m², see Orzell & Bridges 2006), and extreme hyperseasonality (i.e. dry to wet season conditions). Trilisa ×subtropicana was discovered in a large dry prairie unit in the late wet-season following an earlier 2021 prescribed fire (presumably spring), one of multiple prescribed fires that occur in the park on an annual basis. It is likely that, like many of its herbaceous associates in this community, Trilisa ×subtropicana requires frequent fire to persist. Mesic and mesic-wet species commonly associated with Trilisa xsubtropicana include Asclepias pedicellata Walter, Andropogon cabanisii Hack., Andropogon capillipes Nash, Andropogon longiberbis Hack., Carphephorus corymbosus (Nutt.) Torrey & A. Gray, Crotalaria rotundifolia J.F. Gmel., Eleocharis baldwinii (Torr.) Chapm, Eupatorium mohrii Greene, Euthamia caroliniana (L.) Greene ex Porter & Britton, Ilex glabra, Lilium catesbyi Walter, Lyonia fruticosa (Michx.) G.S. Torr., Lyonia lucida (Lam.) K. Koch, Pityopsis tracyi (Small) Small, Rhynchospora ciliaris (Michx.) C. Mohr, Rhynchospora fascicularis (Michx.) Vahl, Schizachyrium stoloniferum Nash, Serenoa repens, Sorghastrum secundum (Elliott) Nash, Trilisa paniculata, Trilisa subtropicana, Utricularia subulata L., and Xyris elliottii Chapm.

KEY TO TRILISA

Modified primarily from on Orzell and Bridges (2017) and Weakley and Southeastern Flora Team (2022):

 Stem densely spreading-pubescent (villoso-hirsute) throughout; upper stem leaves congested, only slightly reduced in size distally; inflorescence columnar or thyrsiform, flowering heads arranged in thyrsiform cymes; leaves (0.5–)1–3(–4) cm wide Trilisa paniculata
1. Stem not densely spreading-pubescent, instead glabrous or glabrescent; upper stems leaves spaced or congested, significantly reduced in size distally; inflorescence widely or narrowly corymbiform (or rarely narrowly sub-paniculate as in <i>T.</i> × <i>subpaniculata</i>); leaves 1–6(–11) cm wide.
2. Inflorescence axis and peduncles moderately to densely viscid or glandular; inflorescence narrowly sub-paniculate
or corymbiform; [rare, c. to s. FL] Trilisa ×subpaniculata
2. Inflorescence axis and peduncles glabrous or glabrescent (only the involucres viscid); inflorescence moderately to
widely spreading or corymbiform; [widespread in the Southeastern Coastal Plain, including c. and s. FL].
3. Fresh plants with very slight or no odor of coumarin/vanilla; basal leaves < 15 cm long and < 4 cm wide; midstem
leaves narrowly elliptic, tightly clasping the stem, the margins entire; inflorescence 0.5–1 \times as tall as broad, the
primary inflorescence branches diverging from the main axis at a 30–45° angle; heads mostly with 10–14 flowers;
[of c. peninsular FL south to s. FL]Trilisa subtropicana
3. Fresh plants with a strong odor of coumarin/vanilla; basal leaves usually > 15 cm long and > 5 cm wide; midstem
leaves broadly elliptic, the apex flared away from the stem, the margins often shallowly toothed; inflorescence
1.5-3x as tall as broad, the primary inflorescence branches diverging from the main axis at a 10–20° angle; heads
mostly with 7–10 flowers; [of c. peninsular FL northwards to se. NC and westwards to e. LA]Trilisa odoratissima

EUPHORBIACEAE

STILLINGIA: On Stillingia tenuis, the narrow-leaved Queen's Delight of southern Florida Primary author: James W. Horn

The genus *Stillingia* Garden ex L. (Euphorbiaceae) exhibits greater morphological and ecological variation in Florida than elsewhere in its range in eastern North America. The patterns of variation present have posed significant challenges for biological and taxonomic interpretation. John Kunkel Small (1869–1938) was probably the first botanist who had extensive, field-based knowledge of *Stillingia* diversity throughout the state, and he ultimately recognized five *Stillingia* species from Florida (1933). In addition to the well-known *S. aquatica* Chapm. and *S. sylvatica* L., he recognized three additional species—*S. angustifolia* (Müll. Arg.) Engelm. ex Watson, *S. spathulata* (Müll. Arg.) Small, and *S. tenuis* Small—which he considered to be endemic (or nearly so, in the case of *S. spathulata*) to peninsular Florida. Excepting Rogers (1951), all three of Small's peninsular *Stillingia* species have seldom been recognized at any taxonomic rank in subsequent, major taxonomic or floristic treatments, which include these three entities within a polymorphic *S. sylvatica* (e.g., Wunderlin & Hansen 2011; Huft 2016).

Rogers (1951) interpreted the substantial variability he observed in *Stillingia* populations of peninsular Florida as being the result of introgressive hybridization between the two species he recognized from eastern North America. The first of these species, *S. sylvatica* (subsp. *sylvatica*, *sensu* Rogers 1951) is a perennial herb with a strongly thickened taproot and has seeds that lack a distinctively differentiated hilum (Fig. 9A). In Florida, *S. sylvatica* is most frequent in dry-mesic to xeric, pine-dominated natural communities that historically experienced frequent fire, particularly *Pinus palustris*-dominated sandhills and *Pinus densa*-dominated scrubby flatwoods. *Stillingia aquatica*, a small, single-stemmed shrub with a candelabra-like crown consisting of 1–20(–30) branches, inhabits depression marshes in pinelands and open wetlands dominated by *Taxodium ascendens*. *Stillingia aquatica* further contrasts with *S. sylvatica* in having a dense, inverted cone-shaped system of lateral roots borne along a short taproot (Rogers 2021) and in its inverted U-shaped hilum (Fig. 9A).

Rogers (1951) also recognized a third entity, *Stillingia sylvatica* subsp. *tenuis* (Small) D.J. Rogers, endemic to pine rocklands of Miami-Dade Co., Florida, which he hypothesized to be of hybrid origin. He differentiated this subspecies from *S. sylvatica* subsp. *sylvatica* by its narrower, linear leaves and, putatively, by an acuminate-caudate apex to the median bract subtending each carpellate subunit of the inflorescence (which is reduced to a single female flower in *Stillingia*). In considering *S. sylvatica* subsp. *tenuis* to be a pine rockland endemic, Rogers apparently overlooked morphologically similar plants from south Florida outside of Miami-Dade Co., which Small treated as *S. angustifolia*. Small, in contrast to Rogers, thought two narrow-leaved *Stillingia* entities occurred in south Florida (aside from *S. aquatica*): 1) the more widespread, herbaceous *S. angustifolia* and 2) *S. tenuis*, which he characterized as an apparently unbranched, small shrub with red-pigmented inflorescences, inhabiting "everglades" (Small 1905). Because of its woody habit, Small (1905, 1933) thought *S. tenuis* was more similar to *S. aquatica*, rather than to *S. sylvatica*. These discrepancies motivated my field-based investigation to find and study populations of plants consistent with Small's concepts of *S. angustifolia* and *S. tenuis* and to ascertain their relationships with *S. sylvatica* and *S. aquatica*.

The results of my research support the reinstatement of *Stillingia tenuis* as a valid species, but with an expanded circumscription that includes plants that Small (1903, 1933) treated as *S. angustifolia*. According to this new interpretation, *S. tenuis* is endemic to Peninsular Florida and primarily distributed in southern Florida. *Stillingia tenuis* is closely related to *S. sylvatica*, from which it is strongly differentiated by ecological niche preferences, leaf shape, and, to a lesser degree, by the shape of the bract that subtends the carpellate subunits of the inflorescence. To analyze leaf shape within *S. tenuis*, I test whether leaf shape is significantly different across 10 populations using the leaf blade length-to-width ratio (L/W) as a proxy for leaf shape. Further, I test whether leaf L/W is significantly different between *S. sylvatica* and *S. tenuis*. I also clarify the lectotypification of the basionyms of two of the *Stillingia* names that Small adopted in his floras (1903, 1933), provide synonymies for these names, and identification notes.



Fi6. 9. *Stillingia tenuis* Small and comparisons of seed morphology among *Stillingia* species present in Florida (photos by J.W. Horn). **A.** Seeds of the three *Stillingia* species indigenous to Florida. Top row, dorsal surface; bottom row, ventral surface. *Stillingia aquatica* (L), *S. tenuis* (Mid.), *S. sylvatica* (R). Note the horseshoe-shaped hilum that distinguishes *S. aquatica*. Scale bar = 2 mm. **B.** Inflorescence in male phase, with fruits at base; Charlotte Co., Florida. **C.** Lectotype specimen (*Small & Wilson 1580*; NY 00148783); image courtesy of the C.V. Starr Virtual Herbarium of the New York Botanical Garden, http://sweetgum.nybg.org/science/vh/. **D.** Below-ground stem caudex (woody rhizome) bearing four, basally woody, aerial axes and a strongly thickened taproot system; Miami-Dade Co., Florida.

METHODS

In *Stillingia sylvatica* and its segregates, the substantial variability in leaf shape and size that exists both within and between individuals in a population (Huft 2016) has hindered a better understanding of species boundaries. Herbarium specimens, typically representing only one individual from a population, with fixed developmental information, and sometimes with just minimal ecological data, are not fully informative of these holistic biological features. On account of this, one can easily gain the impression in examining herbarium specimens of *S. sylvatica* and its segregates from peninsular Florida that leaf shape and size vary continuously, without any apparent pattern.

In examining many plants in the field, in addition to herbarium specimens, it is clear that heteroblasty accounts for a substantial amount of the variation in leaf shape (and absolute dimension) in *Stillingia sylvatica* and its segregates. Heteroblasty is evident both among leaves on a given shoot, where proximal leaves are much smaller, particularly on the initial axis (module) and also between leaves of successive modular branches. In plants that I herein consider to be *S. tenuis*, the leaves of the midstem to distal end of a shoot module are often increasingly longer and proportionately as narrow or narrower on successive modular branches. In *S. sylvatica*, the shape and size of the mid- to distal leaves on the first-order modular branches (*S. sylvatica* plants are rarely branched to more than one order) nearly always contrasts with those of the initial axis, but without a consistent pattern among individuals (although there is a tendency for branch leaves to be shorter and proportionately narrower). Hence, in using leaf blade morphology to investigate *Stillingia* taxonomy, care must be taken to compare developmentally equivalent leaves. To examine leaf shape, I use the leaf blade length-to-width ratio (L/W), which Shi et al. (2020), using the reciprocal width/length ratio, found to be a good proxy for leaf shape in closely related species.

Because leaf shape is both an important characteristic for distinguishing Stillingia tenuis from S. sylvatica and is also highly variable among individuals in a population, I first chose to investigate this trait at the population level in S. tenuis, since within-population rages of L/W are high in this species (Fig. 10). Therefore, I tested whether population-level L/W mean values were homogenous across the range of S. tenuis, originating from the same underlying distribution of values. I selected ten sites (Table 2) spanning the core range of S. tenuis, each containing a population of at least 20 individuals. Because the leaves of Stillingia individuals are only comparable if they are from developmentally equivalent parts of the plant, I measured one leaf from the mid- to distal zone of a first-order modular branch of each plant to ensure morphological consistency of the data. I measured leaves on the plants in the field. Next, I looked for statistically significant differences in the mean values of L/W between S. sylvatica and S. tenuis. The data for S. tenuis in this test is a subset of a pooling of the population data just mentioned (n_{obs} = 403; excludes measurements from sites 3 and 8, see Table 2), because the means of two populations were identified in a post hoc Games-Howell test as being significantly different. I collected the L/W data for S. sylvatica individuals from peninsular Florida counties from both plants in the field as well as from measurements made from digital images of herbarium specimens using ImageJ (v1.53k; Schneider et al. 2012) image analysis software. I measured one leaf from the mid- to distal zone of a first-order modular branch per plant (n_{obs} = 144). I used specimen images from the following herbaria: ARCH, DUKE, FLAS, FSU, FTG, NCU, NEON-ASU, NY, PH, PIHG, UCF, USF, VDB.

I conducted all statistical analyses using R Statistical Software (v4.2.0; R Core Team 2021). To test the assumptions of a normal distribution and homogeneity of variances for L/W for the ten *Stillingia tenuis* populations and the *S. sylvatica* and *S. tenuis* datasets, I performed a Shapiro-Wilk test on each of the data partitions to assess their goodness of fit to a normal distribution and conducted Bartlett's test on each of the full datasets. Neither of the two assumptions was met by any of these data. However, the distributions of L/W values for each of the samples compared in the two tests all had similar, right-skewed shapes. Hence, I used a Welch one-way ANOVA to test the null hypothesis of equality of the L/W means from the ten *S. tenuis* are equal. Both tests adjust for heterogeneity of variance. Even though the assumption of a normal distribution of sample values is violated in these data, the tests are appropriate choices because they are not highly sensitive to





Fi6. 10. Boxplot of the leaf blade length/width ratio (L/W) for 10 populations of *Stillingia tenuis* from southern Florida. The localities of the site numbers and summary statistics for each population are detailed in Table 2. The median value of L/W for each population is given below each site number. The means of L/W across the 10 populations differ significantly (*Welch's F*(9, 140.6) = 2.91, *p* = 0.0035). A *post hoc* test of pairwise comparisons indicates a significant difference in the mean of L/W means exists only between sites 3 and 8 (*p* = 0.023).

deviations from this assumption when the sample distributions are similar in shape (McDonald 2014). In addition to Welch's one-way ANOVA, I conducted a *post hoc* Games-Howell test using the package rstatix (v0.7.0; Kassambara 2021) to identify significantly different, pairwise comparisons among the ten *S. tenuis* populations.

STATISTICAL RESULTS

There was a significant difference in the means of L/W (Table 2) among the ten populations of *Stillingia tenuis* (*Welch's F*(9, 140.6) = 2.91, p = 0.0035). The *post hoc* Games-Howell test showed that means of L/W were significantly different (p = 0.023) only between Site 3 (Babcock/Webb WMA: Yucca Pens) and Site 8 (Big Cypress NP: Wagon Wheel Rd.). All other pairwise comparisons (n = 44) were not significant.

The mean L/W of Stillingia sylvatica was 4.21 (SD = 1.47), whereas the mean L/W of S. tenuis was 13.00

Site #	Site name	County	iNaturalist obs.	n _{obs}	Mean L/W (SD)
1	Myakka State Forest	Sarasota	80679083	58	12.4 (3.66)
2	Babcock/Webb WMA: Tuckers Grade	Charlotte	50721430	40	11.8 (3.90)
3	Babcock/Webb WMA: Yucca Pens	Charlotte	21056410	35	11.6 (3.52)
4	Estero Bay Preserve SP	Lee	20735896	52	12.1 (3.38)
5	Picayune Strand SF: North	Collier	81624438	21	13.5 (3.79)
6	Picayune Strand SF: South	Collier	119342923	93	14.0 (4.87)
7	Big Cypress NP: Bear Island	Collier	118107078	91	13.3 (3.98)
8	Big Cypress NP: Wagon Wheel Rd.	Collier	80047460	42	14.9 (4.59)
9	Big Cypress NP: Florida Trail	Collier	80429886	24	12.5 (5.69)
10	Larry & Penny Thompson Park	Miami-Dade	120736491	24	13.9 (4.08)

TABLE 2. List of ten sites from southern Florida for population-level measurements of *Stillingia tenuis* leaves, associated iNaturalist observations, and summary statistics. GPS coordinates for each site and images of representative plants are provided in the associated iNaturalist observation. The iNaturalist observations may be retrieved by appending the observation number after the final backslash of the following URL: https://www.inaturalist.org/observations/

(SD = 4.23). This difference in means of L/W between the two species was highly significant (*Welch's t*(544.76) = -36.145, $p = 2.2 \times 10^{-16}$, 95% C.I. = [-9.30, -8.34]).

Notes on the lectotypification of basionyms of Stillingia angustifolia and S. spathulata

The following facts bear on two of the names adopted by Small (1903, 1933), *Stillingia angustifolia* (Müll. Arg.) Engelm. ex Watson and *Stillingia spathulata* (Müll. Arg.) Small. Rogers (1951) clearly intended to typify the basionyms of these names, *Stillingia sylvatica* var. *angustifolia* Müll. Arg. and *Stillingia sylvatica* var. *spathulata* Müll. Arg., and designated type specimens from the suite of original material that Müller Argoviensis (1866) cited in his protologues for these names. Rogers (1951) designated the types as follows:

Stillingia sylvatica α. spathulata Muell. Arg. in DC. Prodr. 15(2):1158. 1866. (T.: Bosc s.n.) Stillingia sylvatica γ. angustifolia Muell. Arg. loc. cit. 1866. (T.: Mitchell s.n.)

Because lectotype designations prior to 1990 do not need to specify a conserving institution (Art. 9.22; Turland et al. 2018) and the designated types are present at G-DC as unicate specimens with no known duplicates at other herbaria, Rogers (1951) effectively lectotypified these names. Subsequently, Athiê-Souza et al. (2016) apparently overlooked Rogers' typifications and provided superfluous lectotypifications for these two names.

Stillingia angustifolia (Müll. Arg.) Engelm. ex Watson, Proc. Amer. Acad. Arts 18:154. 1883. Stillingia sylvatica var. angustifolia Müll. Arg., in DC. Prodr. 15(2):1158. 1866. Type: U.S.A. FLORIDA: Orientale, Lat. 29° 20['], 1822, Mitchill s.n. (LECTO-TYPE, designated by Rogers 1951 as "Mitchell s.n.": G-DC G00319646, internet image!) [= Stillingia sylvatica Linnaeus (1767: 126)].

Rogers (1951) misspelled the surname of the collector, Samuel Latham Mitchill (1764–1831). However, because Rogers designated types for Müller Argoviensis' names solely from the original material, the correspondence between the two surnames (and Rogers' intent) is clear (Art. 9.2; Turland et al. 2018). The lectotype specimen is from peninsular Florida at a latitude that intersects Levy, Marion, and Volusia counties. Plants of *Stillingia sylvatica* from northern peninsular Florida—especially many collections from Levy Co. that have rather narrow leaves—closely resemble the lectotype. However, Small's concept of *S. angustifolia* is neither morphologically nor geographically consistent with the lectotype.

Stillingia spathulata (Müll. Arg.) Small, Fl. S.E. U.S. (1903: 704). Stillingia sylvatica var. spathulata Müll. Arg., in DC. Prodr. 15(2):1158. 1866. Type: U.S.A. CAROLINA: locality unknown, without date, Bosc s.n. (LECTOTYPE, designated by Rogers 1951: G-DC G00319748, internet image!) [= Stillingia sylvatica Linnaeus (1767: 126)].

The lectotype specimen (*Bosc s.n.*) consists of a shoot with mid- to distal leaves that are elliptical to slightly obovate in shape and ca. 2× as long as broad. It is quite similar to the lectotype of *Stillingia sylvatica* L. (*Garden s.n.*, Herb. Linn. No. 1147.1 [LINN, online image!]). Both specimens were likely collected from the vicinity of

Charleston, South Carolina, since Alexander Garden (1730–1791) resided in Charleston (Denny 1948) and Louis-Augustin Guillaume Bosc (1759–1828) visited Charleston and made extensive collections there (Brendel 1879). The morphotype of *S. sylvatica* that is typical of the Carolinas closely resembles both lectotype specimens. Consequently, *S. spathulata* should unquestionably be synonymized under *S. sylvatica*, and the type *Bosc s.n.* is incongruent with Small's concept of *S. spathulata* in both morphology and geographic range.

Plants Small considered to be typical of *S. spathulata* are represented by a *S. sylvatica* morphotype that is common in northern and central peninsular Florida. These plants have oblanceolate to widely obovate leaves and often have stems and, to a lesser degree, leaves (and rarely inflorescences) that are suffused with a redcrimson pigment. Plants of *S. sylvatica* of the Carolinas typically lack red pigmentation and have leaves that are regularly elliptical to slightly obovate. Plants of *Stillingia sylvatica* in peninsular Florida are much more variable with regard to leaf shape than those of the Carolinas.

Congruent with this observation, peninsular Florida populations of *S. sylvatica* sometimes have individuals with leaf shapes typical of plants of the Carolinas mixed with plants that correspond well to Small's concept of *S. spathulata*. Small (1903, 1933) also contrasted his concept of *S. spathulata* with *S. sylvatica* on the bases of capsule diameter and seed length, although Rogers (1951) thought these traits were of limited to no taxonomic utility in *Stillingia*. Further, plants of *S. sylvatica* throughout its range are ecologically similar in occupying dry-mesic to xeric, fire-maintained pinelands on acidic soils. For these reasons, Weakley and Southeastern Flora Team (2022) included plants corresponding to Small's concept of *S. spathulata* within *S. sylvatica*.

Stillingia tenuis is a distinct species

Stillingia tenuis Small, Bull. New York Bot. Gard. 3:429. 1905. (Fig. 9). Type: U.S.A. FLORIDA. Miami-Dade Co.: in everglades between Homestead and Camp Jackson, 4–11 May 1904, Small & Wilson 1580 (LECTOTYPE, designated by Athiê-Souza et al. 2016: NY00148783, internet image!; ISOLECTOTYPES: NY00148782, internet image!; US00096661, internet image!).

Stillingia tenuis is here recognized as distinct from *S. aquatica* and *S. sylvatica* on the basis of both morphology and ecology. The circumscription adopted here differs from that of Small (1905, 1933) and that of Rogers (1951) (of this entity at the rank of subspecies), as it also includes plants that Small regarded as *S. angustifolia*. Small's *S. angustifolia* is conceptually equivalent to *Stillingia* sp. 1 in Weakley (2020) and Weakley and Southeastern Flora Team (2022); hence plants previously keyed to this provisional name should now be identified as *S. tenuis*. *Stillingia tenuis* is endemic to southern Peninsular Florida (excluding the Florida Keys), with a majority of the known, extant populations occurring c. 25 km inland from the coastline in Charlotte, Collier, Lee, and Miami-Dade cos. The range of *S. tenuis* extends northward to Manatee Co. along the Gulf Coast (E.L. Bridges, pers. comm.), and along the Atlantic Coast to at least Indian River Co. (and likely to southeastern Brevard Co.; https://www.inaturalist.org/observations/67553419). *Stillingia tenuis* is present in the interior of central peninsular Florida, northward to Osceola and Polk cos., though is very rare in this region (E.L. Bridges, pers. comm.).

Within this range, two ecological niches are typical for *S. tenuis* and also support the largest populations: 1) wet, *Pinus densa* dominated flatwoods with soils that are underlain by limestone or marl and 2) the short-hydroperiod transition zone between pinelands (dominated by *P. densa*, including pine rocklands) and marl prairies. Frequent associates occurring within 1 m of *S. tenuis* individuals in these communities include: *Cladium jamaicense* Crantz, *Pluchea baccharis* (Mill.) Pruski, *Euthamia caroliniana* (L.) Greene ex Porter & Britton, *Melanthera angustifolia* A. Rich., *Morella pumila* Small, *Serenoa repens* (W. Bartram) Small, *Schizachyrium rhizomatum* (Swallen) Gould, *Muhlenbergia sericea* (Michx.) P.M. Peterson, *Hyptis alata* (Raf.) Shinners, *Rhynchospora divergens* Chapm. ex M.A. Curtis, *Lachnocaulon anceps* (Walter) Morong, and *Piriqueta glabra* Chapm. Populations may extend into adjacent mesic flatwoods or occur in pine rockland communities that are seasonally wet (and have many of the associates from the above list) or particularly sandy, and then frequently associated with *Quercus elliottii* Wilbur (= *Q. pumila* Walter), *Serenoa repens*, *Rhus copallinum* L., *Andropogon longiberbis* Hack., and *Schizachyrium sanguineum* (Retz.) Alston. Notably, *S. tenuis* is

apparently scarce in upland pine rocklands in Miami-Dade Co. Further, it is nearly absent from scrubby flatwoods (it is uncertain to me if these few individuals represent hybrid/ introgressed individuals with *S. sylvatica*) and absent from Florida Scrub communities that exist within its range.

Initially, it was unclear to me if Stillingia tenuis in its strict sense as a woody plant was distinct from the apparently more herbaceous S. angustifolia (sensu Small 1903, 1933). Plants of S. tenuis similar in both morphology and ecological niche to the type specimen occur in the Everglades National Park in the transition zone between pine rocklands and marl prairies of the transverse glades that dissect Long Pine Key. Here, mature individuals of S. tenuis produce aerial shoot systems (with apparently old individuals bearing several) that may last for more than a year (although probably no more than 2–3 years). The first consequence of this extended shoot system duration is that the initial axis (and sometimes also the proximal modular branches) develops a thin, tight, brown bark and secondary xylem accumulates at the base of the initial axis such that it can attain a diameter of up to c. 8 mm at its junction with the rhizome (Fig. 9D). Second, each shoot system may become sympodially branched to up to six orders. The most frequent manifestation of this sympodial shoot development is that only a single modular branch develops from below the terminal inflorescence of the previous modular branch (or initial axis) so that with successive branching events, an apparently unbranched, linear sympodium develops that may be up to c. 1.2 m in height (Fig. 9C). Less commonly, two (or rarely three) modular branches initiate below the inflorescence of the initial axis or early-order modular branch so that the developing shoot system becomes widely branched in appearance. Such plants have the appearance of young, little-branched individuals of S. aquatica, prompting both Small (1905) and Horn and Weakley (Weakley 2020; Weakley & Southeastern Flora Team 2022) to draw an inappropriate comparison between the two. In contrast with S. aquatica, but similar to S. sylvatica, S. tenuis plants lack a U-shaped hilum (Fig. 9A), iteratively develop many aerial shoot systems over the lifetime of an individual from a below-ground, woody rhizome, and have a strongly thickened taproot system (Fig. 9D).

Upon examining the range of *S. tenuis* plants that are congruent with Small's concept of *S. angustifolia*, both within and (especially) outside of Miami-Dade Co, it became apparent that plants similar to the lectotype specimen of S. tenuis exist at an extreme on a spectrum of habit. Outside of Miami-Dade Co., plants of S. tenuis produce aerial shoot systems that are annual in duration and not typically branched beyond three orders. However, by the end of a growing season, the initial axis of a given shoot system develops a continuous periderm layer. Secondary xylem accumulation is not obvious but is clearly present when the base of the initial axis is manually broken. It remains unknown whether S. tenuis plants from Miami-Dade Co. produce shoot systems that last only a single growing season, but here it is likely that the difference in habit that Small perceived between S. tenuis and S. angustifolia is merely due to differences in both shoot and plant age. Specimens from Miami-Dade Co. identified as S. angustifolia by Small and others consist of plants with young shoot systems that are not branched beyond one order. These specimens were collected from areas that had either recently burned or likely represent young individuals. My observations of S. tenuis at Larry and Penny Thompson Memorial Park established that young plants growing next to the trails through the pine rockland produced shoot systems very similar in aspect to typical plants from southwest Florida, whereas large and apparently older individuals growing in less disturbed vegetation off the trail had more extensively branched, woody stems c. 1 m in length. Thus, it appears that Small's contrast between S. tenuis and S. angustifolia on the basis of woody vs. herbaceous habit has no validity.

In contrast to habit, it is clear that most of the substantial range of variation in leaf shape in *Stillingia tenuis*, as approximated by L/W, exists within populations rather than between them (Table 2, Fig. 10). Although the differences among the means of L/W for the ten populations of *S. tenuis* that I sampled is significant, *post hoc* pairwise comparisons of the populations identified a significant difference in L/W means only between the Yucca Pens (Site 3) and Wagon Wheel Rd. (Site 8) populations, which represent the extremes in the range of means across the 10 populations (Table 2). These results are consistent with the findings of other studies regarding among-population variation in leaf shape within a species (Brushi et al. 2003; Consea et al. 2012). What is perhaps most surprising about the results from *S. tenuis* is that given the large magnitude of

L/W range within each population, the population L/W means are, nevertheless, relatively uniform. Therefore, these results support the idea that populations of *S. tenuis* are phenotypically cohesive with regard to leaf shape.

If populations of *Stillingia tenuis* show evidence of phenotypic cohesiveness, then one may first ask to what extent does this cohort of populations differ from its putatively closest relative, S. sylvatica. The approximately threefold difference in mean values of L/W between S. tenuis and S. sylvatica from Peninsular Florida is statistically highly significant (Fig. 11), and many individuals may be distinguished solely on the basis of L/W of the mid- to upper stem leaves of the first order modular branches. However, there is considerable overlap in the ranges of L/W values between the two species. A second morphological character that likely has diagnostic value but needs further investigation is the shape of the apex of the median bract that subtends the single-flowered, carpellate inflorescence subunits. These carpellate inflorescence subunits ("cymules") are proximal to the terminal, staminate portion of the spike-like, terminal inflorescence (Fig. 9). Rogers (1951) described the apex shape of these bracts as being "caudate-acuminate" in plants here considered to be S. tenuis, though I have yet to see such bracts having a long, tail-like apex. In my observations of S. tenuis, these bracts have an acute apex and sometimes long-acute apex. In contrast, such bracts in S. sylvatica from peninsular Florida have an unpointed apex that is typically widely obtuse. Nevertheless, this trait may not hold for S. sylvatica west of the Mississippi River (Johnston & Warnock 1963). The third biological aspect by which these two species are contrasted is ecological niche, and this contrast is strongly marked. Stillingia tenuis is an element of natural communities that are frequently subject to short periods of inundation and/or saturation during the wet season and are situated on soil underlain by limestone or marl. In contrast, S. sylvatica is an element of strictly upland and often xeric natural community types on acidic soils. Because these ecological differences are strongly related to geography, populations of the two species have little opportunity for contact, and there is no evidence that they are ecologically interchangeable.

Given these differences, the second question one may ask is if they justify the recognition of S. tenuis at species rank, distinct from S. sylvatica. The main argument against recognizing S. tenuis is that there is evidence of limited introgressive hybridization between these two entities based on examination of plants in the field and corresponding molecular data (J.W. Horn, unpublished data). Sites I have visited that I think consist of potentially introgressed individuals occur in northern and eastern Charlotte Co., northeastern Collier Co, and Hendry Co. These populations consist of fewer than c. 15 plants, which are typically intermediate in morphology between the two parents, and occur in mesic to scrubby flatwoods. Examination of digital herbarium specimens on SERNEC indicates that this contact zone extends to Sarasota and Manatee cos., Highlands Co. south of Lake Placid, Glades Co., and to several southeastern Florida counties. However, populations representing introgressed plants are infrequent and both species have geographically distinct core ranges where populations are seemingly isolated from interspecific genetic exchange. Thus, the large range of L/W ratios for leaves that are morphological equivalents among individuals within discrete populations of S. tenuis is likely due to inherent phenotypic plasticity with regard to leaf shape and size rather than introgression. Both species are morphologically and ecologically distinct, yet each is a cohesive entity along both these lines. Preliminary molecular phylogenetic data largely supports, and does not reject, the hypothesis that the individuals of S. tenuis sampled derive from a single evolutionary lineage (J.W. Horn, unpublished data). Individual specimens of non-introgressed individuals are unambiguously diagnosable by a combination of morphological and ecological information. Hence, recognizing S. tenuis to be distinct from S. sylvatica is the best supported taxonomic hypothesis, given all available evidence.

Representative specimens of *Stillingia tenuis*: U.S.A. FLORIDA. Charlotte Co.: Cecil M. Webb Wildlife Management Area, N of intersection of Tram Grade and Oilwell Grade, 9 May 1996, *Gann & Bradley 615* (FTG); N side of Zemel Rd., from 1.0–1.4 mi W of its intersection with US 41, 10 May 1990, *Orzell & Bridges 13475* (NY, USF); Caloosa Experimental Range, U.S. Forest and Range Station, SE Charlotte Co., 10 Jun 1956 *Adams 184* (USF, VDB). **Collier Co.:** CR 856 0.5 mi. W of its intersection with Hwy. 84, 28 Jun 1985, *Taylor 5078* (DUKE); along Old Marco Rd. about 10 mi. se of Naples, 18 Feb 1941, *Deam 60802* (DUKE, IND); 10 mi. SE of Naples, 1 Mar 1969, *Porter & Porter 10641* (DUKE, NY); S side of FL 837 (Wagon Wheel Rd.), ca. 2.3 mi. W of FL 839 (FL 840A, Turner River Rd.), Big Cypress National Preserve, 8 Feb 1991, *Orzell & Bridges 15963* (FTG); Along Route 839, E of Jerome, 12 May 1981, *Correll & Correll 51772* (NY, USF); Along Fla. 837, ca.



Leaf blade length/width ratio for Stillingia sylvatica vs. S. tenuis

Fi6. 11. Boxplot of the leaf blade length/width ratio (L/W) for *Stillingia sylvatica* (individuals from peninsular Florida) and *S. tenuis*. The difference in the mean values of L/W is highly significant between the two species (*Welch's* t(544.76) = -36.145, *p* = 2.2×10⁻¹⁶, 95% C.I. = [-9.30, -8.34]).

5 mi. E of Jerome, 20 Sep 1965, *Ward et al.* 5215 (FLAS); Corkscrew Swamp Sanctuary, 15 Jul 1994, *Abbott & Judd* 7298 (FLAS); Scenic Drive NW of Copeland, off Fla. 29. Vicinity of Fakahatchee, 20 April 1967, *Lakela & Almeda* 30709 (NCU, USF). **Hendry Co.**: FL 80, 5 mi. E of LaBelle, 18 Mar 1982, *Baltzell* 11522 (FLAS). **Indian River Co.**: Vero Beach, 20 Jun 1951, *Hood* 4331 (FLAS). **Lee Co.**: Flint Pen Swamp wetlands, just S of Corkscrew Rd., ca. 5 air mi E of 1-75, 24 Jun 1997, *Anderson* 17811 (FTG, SEL); vicinity of Fort Myers, 14 Mar 1916, *Standley* 16 (NY); Central Sanibel [Island], 3 Mar 1972, *Brumbach* 7853 (FLAS, MICH, NY); Sawgrass Road, Sanibel, 21 Jul 1954, *Cooley* 2277 (FLAS, USF); between Ft. Myers and Bonita Springs, 10 Jun 1961, *Godfrey & Reinert* 60983 (NCU); Alva Scrub Preserve, ca. 0.7 mi. ESE of the jct. of Goggin Rd. and Langford Rd., 15 May 2010, *Chicone* 735 (USF). **Martin Co.**: Danforth Park, 18 Mar 2000, *Woodmansee* 464 (FTG). **Miami-Dade Co.**: Between the main campus of the University of Miami and Dixie Highway (US 1) in Coral Gables, 1 Apr 1964, *Stimson* 258 (DUKE); near Redland, 30 Mar 1964, *Stimson* 219 (DUKE); Cutler to Black Point Creek, 1 Jul 1915, *Small, Mosier & Small* 6724 (DUKE; FLAS); Between Perrine & Cutler, c. 0.7 mi. W of Eureka Rd.—Old Cutler Rd. intersection, 21 Jun 1960. *Webster & Williams* 10028 (DUKE); Tamiami Pinelands, SW 137 Ave – 128 St. Kendall, 14 Jan 1979, *Hendon* 96 (LSU); W side of Block B, Long Pine Key, Everglades National Park, 17 May 1991, *Herndon* 3053 (LSU); Long Pine Key, Everglades National Park, 27 Mar 1986, *Herndon* 1440 (FTG, NY) Deering

Estate, Cutler, 26 Aug 1978, Correll & Pompenoe 50071 (FTG, NCU); Larry & Penny Thompson Park, 5 May 1998, Bradley 1651 (FTG); Pinelands about Goodburn Hammock, 17 Mar1915, Small & Mosier 5900 (NY). Palm Beach Co.: Lake Worth, 19 Apr 1941, Cummings s.n. (FLAS). Sarasota Co.: SW corner of Knight's Trail County Park, near Cow Pen Slough and Rustic Road, 30 Jun 1997, Holst et al. 6074 (SEL, USF)

KEY TO STILLINGIA SPECIES IN FLORIDA

- 1. Stems herbaceous to weakly woody, several from the crown of a woody rhizome that also bears a strongly thickened taproot system; aerial stems sympodially branched to 1–3(–6) orders; aerial shoot systems typically annual in duration (uncommonly persisting to ~3 years and becoming woody); leaves linear, elliptic, oblanceolate, or narrowly obovate, widest near the midpoint or towards the apex, newly developed shoot modules appearing evenly leafy, at least to June/July; caruncle of the seed broadly crescent-shaped when well-developed, > 1 mm wide, largely concealing the small, irregularly semicircular hilar scar; [of upland, dry habitats, or wet pinelands that are only sporadically inundated].
 - 2. Leaf blades < 9 mm wide at widest point (typically 3.4–6.2 mm wide), L/W ratio (5–)10–17.5(–28), typically broadest near the middle; median bract subtending the pistillate cymule with an acute apex; [of calcareous, wet/mesic pine flatwoods or pineland/marl prairie transitions that are sporadically inundated; endemic to c. & s. FL] ______ Stillingia tenuis
 - Leaf blades > 9 mm wide at widest point, L/W ratio (1.3–)2.3–5.5(–9.1), frequently broadest towards the tip; median bract subtending the pistillate cymule typically with an obtuse apex (rarely widely acute); [of sandhills and scrubby flatwoods; widespread in the panhandle south to c. FL, rare in s. FL] ______ Stillingia sylvatica

FABACEAE

DESMODIUM: The identity of Desmodium dillenii Darl.

Primary author: Steven P. Grund

The *Desmodium paniculatum* complex (*sensu* Schubert 1950) has plagued botanists with difficult issues of confusing morphology and species circumscription. *D. glabellum* (Michx.) DC. and *D. perplexum* B.G. Schub. are included in a broad concept of *D. paniculatum* (L.) DC. by Ohashi (2013), but the species have been maintained, sometimes with expressed trepidation, by other recent authors (e.g. Gleason & Cronquist 1991; Haines 2011; Voss & Reznicek 2012; Weakley et al. 2012; Weakley 2020; Weakley & Southeastern Flora Team 2022). The hesitation in accepting these species seems to have been largely due to the inadequacy of the pubescence characters usually used to distinguish the taxa in keys, but this appears to have been resolved by recent work identifying more consistent morphological features (Thomas 2020). In a study of Pennsylvania *Desmodium* intended for publication, we have found Thomas's work to be a welcome elucidation of a formerly perplexing pair of species, and the most striking result of our examination of roughly one thousand specimens is that, contrary to previous conclusions, *D. glabellum* is considerably more common in Pennsylvania than *D. perplexum* (Rachel Goad et al., unpublished data).

The name *Desmodium dillenii* Darl. was long used to encompass both *D. glabellum* and *D. perplexum* until Schubert (1950) declared it a *nomen confusum*, a term without standing in the current code (Turland et al. 2018), on the basis of her interpretation that Darlington used original material representing what she considered to be two different elements. In the protologue (Darlington 1837), the phrase in the first paragraph, "ICON, Dill. Hort. Eltham. tab. 144. f. 171" (referencing Dillenius 1732) establishes that illustration as the holotype (informally an iconotype). It is understandable that Schubert was unable to determine which of the concepts she recognized was represented, as the type illustration reveals nothing about the nature of the trichomes central to distinguishing those concepts at that time. She refers to specimens in Darlington's herbarium as the original material representing two different elements, which matters not if there exists an identifiable holotype. In light of the clarification provided by Thomas (2020), it becomes clear by examining leaf shape and phyllotaxy that the holotype represents *D. glabellum*, which has priority (comb. Candolle 1825). We recommend that *Desmodium dillenii* Darl. be treated as a junior synonym of *D. glabellum* (Michx.) DC.

JUNCACEAE

JUNCUS: Typification of *Juncus anthelatus* (Juncaceae, *Juncus sect. Steirochloa*) Primary authors: Wesley M. Knapp & Derick B. Poindexter

Juncus section *Steirochloa* Griseb. is a widespread section found in nearly all temperate regions, except for South Africa (Kirschner 2002). As presently circumscribed, it consists of 35 species, with its main centers of diversity located in eastern and western North America, Central Asia, and temperate South America (Kirschner 2002). Nomenclatural investigations of North American members of this section by the first author revealed the need to typify a well-known but often misidentified species in the group, *Juncus anthelatus* (Wiegand) R.E. Brooks.

Juncus anthelatus is a common and widespread taxon found over much of the eastern United States and southern Canada in exposed or partially shaded sites of moist or seasonally wet soils. Rarely it is encountered in the western U.S. as an introduction. Wiegand (1900) distinguished *Juncus tenuis* Willd. var. *anthelatus* Wiegand from the typical var. *tenuis* by its tall and rather stiff stems, very large, diffuse inflorescence, and smaller capsules. Brooks and Whittemore (1999) elevated Wiegand's variety to the species-level by making the combination *J. anthelatus* (Wiegand) R.E. Brooks. Their rationale for this change in status was attributed to reported differences from *J. tenuis* with regard to morphology, habitat, phenology, and isozyme profile.

Brooks and Whittemore (1999) acknowledged that the basionym for this taxon (*Juncus tenuis* var. *anthelatus*) had not been properly assigned, stating within the protologue "Type: not designated." Furthermore, they neglected to correct this deficiency by designating a representative lectotype. Thankfully, Wiegand (1900) cited numerous collections when describing *J. tenuis* var. *anthelatus* and as none were specified as the intended holotype any of these specimens are eligible for the typification of this name. Of all Wiegand's cited specimens (i.e., syntypes) only one contains a collection number (*E. Hall 663*, GH-00061742) and an annotation in Wiegand's hand. Therefore, we feel *E. Hall 663* has the greatest utility and basis as a lectotype.

Typification:

- Juncus anthelatus (Wiegand) R.E. Brooks, Novon 9:11 (1999). BASIONYM: Juncus tenuis Willd. var. anthelatus Wiegand, Bull. Torrey Bot. Club 27:523–524. 1900. Juncus macer A. Gray var. anthelatus (Wiegand) Fernald, J. Bot. 68:367. 1930. Juncus macer A. Gray f. anthelatus (Wiegand) FJ. Herm., Rhodora 40(471):81. 1938. Juncus tenuis Willd. f. anthelatus (Wiegand) FJ. Herm., Castanea 10:23. 1945. Juncus tenuis Willd. ssp. anthelatus (Wiegand) Verloove & Lambinon, New J. Bot. 1(1): 39. 2011. Type: U.S.A. TEXAS: Houston, prairies, 20 Apr 1872, E. Hall 663 (Lectotype, designated here: GH-00061742.
 - Juncus macer A. Gray f. discretiflorus F.J. Hermann, Rhodora 40: 82. 1938. Juncus tenuis Willd. f. discretiflorus (F.J. Hermann) Fernald, Rhodora 47: 123. 1945. Type: U.S.A. Indiana: Harrison Co: 13 Jul1935, Deam 56381 (HOLOTYPE: GH; ISOTYPE: IND).

PRIMULACEAE

STEIRONEMA: Comments on genera in the Lysimachieae and a new combination in *Steironema* Primary authors: Alan S. Weakley & Derick B. Poindexter

Authors have differed in their interpretations of the circumscription of *Lysimachia*. In general, *Lysimachia* has been variously interpreted to include or exclude (in various combinations) *Anagallis, Centunculus, Glaux, Naumburgia, Steironema*, and *Trientalis* (generic names not used in the past century are excluded from this list). Generally, *Anagallis, Centunculus, Glaux,* and *Trientalis* were recognized as separate from *Lysimachia*, with *Naumburgia* and *Steironema* included, though Ståhl & Andeberg (2004) combined *Centunculus* into *Anagallis,* and (in eastern North America) *Steironema* and *Naumburgia* were separated from *Lysimachia* at genus rank by Small (1903, 1913, 1933), Gleason and Cronquist (1952), and Mohlenbrock (2014). In the first decade of the 21st century, phylogenetic analyses resulted in a trend of lumping all these genera together as *Lysimachia,* with, for instance, Manns and Anderberg (2009) arguing that "merging all the genera in *Lysimachia* is here considered better than splitting the latter into several smaller genera."

Not all have been comfortable in following the expansion of *Lysimachia* to the same circumscription as tribe Lysimachieae. Cholewa (2009) in *Flora of North America* retained traditional *Trientalis* at genus rank,

and *Anagallis* (with *Centunculus* included), but did include *Glaux* in *Lysimachia*, while noting that "future taxonomic realignments at the familial and generic levels are to be expected." A recent phylogenetic study of tribe Lysimachiae (Yan et al. 2018) stated that they were using a taxonomy recognizing "*Lysimachia* (211 species), *Anagallis* (31), *Trientalis* (3), *Glaux* (1), *Asterolinon* (2), and *Pelletiera* (2)," but also that "we followed the traditional classification, but our results also support expansion of *Lysimachia*; we therefore place these genera in quotation marks." Yan et al. (2018) interpreted their phylogenetic tree as eleven numbered clades (I through XI). The "first branching" or "basal" branches represent clades that largely correspond with traditional genera. Clade XI is equivalent to *Trientalis*, Clade X includes two tropical American species of montane or cloud forest habitats (*L. andina*, *L. mexicana*), and Clade IX consists of *Steironema*. Clades IX, X, and XI group together in a clade that is sister to the remaining clades I-VIII. Next branching is Clade VIII, which includes the type of *Anagallis*, *Asterolinon*, *Pelletiera*, and *Lysimachia* (2 sampled species: *L. nemorum*, and *L. serpyllifolia*). The remaining clades I-VI are mainly Asian and Hawaiian (with a few European or circumboreal species), and encompase a broad range of morphological variation.

As is very often the case, the results of a particular phylogenetic tree may support a particular classification involving lumping, and equally support an alternative classification involving splitting. It is beyond the scope of this paper to fully address generic issues in tribe Lysimachieae, but we feel that the phylogenetic, morphological, and evolutionary diversity of the group is not well served by combining all into a large and very heterogeneous *Lysimachia*, and that such an approach is also not comparable with genus rank as it is applied in other closely allied groups in Primulaceae s.l. We therefore choose to recognize the "basal" clades represented in the southeastern United States at genus rank: *Trientalis, Steironema, Anagallis, Centunculus*, and a broad *Lysimachia*, based on morphology, biogeography, tradition, and their monophyly in recent phylogenetic analyses, including Yan et al. (2018) and Hao et al. (2004). This leaves *Lysimachia* as still rather broadly defined and morphologically heterogeneous, but largely north temperate and boreal (with a radiation in Hawaii), and with a center of diversity in eastern Asia.

A single combination is needed to apply this largely traditional taxonomic scheme to the species of Lysimachieae native or naturalized in the Southeastern United States region. The recently named (2015) *Lysimachia lewisii* D. Estes, J.T. Shaw, & Maus.-Moon. lacks a name in *Steironema*, which we here provide.

Steironema lewisii (D. Estes, J.T. Shaw, & Maus.-Moon.) Weakley & D.B. Poind., comb. nov. BASIONYM: Lysimachia lewisii D. Estes, J.T. Shaw, & Maus.-Moon, Phytoneuron 2015-17:1, Figs. 1–2. TYPE: TENNESSEE. LEWIS CO.: Meriwether Lewis National Monument off Natchez Trace Parkway, 9.6 km by air SE of Hohenwald, on hiking trail NE of Old Spring, growing on SE-facing mid-slope in hollow that leads to Little Swan Creek, 31 Jul 2008, T. Duke 106 with D. Estes (HOLOTYPE: APSC; ISOTYPES: FSU, GA, GH, LSU, MO, NCU, NY, TENN, UARK, US, UWAL, VDB) (Figs. 1–2).

SELAGINELLACEAE

BRYODESMA, GYMNOGYNUM, and **STACHYGYNANDRUM:** Recognition of segregate genera in *Selaginella* s.l. for the *Flora of the Southeastern United States*, with four new combinations needed Primary author: Alan S. Weakley

Linnaeus and other 18th and 19th century taxonomists did not deal well with family and genus concepts in the ferns and lycophytes, and only in the 20th century and especially the 21st have realistic, meaningful, comparable, and coherent concepts and circumscriptions of these mid- to lower-level taxonomic ranks clarified. In the surviving lycophytes, a three (to four) family system has emerged and been almost universally recognized—Lycopodiaceae (sometimes with Huperziaceae separated at family rank), Isoetaceae, and Selaginellaceae. Lycopodiaceae was long treated as a monogeneric family, an approach that was the consensus taxonomy until the 1980s, during and after which deep phylogenetic differences and correlated and profound morphological, cytological, and other differences have been used to craft a more informative classification. The PPG I classification (PPG I 2016) treated the Lycopodiaceae as three subfamilies and sixteen genera, and that approach has been broadly followed, with minor variations, such as the 2022 proposal of a seventeenth

genus (Chen et al. 2022) An alternative approach of three genera (each in a monogeneric subfamily) has been promoted by Christenhusz and Chase (2014, 2018) and countered by Schuettpelz et al. (2018).

Selaginellaceae has long been generally treated as a monogeneric family, and the relatively simple structure of the plants has been used to justify and enable this approach; contrastingly, the significant and obvious diversity within Selaginellaceae has also suggested the recognition of multiple groups at subgenus, section, or sometimes genus (i.e., Soják 1993) rank. Recent phylogenetic analyses have resulted in the recognition of 6–7 subgenera based on deep phylogenetic clades and correlated morphology (Weststrand & Korall 2016a, 2016b; Zhou & Zhang 2015; Zhou et al. 2016; Klaus et al. 2017), and we seem to be at the point where the major monophyletic and morphology-based groups are clearly resolved. At what rank should these groups be recognized?

Non-specialist users of plant taxonomy and nomenclature make up the vast majority of our "clients," and taxonomy needs to reach and be relatively user-friendly for non-specialists and specialists. Non-specialists use two ranks consistently (genus and species), and three other ranks to some degree (family, and the infrataxon ranks, subspecies and variety), while intermediate ranks (subgenus, section, subfamily, etc.) and higher ranks (above family) are generally out of sight to them. Christenhusz & Chase (2018) argue that "it is often more preferable in the long run to lump these clades in the beginning, leaving it up to the specialists to sort out which subfamilies/subgenera should be recognized and allowing the rest of the user community to enjoy stability of at least family and genus names—the ranks most used—recognizing that the component taxa may in fact be changing subfamilial and subgeneric positions." This comes close to advocating a "dark taxonomy," where important changes are conducted at ranks not noticed by most of the user community.

I'd like to assert that name changes reflecting new understanding of relationships are a feature and not a bug of our binomial taxonomy! As much as name changes can elicit irritation or even occasional rebellion in the user community, they also convey important information and are generally assimilated after a period of a decade (or sometimes a generation). For instance, in Asteraceae, the division of heterogeneous and non-monophyletic genera such as Eupatorium and Aster have been fully assimilated by specialist and non-specialist communities, and usage of "split" genus names (e.g. *Eutrochium, Ageratina, Fleischmannia, Symphyotrichum, Eurybia, Doellingeria*) enhances accurate evolutionary information, understanding of diversity, and even practical identification. And of course, the argument that such changes can be hidden at invisible ranks ignores that most name changes are created by lumping or splitting necessitated by monophyly, not by "optional" upranking or downranking.

The genus rank is a critical one in our system of taxonomy and nomenclature, as part of the binomial name of species, but also because it is the first "grouping level" in the taxonomic hierarchy above the species that is routinely seen by most of the user community, and often serves a critical role in teaching taxonomy and species identification. Christenhusz & Chase (2018) argue that finely split genera are difficult for the non-specialist, as not intuitively recognizable, but this argument can cut both ways, as in the case of *Selaginella* of eastern North America. The major clades are so different in appearance as to suggest that they are unrelated; the non-specialist regularly mistakes *Selaginella apoda* for a leafy liverwort, *Selaginella rupestris* for a robust moss (like *Polytrichum*), and *Selaginella selaginoides* (with its strobilus on an ill-defined 'strobilus stalk') for a *Lycopodium*.

"Floras" (as books, apps, websites) are where the results of plant systematics research (and associated studies of distributions, habitats, etc.) are synthesized for use by the broad user community, which includes conservationists, farmers, weed scientists, natural resource specialists, rangers, land managers, ecologists, teachers, and students. Larger floras, such as the *Flora of North America north of Mexico*, are of necessity written as compilations of contributed treatments, parsed by genus or family, and this can lead to very disparate taxonomic philosophies being employed in closely related groups. For the *Flora of the Southeastern United States* (Weakley & Southeastern Flora Team 2022), we have tried to "smooth" these differences and to have a relatively consistent taxonomic philosophy applied to taxonomic recognition and rank assignment. The conventional treatment of "taxonomic groups" in Selaginellaceae (as a monolithic genus with subgenera)

contrasts starkly with the treatment that has evolved in Lycopodiaceae, in which 16–17 groups are accorded genus status, because they are each monophyletic, they are readily recognizable macroscopically, they are old to very old clades, their recognition provides a more accurate and meaningful basis for understanding plant biodiversity above the species level, and their recognition makes effective use of the primary hierarchical ranks—without simply repeating a circumscription at successive hierarchical ranks (i.e., that *Lycopodium*, Lycopodiaceae, and Lycopodiales all have the same circumscription and membership). The age and morphological distinctiveness of the major clades of Selaginellales continues to be corroborated, with Schmidt et al. (2020) reporting a diversity of fossils of *Stachygynandrum* from the mid-Cretaceous, ca. 100 Ma, and Klaus et al. (2017) estimating the divergence of *Selaginella* s.s. and the other clades of *Selaginella* s.l. at about 370 Ma, in the Devonian.

In this regard, *Selaginella* and Selaginellaceae seem roughly analogous to *Lycopodium* and Lycopodiaceae—or for that matter to *Thelypteris* and Thelypteridaceae—where a new classification based on major monophyletic clades with morphological synapomorphies has emerged from more than a century's controversy (Fawcett & Smith 2021; Fawcett et al. (2021). These three cases are even analogous in that in each the type species is part of a depauperate boreal clade, and that a split generic taxonomy results in (temporarily) the greatest possible disruption, as the previously broadly used genus is reduced to one or a few species, and hundreds of species change genera.

In order to implement a comparable taxonomy in Selaginellaceae for the *Flora of the Southeastern United States* by treating the major clades at genus rank, several new combinations are needed. Weststrand and Korall (2016b) recognized six subgenera of *Selaginella*, and we follow the circumscription of these entities, but treat them at genus rank.

For the Southeastern United States, three of these groups are present:

Bryodesma Soják, Preslia 64:154. 1993 [1992] [≡ subg. Rupestrae Weststrand and Korall (2016b)] Gymnogynum P. Beauv., Mag. Encycl. 9(5):480. 1804 [≡ subg. Gymnogynum Weststrand and Korall (2016b)] Stachygynandrum P. Beauv. ex Mirb. in Lam. & Mirb., Hist. Nat. Vég. 3:477. 1803 [≡ subg Stachygynandrum (P. Beauv. ex Mirb.) Baker, J. Bot. 21:3. 1883, sensu Weststrand and Korall (2016b)]

Bryodesma corallina (Riddell) Weakley, comb. nov. BASIONYM: Lycopodium corallina Riddell, New Orleans Medical and Surgical J. 9:617. 1853. Selaginella corallina (Riddell) Wilbur & Whitson, Amer. Fern J. 95:162. 2005. Type: U.S.A. Texas: San Saba Co.: [interpreted; ?], on dry granular quartz rocks at Kaolin Creek, near the San Saba, Nov 1839, Riddell s.n. (SYNTYPE, GH!).

Selaginella riddellii Van Eselt., Contr. U.S. Natl. Herb. 20(5):162–163, pl. 15, f. 63. 1918. Selaginella arenicola subsp. riddellii (Van Eselt.) R.M. Tryon. Ann. Missouri Bot. Gard. 42(1):24. 1955.

I recognize this taxon at species rank, agreeing with Wilbur and Whitson (2005) and Diggs and Lipscomb (2014).

- Gymnogynum kraussianum (Kunze) Weakley, comb. nov. BASIONYM: Lycopodium kraussianum Kunze, Linnaea 18:114.
 1844. (24–26 Oct 1844). TYPE: SOUTH AFRICA: "In sylvis Zitzikamma districtus Uitenhage in terra detexit Kraus Martio 1839— Ad portum Natalensem inter Omfondi et Tagela in sylvis umbrosis humidis, et in coronis rupium saxis adpressum; nec non in faucibus umbrosis sylvarum prope rivulum haud procul a Chakas-Kraal legit Gueinzius. Lectotype (designated by Bizzarri 1975: 577): "Port. Natal.," Guenzius (K 000351292; isolectotype: P 00065023); paralectotypes in FI and W. Homotypic synonyms: Didiclis kraussiana (Kunze) Rothm., Feddes Repert. 54:71. 1944. Lycopodioides kraussiana (Kunze) Kuntze, Revis. Gen. Pl. 1–2:826.
 1891. Selaginella kraussiana (Kunze) A. Braun, Index sem. hort. bot. berol. 1859:22. 1860.
- Stachygynandrum eatonii (Hieron. ex Small) Weakley, comb. nov. BASIONYM: Selaginella eatonii Hieron. ex Small, Ferns of Tropical Florida 67. 1918. Diplostachyum eatonii (Hieron. ex Small) Small, Ferns of the Southeastern States 422. 1938. TYPE: U.S.A. FLORIDA: Miami-Dade Co.: about lime sinks, border of Everglades, Black Point Creek, A.A. Eaton 265 (LECTOTYPE: NY).
- Stachygynandrum eclipes (W.R. Buck) Weakley, comb. nov. BASIONYM: Selaginella eclipes W.R. Buck, Canad. J. Bot. 55:366–367. 1977. TYPE: U.S.A.: MISSOURI: Douglas Co.: 27 Sep 1974, Warren L. Wagner 74159 (MICH1190987).

MISCELLANEOUS FAMILIES

New and Notable Vascular Plant Records from North Carolina

Primary author: Eric A. Ungberg

Herbarium work and *de novo* field surveys carried out between 2019 and 2021 resulted in records for several native taxa either new to or historic for North Carolina. New state records include *Chenopodium berlandieri* Moq. var. *macrocalycium* (Aellen) Cronquist (Carteret County), *Croton michauxii* G.L. Webster (Brunswick County), *Eleocharis compressa* Sull. var. *compressa* (Granville County), *Rhynchospora compressa* J. Carey ex Chapm. (Brunswick County), and *Rhynchospora sulcata* Gale (Scotland County). New records of species considered state-historic by the North Carolina Natural Heritage Program include *Carex barrattii* Torr. ex Schwein. (Montgomery County), *Carex vestita* Willd. (Montgomery County), and *Helanthium tenellum* (Mart. ex Schult. f.) Britton (Scotland and Richmond counties).

Helanthium tenellum [Alismataceae]

Helanthium tenellum is reported for two new counties in North Carolina based on collections in 2019 (Scotland County) and 2020 (Richmond County) by Bruce Sorrie and Eric Ungberg respectively. This plant has not been collected or otherwise reported for North Carolina since three collections from the 1980s taken in Brunswick (1985) and Robeson Counties (1983, 1984). The Scotland Co. population was found in a recently clear-cut clay-based Carolina Bay at roughly the same location as described for *Rhynchospora sulcata* below. B.A. Sorrie estimated the population to be roughly 5,000 plants. The Richmond Co. population was found along the margins of a shallow sandhills depression pond and was estimated to have between 3,500 and 17,000 plants (personal communication, H. LeGrand 2021) (Fig. 12).

Though this species is widely distributed throughout the eastern United States, it is rare across that range, having a conservation ranking of S1, S2, SX, or SH in nearly every state where it is found (NatureServe 2000). In North Carolina it is considered imperiled (S1) and is listed as Endangered by the N.C. Plant Conservation Program and N.C. Natural Heritage Program. Though it is currently ranked as "secure" globally (G5) and "no ranking" nationally (NNR), these designations should be revisited given its apparent rarity throughout its range in North America.

Voucher Specimens: **NORTH CAROLINA. Scotland Co.:** Big Cypress Meadow, just S of Tunstall's Bay, E margin at old vehicle track, Carolina bay, probably clay based, about half of it clear-cut to remove loblolly pines, now with abundant saplings of *Quercus nigra*, *Liquidambar styraciflua*, *Rubus argutus*, flooded from 2018 hurricane, now mostly 1 foot deep, abundant on exposed bottom, estimate 5000 fruiting plants plus some still with flowers, 18 Oct 2019, *B.A. Sorrie* 13787 (NCU00436031). **Richmond Co.:** Sandhills Game Lands ca. 1500 ft ESE of intersection of Route 1 and Route 177 in sandhills depression pond, with *Eleocharis tricostata*, *Eleocharis melanocarpa*, *Persicaria hirsuta*, 39.975486, –79.595714, 25 Jun 2021, *E. Ungberg s.n.* (NCU00434538).

Chenopodium berlandieri var. macrocalycium [Chenopodiaceae]

A collection of *Chenopodium berlandieri* var. *macrocalycium* is reported from Carteret County, North Carolina. While the species account in the Flora of North America (Clemants & Mosyakin 2002) reports this taxon as occurring in North Carolina, no existing herbarium specimens are known, based on searches of SERNEC, the Consortium of Midwest Herbaria, and several other large herbaria. Existing specimens of *Chenopodium berlandieri* in the broad sense, and even of *C. album* L. (given the inclusion of *C. berlandieri* in *C. album* in the influential Radford et al. 1968 manual) should be evaluated and will likely result in additional records of *C. berlandieri* var. *macrocalycium* for North Carolina.

Voucher Specimen: NORTH CAROLINA. Carteret Co.: Theodore Roosevelt Natural Area, near E end of nature trail on northern shore, sandy bank above salt marsh, with *Spartina alterniflora*, *Borrichia frutescens*, *Cyperus* spp., *Juniperus virginiana* var. silicicola, 34.697283, –76.838949, 15 Aug 2021, E. Ungberg 559 (NCU00444045).

Carex barrattii [Cyperaceae]

Carex barrattii (Barratt's Sedge, G4) is reported from a complex of Piedmont Boggy Streamheads occurring in a matrix of Dry and Wet Piedmont Longleaf Pine Forest in the Uwharrie National Forest, Montgomery County, North Carolina (Figs. 13, 14). These plant communities are globally rare (Schafale 2012) and have a



FiG. 12. Helanthium tenellum. Sandhills Game Lands, Richmond Co., NC. Shallow margins of sandhills depression pond. Photo by E.A. Ungberg.



Fig. 13. Carex barrattii. Uwharrie National Forest, Montgomery Co, NC. Margins of Piedmont boggy streamhead community type embedded within a matrix of Wet Piedmont Longleaf Pine Forest. Photo by E.A. Ungberg.



Fig. 14. Habitat of Carex barrattii and C. vestita. Wet Piedmont Longleaf Pine Forest, Uwharrie National Forest. Photo by E.A. Ungberg.

distinctive component of Coastal Plain flora not often found in the Piedmont, including a canopy of *Pinus palustris* Mill. and conservative herbaceous species like *Calamovilfa brevipilis* (Torrey) Scribn., *Iris prismatica* Pursh, and *Danthonia epilis* Scribn.

Carex barrattii is found primarily in the mid-Atlantic Coastal Plain centered around New Jersey and occurs only sporadically further south. Except for New Jersey, it has conservation rankings of S3 or lower in all states in which it is found. Weakley and Southeastern Flora Team (2022) gives its habitat as "peaty bogs and marshes, especially in depression ponds, depression swamps, and sinkhole ponds" and remarks that inland occurrences are often habitats with "Coastal Plain affinities." This species can be easily overlooked due to its tendency to produce very few reproductive culms relative to the number of vegetative clumps or clusters in a population.

Prior to the discovery of these Montgomery Co. populations, *Carex barrattii* was known from only a handful of counties in North Carolina, with collections from Harnett (1957), Haywood (1949), Henderson (1936, 1956), and Wake (No date) counties. The Wake Co. collection is undated but likely from the early 1900s at the latest, based on the appearance of the specimen (NYBG9723).

While the Uwharrie populations are rather large in terms of number of clumps or ramets, they may represent relatively few genetic individuals due to the extensively rhizomatous habit. We propose a state conservation ranking of S1 and its inclusion on the state list of rare and tracked species as "Significantly Rare – Periphery" (SR-P).

Voucher Specimen: NORTH CAROLINA: Montgomery Co.: Lomax Church longleaf pine forest. North of Dusty Level Road at gate about 0.75 mi W of Mount Carmel Church Road, Piedmont boggy streamhead complex, with Osmundastrum cinnamomeum, Carex mitchelliana, Viburnum nudum, Andropogon glomeratus, Oxypolis rigidior, 35.372882, –79.973972, 29 Apr 2022, E. Ungberg 1014 (NCU00438341).

Carex vestita [Cyperaceae]

Carex vestita (Velvet Sedge, G5) is reported from the same complex of Piedmont Boggy Streamheads mentioned in the *Carex barrattii* account (Figs. 14, 15). *Carex vestita* in North Carolina is previously only known from a single 1959 collection near the Durham/Orange County line, with the vague habitat description: "edge of roadside near woods." In 2013, a population in Polk County, North Carolina was reported to the North Carolina Natural Heritage Program. To our knowledge, the latter report is not associated with an herbarium specimen, and we are unable to confirm its veracity. The stated habitat for the Polk County occurrence is "along banks of Walnut Creek […] growing under mature *Asimina triloba*."

Like *Carex barrattii*, this species is found predominantly along the mid-Atlantic Coastal Plain but ranges further inland and north, with fewer disjunct occurrences in the south. Weakley and Southeastern Flora Team (2022) gives its habitat as "low forests, bogs, seepage swamps, wet clearings, and depressions." It is easily identified by the distinctive combination of elongate, cord-like rhizomes, and densely hairy perigynia on erect-ascending spikes, these clustered distally on each culm. Like *Carex barrattii*, it has a tendency to produce relatively few reproductive culms, and those present are relatively short and easily overtopped by taller vegetation.

Thus far, three populations have been located, all in the Uwharrie National Forest. The first two were found several miles west of Troy, North Carolina and are about a mile apart. Each has relatively few clumps or ramets and presumably even fewer genetic individuals, due to its long-rhizomatous growth habit. The third, which is of similar size and extent, was found in June of 2022 about 8 miles southeast of the first two, again on the margins of a Piedmont Boggy Streamhead embedded within a Wet Piedmont Longleaf Pine Forest community type.

Given both its current and historic rarity, and its association with a globally rare community type, we propose a state conservation ranking of S1 and its inclusion on the state list of rare and tracked species as "Significantly Rare – Periphery" (SR-P).

Voucher Specimen: NORTH CAROLINA. Montgomery Co.: S of Correll Road on margin of Piedmont boggy streamhead, occurring with Iris prismatica, Solidago austrina, Viburnum nudum, Oxypolis rigidior, Rhynchospora recognita, and Polygala lutea, 35.384374, –79.970420, 29 Apr 2022; E. Ungberg 1013 (NCU00438342).

Eleocharis compressa var. compressa [Cyperaceae]

Eleocharis compressa var. *compressa* is reported from a collection taken in Granville County, North Carolina and is the first record of this species from the state. This species was observed in a globally rare Diabase Glade (NatureServe 1998; Schafale 2012) and co-occurring with many other North Carolina tracked and rare plant species including *Trichostema brachiatum* L., *Ruellia humilis* Nutt., *Phemeranthus piedmontanus* S. Ware, *Berberis canadensis* Mill., *Scutellaria nervosa* Pursh, *Symphyotrichum depauperatum* (Fernald) Nesom, and *Isoetes piedmontana* (N.E. Pfeiff.) C.F. Reed.

The nearest records of *Eleocharis compressa* are from Virginia, in Pittsylvania Co. (Kartesz 2015). These records are misidentified and are in fact *Eleocharis wolfii* (A. Gray) A. Gray ex Patt., as are all other county records from western Virginia (personal communication, J. Townsend 2021). The nearest collections of *Eleocharis compressa* are therefore from either frequently flooded scour areas over mafic and calcareous substrates on the Potomac River in northern Virginia (~250 miles north), or a region in the mountains of southern West Virginia (~160 miles northwest). At this time, no attempt has been made to confirm the identities of West Virginia collections.

Given the large disjunction from the nearest populations, and its occurrence at only a single site in the state, we recommend that *Eleocharis compressa* var. *compressa* be given a state ranking of S1 in North Carolina. At a minimum, its inclusion on the state list of tracked and rare species as "Significantly Rare – Periphery" (SR-P) should be considered, though a more conservative ranking is likely warranted given the lack of Diabase Glade habitat elsewhere in the state, the limited extent of the existing habitat, the presence of invasive species at the site (namely *Ligustrum quihoui* Carrière and *Nandina domestica* Thunb.), and the small number of *E. compressa* var. *compressa* plants present.



Fig. 15. Carex vestita. Margin of Piedmont Boggy Streamhead and Wet Piedmont Longleaf Pine Forest, Uwharrie National Forest. Photo by E.A. Ungberg.

Voucher Specimen: NORTH CAROLINA. Granville Co.: B Street glade, Butner, occurring N of main glades in damp, thin soil near exposed rock, growing with *Isoetes piedmontana*, various mosses, *Packera* spp., 36.110, –78.779, 16 May 2021, *E. Ungberg, with E. Bridges and M. Pyne* (NCU00443487).

Rhynchospora compressa [Cyperaceae]

Rhynchospora compressa is reported as a part of the native flora of North Carolina from a single collection from Brunswick County taken in August of 2019. The overall status of the population is unknown at this time as it was not identified for some time after its original collection. The collection was made from a Very Wet Loamy Pine Savanna (Schafale 2012) community of marginal quality, having been bedded for silvicultural purposes in the past, though still with numerous rare and tracked plant species, such as *Helenium pinnatifidum* (Schwein. ex Nutt.) Rydb., *Thalictrum cooleyi* H.E. Ahles, *Parnassia caroliniana* Michx., and *Macbridea caroliniana* (Walter) S.F. Blake. *Rhynchospora compressa* is most similar to *R. torreyana* and *R. perplexa* but differs in having larger achenes (1.4–1.6 mm versus 0.7–1.3 mm wide), longer achene tubercles (0.6–0.8 mm versus 0.2–0.5 mm long) and wider leaves (3–5 mm versus 1–3 mm wide).

Presuming that this population remains extant since the time of collection, it would now represent the northern-most occurrence of this species, previously known only as far north as Wardfield Savanna in South Carolina (pers. comm., K. Bradley 2022), this latter population itself disjunct from the center of its distribution along the Gulf coast and in southwestern Georgia.

Voucher Specimen: NORTH CAROLINA. Brunswick Co.: Camp Branch Savanna, N of Myrtlehead Road NW, ca. 1.1 mi E of its intersection with Parker Road NW, in disturbed very wet loamy pine savanna, occurring with *Tiedemannia filiformis*, *Iris tridentata*, *Rhynchospora* spp., *Sporobolus teretifolius*, *Carex striata* var. brevis, *Cyrilla racemiflora*, *Clethra alnifolia*, *Ilex glabra*, 34.147107, –78.491226, 9 Aug 2019, E. *Ungberg* 446 (NCU, not yet accessioned).

Rhynchospora sulcata [Cyperaceae]

Rhynchospora sulcata (Grooved Beaksedge, G3) is reported as part of the native flora of North Carolina from two collections, both taken in Scotland County (Fig. 16). In August of 2020, visits to a Carolina Bay complex northeast of Laurinburg, North Carolina resulted in a collection of *Rhynchospora sulcata*. The plant was dominant to co-dominant in several places along the eastern margin of the flooded bay. Following this, an evaluation of herbarium specimens from the same site revealed an earlier collection by B.A. Sorrie from 1992, originally determined to be *Rhynchospora microcarpa* Baldwin ex A. Gray. Compared to *Rhynchospora sulcata* has lateral inflorescences along a greater portion of the culm and more deeply scalloped alveoli on the achene surfaces.

Given the frequent lumping of *Rhynchospora sulcata* within *Rhynchospora microcarpa*, specimens of the former have often been erroneously attributed to the latter. McMillan annotated a number of these specimens during herbarium work supporting his volume *Rhynchospora (Cyperaceae) of South Carolina and the Eastern United States*, but there remain several collections of *Rhynchospora microcarpa* from the inner Coastal Plain of South Carolina that are clearly *Rhynchospora sulcata*. While the *Flora of the Southeastern United States* (Weakley & Southeastern Flora Team 2022) indicates that *Rhynchospora microcarpa* inhabits Carolina bays, this statement is likely based on these erroneous identifications. In North Carolina, *Rhynchospora microcarpa* occurs exclusively in the outer Coastal Plain, and often in areas with some calcareous influence, such as coastal marshes, maritime woodlands, and calcareous savannas. *Rhynchospora sulcata* inhabits Carolina bays and limesink ponds or dolines and should be sought in these habitats elsewhere in North Carolina are likely to represent *Rhynchospora microcarpa* from the inner Coastal Plain of North and South Carolina are likely to represent *Rhynchospora sulcata*.

The discovery of this species in North Carolina represents a significant northward range expansion. The nearest collections are from several South Carolina counties near the Georgia state line, some 150 miles to the southwest. Given that this is the northernmost population of a globally vulnerable taxon (G3; NatureServe 1997) by a considerable distance, and to date the only one known for North Carolina, we propose a state conservation ranking of S1 and its inclusion on the state list of tracked and rare species as "Significantly Rare – Throughout" (SR-T).



Fig. 16. Rhynchospora sulcata. Margin of clay-based Carolina bay, Tunstall's Bay, Scotland Co. NC. Photo by E.A. Ungberg.

Voucher Specimens: **NORTH CAROLINA. Scotland Co.:** Tunstall's Bay, Route 401 NE of Laurinburg, graminoid dominated, no standing water, common on exposed bottom with *Rhynchospora filifolia*, *Panicum hemitomon*, *Scleria reticularis*, *Ludwigia suffruticosa*, 34.847938, –79.399927, 11 Jul 1992, B.A. Sorrie 6606 (NCU0011485); E margin of Big Cypress Meadow in ground disturbed by vehicle tracks, with *Rhynchospora careyana*, *Rhynchospora nitens*, *Dichanthelium wrightianum*, *Pinus taeda*, 34.848497, –79.399868, 6 Aug 2020, E. Ungberg s.n. (NCU, not yet accessioned) (Fig. 16)

Croton michauxii [Euphorbiaceae]

Croton michauxii is reported as occurring in North Carolina from two specimens collected in Brunswick Co , first in 2006 and again in 2020. Weakley and Southeastern Flora Team (2022) notes its habitat as longleaf pine sandhills and disturbed sandy soils, habitats easily found in adjacent areas of North Carolina. *Croton michauxii* and *Croton willdenowii* G.L. Webster are variously treated as separate species or as two varieties of a broadly considered *Croton michauxii*. *Croton willdenowii* occurs widely throughout the Piedmont and mountain regions of North Carolina, most often on or near rock outcrops, barrens, and glades. *Croton willdenowii* is also found in the sandhills but is otherwise absent from the Southeastern Coastal Plain – thus its presence in Brunswick Co. was somewhat unusual. The determination of Brunswick Co. specimens to represent *Croton michauxii* makes biogeographical sense given its predominantly Coastal Plain distribution and presence in Horry Co., South Carolina, immediately adjacent to Brunswick Co.

Differences between the two taxa are subtle, and certain characters, such as leaf-width, overlap. The most informative morphological differences for identifying *Croton michauxii* include greater inflorescence length (greater than or equal to 1 cm versus less than 0.5 cm), number of capsules per inflorescence (3–6 versus 1–2), and the density/diameter of leaf adaxial surface stellate trichomes (not strongly overlapping or intersecting).

The collection from 2006 (NCU00096918) was originally correctly identified as *C. michauxii* but subsequently annotated to *C. willdenowii*. After making my 2020 collection, I reviewed other *Croton* specimens from the area and agreed with the original determination by J.C. Morris. B.A. Sorrie has since reviewed both specimens and concurred with the determinations of *C. michauxii*.

Given the lack of specimens for this taxon from the otherwise heavily collected Brunswick County, we recommend that *Croton michauxii* be given a state conservation ranking of S1 in North Carolina and be included on the state list of tracked and rare species as "Significantly Rare – Periphery" (SR-P).

Voucher Specimens: NORTH CAROLINA. Brunswick Co.: Boiling Springs Lakes Preserve, Beaver Dam Quad, in longleaf pine savanna at edge of large doline pond with *Pinus palustris*, *Aristida stricta*, and *Vaccinium crassifolium*, 20 Sep 2006, *J.C. Morris 060606-15* (NCU00096918); Boiling Springs Lakes, E side of Lee Buck Road SE at intersection with Creek Walker Trail, SE. 34.127, –78.038, 6 Oct 2020; *E. Ungberg 654* (NCU00443955).

ACKNOWLEDGMENTS

SGW thanks Carol Ann McCormick and Shanna Oberreiter for physical and digital voucher preparation and USF herbarium staff for providing open access to their numerous digital herbarium records. He thanks Steve Orzell and Edwin Bridges for insights on the description of *Trilisa subtropicana* and discussions on variation within Florida Peninsula composites. SPG thanks Justin Thomas for encouragingly reviewing a very early draft, and for examining the type illustration and confirming its identity. Melanie Schori reviewed and suggested important adjustments to a draft. Rachel Goad has led, and Claire M. Ciafré has partnered, in our study of Pennsylvania *Desmodium*. JWH thanks Melanie Schori for nomenclatural advice, Sherri Emer (FGCU) for help with imaging seeds, and the Florida Native Plant Society for funding. ASW thanks Arthur Haines, Michael Hassler, Petra Korall, Carl Rothfels, Alan R. Smith, Iván Valdespino, Stina Weststrand, and LiBing Zhang for discussions and diverse and divergent opinions about the circumscription of genera in Selaginellaceae. We thank ARCH, CM, DUKE, FLAS, FSU, FTG, GA, GH, IND, LSU, MICH, MO, NCU, NEON-ASU, NY, PH, PIHG, SEL, TENN, UARK, UCF, US, USF, UWAL, VDB, WYU, and other herbaria, as well as SERNEC and other specimen portals, for the important work they do in curating and making available the accumulated scientific information of centuries of collection. We express our deep appreciation for support received from an anonymous donor supporting work on the Southeastern Flora Project. We thank Edwin

Bridges and Richard Carter for their helpful reviews, and Barney Lipscomb and other editorial staff at JBRIT for their careful attention to this manuscript.

REFERENCES

ALABAMA PLANT ATLAS. 2021. https://flora of Alabama.org.

- ATHIE-SOUZA, S.M., A.L. DE MELO, M.J. DA SILVA, & M.F. DE SALES. 2016. New synonyms and typifications of *Stillingia* (Euphorbiaceae). Phytotaxa 266:183–194.
- BRENDEL, F. 1879. Historical sketch of the science of botany in North America from 1635 to 1840. Amer. Naturalist 13:754–771.
- BROOKS, R.E. & A. WHITTEMORE. 1999. Juncus anthelatus (Juncaceae, Juncus subg. Pioiphylli), a new status for a North American taxon. Novon 9:11–12

BRUSCHI, P., P. GROSSONI, & F. BUSSOTTI. 2003. Within- and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. Trees 17:164–172.

CANDOLLE, A.P. DE. 1825. Prodromus Systematis Naturalis Regni Vegetabilis. Vol. 2. Treuttel & Würtz.

CHEN, D.-K., X.-M. ZHOU, C.J. ROTHFELS, L.D. SHEPHERD, R. KNAPP, L. ZHANG, N.T. LU, X.-P. FAN, X. WAN, X.-F. GAO, H. HE, & L.B. ZHANG. 2021. A global phylogeny of Lycopodiaceae (Lycopodiales: Lycophytes) with the description of a new genus, *Brownseya*, from Oceania. Taxon 71:25–51.

CHOLEWA, A.F. 2009. *Lysimachia*. In: Flora of North America Editorial Committee. Flora of North America north of Mexico. Volume 8, Magnoliophyta: Paeoniaceae to Ericaceae. Oxford Univ. Press, New York, NY, U.S.A.

CHRISTENHUSZ, M.J.M. & M.W. CHASE. 2014. Trends and concepts in fern classification. Ann. Bot. (Oxford) 113:571–594.

CHRISTENHUSZ, M.J.M. & M.W. CHASE. 2018. PPG recognizes too many fern genera. Taxon 67:481–487.

CLEMANTS, S.E. & S.L. MOSYAKIN. 2003. Chenopodium. In Flora of North America Editorial Committee. 2003b. Flora of North America north of Mexico. Volume 4, Magnoliophyta: Caryophyllidae, part 1. Oxford Univ. Press, New York, NY, U.S.A.

CONSEA, M.À., M. MUS, & J.A. ROSSELLÓ. 2012. Leaf shape variation and taxonomic boundaries in two sympatric rupicolous species of *Helichrysum* (Asteraceae: Gnaphalieae), assessed by linear measurements and geometric morphology. Biol. J. Linn. Soc. 106:498–513.

CONSORTIUM OF NORTHEASTERN HERBARIA. 2021. https://neherbaria.org

CRONQUIST, A. 1947. Notes on the Compositae of the northeastern United States. V. Astereae. Bull. Torrey Bot. Club 74:142–150.

CRONQUIST, A. 1980. Vascular flora of the southeastern United States. I. Asteraceae. Univ. North Carolina Press, Chapel Hill, U.S.A.

DARLINGTON, W. 1837. Flora Cestrica: An attempt to enumerate and describe the flowering and filicoid plants of Chester County, in the State of Pennsylvania. Simon Seigfried. https://www.biodiversitylibrary.org/page/39674806.

DELANEY, K., N. BISSETT, & J.D. WEIDENHAMER. 1999. A new species of *Carphephorus* (Asteraceae; Eupatorieae) from peninsular Florida. Bot. Explor. 1:1–15

DENNY, M. 1948. Linnaeus and his disciple in Carolina: Alexander Garden. Isis 38:161–174.

DIGGS, G.M., JR. & B.L. LIPSCOMB. 2014. The ferns and lycophytes of Texas. Bot. Res. Inst. Texas, Fort Worth, TX, U.S.A.

DILLENIUS, J.J. 1732. Hortus Elthamensis Seu Plantarum Rariorum Quas In Horto Suo Elthami In Cantio. Vol. 1. 2 vols. London. https://bibdigital.rjb.csic.es/idurl/1/10700.

ESTES, D., J. SHAW, & C. MAUSERT-MOONEY. 2015. *Lysimachia lewisii* (Primulaceae): A new species from Tennessee and Alabama. Phytoneuron 2015-17:1–15.

FAWCETT, S., & A.R. SMITH. 2021. A generic classification of the Thelypteridaceae. J. Bot. Res. Inst. Texas Press, Fort Worth, TX, U.S.A.

FAWCETT, S., A.R. SMITH, M. SUNDUE, J.G. BURLEIGH, E.B. SESSA, L.-Y. KUO, C.-W. CHEN, W.L. TESTO, M. KESSLER, GOFLAG CONSORTIUM, & D.S. BARRINGTON. 2021. A global phylogenomic study of the Thelypteridaceae. Syst. Bot. 46:891–915.

FERNALD, M.L.1940. A century of additions to the flora of Virginia. Rhodora 42:492–495; pl. 647, 648.

FERNALD, M.L. 1950. Gray's Manual of Botany. 8th Edition. Van Nostrand, New York, U.S.A.

GLEASON, H.A. & A. CRONQUIST. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden and Hafner Press, New York, N.Y., U.S.A.

GLEASON, H.A. & A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. Subsequent edition. New York Botanical Garden, Bronx, N.Y., U.S.A.

HAINES, A.A. 2011. New England Wildflower Society's Flora Novae Angliae, a manual for the identification of native

and naturalized higher vascular plants of New England. New England Wildflower Society and Yale Univ. Press, New Haven, CT, U.S.A.

- HAO, G., Y.-M. YUAN, C.-M. HU, X.-J. GE, & N.-X. ZHAO. 2004. Molecular phylogeny of *Lysimachia* (Myrsinaceae) based on chloroplast *trn*L-F and nuclear ribosomal ITS sequences. Molec. Phylogen. Evol. 31:323–339.
- HUFFMAN, J. M. & W. S. JUDD. 1998. Vascular flora of Myakka River State Park, Sarasota and Manatee counties, Florida. Castanea 63:25–50.
- HUFT, M.J. 2016. *Stillingia*. In: Flora of North America Editorial Committee, eds. Flora of North America North of Mexico. Oxford University Press, New York, U.S.A., and Oxford, U.K. 12:233–234.
- JOHNSTON, M.C. & B.H. WARNOCK. 1963. The three species of *Stillingia* (Euphorbiaceae) in far western Texas. S. W. Naturalist 8:100–106.
- KARTESZ, J. 2020. BONAP: North American Plant Atlas. http://bonap.net/napa.
- KASSAMBARA, A. 2021. rstatix: pipe-friendly framework for basic statistical tests, version 0.7.0. Available at: https://cran.rproject.org/web/packages/rstatix/.
- KIRSCHNER, J. 2002. Juncaceae 3: *Juncus* subg. *Agathryon*. In: A. E. Orchard, J. Bleverveen, A.J.G. Wilson & B. Kuchlmayer, eds. Species plantarum: flora of the world, part 8. Biological Resources Study, Canberra, Australia.
- KLAUS, K.V., C. SCHULZ, D.S. BAUER, & T. STÜTZEL. 2017. Historical biogeography of the ancient lycophyte genus *Selaginella*: Early adaptation to xeric habitats on Pangea. Cladistics 33(5):469–480.
- MANNS, U. & A. ANDERBERG. 2009. New combinations and names in *Lysimachia* (Myrsinaceae) for species of *Anagallis*, *Pelletiera* and *Trientalis*. Willdenowia 39:49–54.
- McDonald, J.H. 2014. Handbook of biological statistics, third edition. Sparky House Publishing, Baltimore, MD, U.S.A.
- MOHLENBROCK, R.H. 2014. Vascular flora of Illinois: A field guide, 4th edition. SIU Press, Carbondale, IL, U.S.A.
- MÜLLER ARGOVIENSIS, J. 1866. Euphorbiaceae (excl. Euphorbieae). In: Candolle, A.L.P.P. de, ed. Prodromus systematis naturalis regni vegetabilis. Treuttel et Würtz, Paris, France. 15(2):189–1286.
- NESOM, G.L. 2006. Carphephorus odoratissimus. In: Flora of North America, Vol. 21. Magnoliophyta: Asteridae: Asteraceae. Oxford Univ. Press, New York, U.S.A. and Oxford, U.K. P. 536.
- OHASHI, H. 2013. New combinations in North American *Desmodium* (Leguminosae: Tribe Desmodieae). J. Jap. Bot. 88:166–75.
- ORZELL, S. L. & E. L. BRIDGES. 2002. Notes on Carphephorus odoratissimus (Asteraceae) in peninsular Florida, U.S.A. Sida 20:559–569.
- ORZELL, S. L. & E.L. BRIDGES. 2006. Species composition and environmental characteristics of Florida dry prairies from the Kissimmee River region of south-central Florida. In R.F. Noss, ed. Land of fire and water: Proceedings of the Florida Dry Prairie Conference. E.O. Painter, DeLeon Springs, Florida. U.S.A. Pp. 100–135
- ORZELL S.L. & E.L. BRIDGES. 2017. The "subtropicana" entity warrants species rank, now in *Trilisa*. In: Weakley, A.S. (& 14 others). New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. II. J. Bot. Res. Inst. Texas 11:291–325.
- R CORE TEAM. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.
- RADFORD, A.E., H.E. AHLES, & C.R. BELL. 1968. Manual of the vascular flora of the Carolinas. UNC Press, Chapel Hill, N.C., U.S.A. ROGERS, D.J. 1951. A revision of *Stillingia* in the New World. Ann. Missouri Bot. Gard. 38:207–259.
- ROGERS, G. 2021. Notes of the natural history of *Stillingia aquatica* (Euphorbiaceae): With special attention to reproductive biology. J. Bot. Res. Inst. Texas 15:183–199.
- Schilling, E.E. 2011. Hybrid genera in Liatrinae (Asteraceae: Eupatorieae). Molec. Phylogen. Evol. 59:158–167.
- SCHNEIDER, C.A., W.S. RASBAND, & K.W. ELICEIRI. 2012. NIH Image to Image: 25 years of image analysis. Nat. Methods 9:671–675.
- SCHMIDT, A.R., L. REGALADO, S. WESTSTRAND, P. KORALL, E.-M. SADOWSKI, H. SCHNEIDER, E. JANSEN, J. BECHTELER, M. KRINGS, P. MÜLLER, B. WANG, X. WANG, J. RIKKINEN, & L.J. SEYFULLAH. 2020. Selaginella was hyperdiverse already in the Cretaceous. New Phytol. 228:1176–1182.
- SCHUBERT, B.G. 1950. Desmodium: Preliminary studies -- III. Rhodora 52:135–55.
- Schuettpelz, E., G. Rouhan, K.M. Pryer, C.J. Rothfels, J. Prado, M.A. Sundue, M.D. Windham, R.C. Moran, & A.R. Smith. 2018. Are there too many fern genera? Taxon 67:473–480.
- SHI, P., K. Yu, Ü. NIINEMETS, & J. GIELIS. 2020. Can leaf shape be represented by the ratio of leaf width to leaf length? Evidence from nine species of *Magnolia* and *Michelia* (Magnoliaceae). Forests 12:41. doi:10.3390/f12010041

- SEMPLE, J.C. & J.G. CHMIELEWSKI. 2006. *Doellingeria*. Flora of North America. Vol. 20, Magnoliophyta: Asteridae (in part): Asteraceae, part 2. Oxford Univ. Press, New York, U.S.A.
- SEMPLE, J.C., J.G. CHMIELEWSKI, & C. LEEDER. 1991. A multivariate morphometric study and revision of Aster subg. Doellingeria sect. Triplopappus (Compositae: Astereae): The Aster umbellatus complex. Canad. J. Bot. 69:256–275.

SERNEC (SOUTHEASTERN REGIONAL NETWORK OF EXPERTISE AND COLLECTIONS). 2021. https://sernecportal.org

SMALL, J.K. 1898. Studies in the botany of the southeastern United States -- XV. Bull. Torrey Bot. Club 25:605–621.

SMALL, J.K. 1903. Flora of the southeastern United States: Being descriptions of the seed-plants, ferns and fern-allies growing naturally in North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, Louisiana and the Indian territory and in Oklahoma and Texas east of the one-hundredth meridian. Published by the author, New York, New York, U.S.A.

SMALL, J.K. 1905. Additions to the flora of subtropical Florida. Bull. New York Bot. Gard. 3:419–453.

- SMALL, J.K. 1913. Flora of the southeastern United States, being descriptions of the seed-plants, ferns and fern-allies growing naturally in North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, and in Oklahoma and Texas east of the one hundredth meridian, second edition. Published by the author, New York, NY, U.S.A.
- SMALL, J.K. 1933. Manual of the southeastern flora: Being descriptions of the seed plants growing naturally in Florida, Alabama, Mississippi, eastern Louisiana, Tennessee, North Carolina, South Carolina and Georgia. University of North Carolina Press, Chapel Hill, North Carolina, U.S.A.

STÄHL, B. & A.A. ANDERBERG. 2004. Myrsinaceae. In Kubitzki, K., ed. 2004. The families and genera of vascular plants. VI. Flowering plants – Dicotyledons – Celastrales, Oxalidales, Rosales, Cornales, Ericales. Springer, Berlin, Germany.

- THOMAS, J.R. 2020. *Desmodium glabellum* and *D. perplexum* (Fabaceae): A morphological reevaluation. Missouriensis 38:29–50.
- TURLAND, N.J. (& 15 OTHER EDS.). 2018. International code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Veg. 159. Koeltz Botanical Books, Glashütten, Germany. doi:10.12705/Code.2018
- Voss, E.G. & A.A. REZNICEK. 2012. Field manual of Michigan flora. University of Michigan Press, Ann Arbor, MI, U.S.A.
- WEAKLEY, A.S. 2020. Flora of the southeastern United States. Edition of 20 October 2020. UNC Chapel Hill Herbarium and NC Botanical Garden, Chapel Hill, NC, U.S.A.
- WEAKLEY, A.S. & SOUTHEASTERN FLORA TEAM. 2022. Flora of the southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC, U.S.A.
- WEAKLEY, A.S., J.C. LUDWIG, & J.F. TOWNSEND. 2012. Flora of Virginia. 1st ed. Bland Crowder ed. Foundation of the Flora of Virginia Project, Richmond. Fort Worth: Botanical Research Institute of Texas Press, Fort Worth, TX, U.S.A.
- WEAKLEY, A.S., R.J. LEBLOND, B.A. SORRIE, C.T. WITSELL, L.D. ESTES, K.G. MATHEWS, A. EBIHARA, & K. GANDHI. 2011. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. J. Bot. Res. Inst. Texas 5:437–455.
- WEAKLEY, A.S., D.B. POINDEXTER, R.J. LEBLOND, B.A. SORRIE, C.H. KARLSSON, P.J. WILLIAMS, E.L. BRIDGES, S.L. ORZELL, B.R. KEENER, A. WEEKS, R.D. NOYES, M. FLORES-CRUZ, J.T. DIGGS, G.D. GANN, & A.J. FLODEN. 2017. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. II. J. Bot. Res. Inst. Texas 11:291–325.
- WEAKLEY, A.S., D.B. POINDEXTER, R.J. LEBLOND, B.A. SORRIE, E.L. BRIDGES, S.L. ORZELL, A.R. FRANCK, M. SCHORI, B.R. KEENER, A.R. DIAMOND, JR., A.J. FLODEN, & R.D. NOYES. 2018. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. III. J. Bot. Res. Inst. Texas 12:27–67.
- WEAKLEY, A.S., B.A. SORRIE, R.J. LEBLOND, D.B. POINDEXTER, A.J. FLODEN, E.E. SCHILLING, A.R. FRANCK, & J.C. KEES. 2018. New combinations, rank changes, and nomenclatural and taxonomic comments in the vascular flora of the southeastern United States. IV. J. Bot. Res. Inst. Texas 12:461–480.
- WEAKLEY, A.S., R.K.S. McClelland, R.J. LeBlond, K.A. Bradley, J.F. Matthews, C. Anderson, & A.R. Franck. 2019. Studies in the vascular flora of the southeastern United States: V. J. Bot. Res. Inst. Texas 13:107–129.
- WEAKLEY, A.S., D.B. POINDEXTER, H.C. MEDFORD, B.A. SORRIE, C.A. MCCORMICK, E.L. BRIDGES, S.L. ORZELL, K.A. BRADLEY, H.E. BALLARD, JR., R.N. BURWELL, S.L. LOCKHART, & A.R. FRANCK. 2020. Studies in the vascular flora of the southeastern United States. VI. J. Bot. Res. Inst. Texas 14(2):199–239.
- WEAKLEY, A.S., D.B. POINDEXTER, H.C. MEDFORD, A.R. FRANCK, K.A. BRADLEY, J. SADLE, & J.M. KELLEY. 2021. Studies in the vascular flora of the southeastern United States. VII. J. Bot. Res. Inst. Texas 15:23–56.
- WERIER, D. 2017. Catalogue of the vascular plants of New York state. Mem. Torrey Bot. Soc. 27.

WESTSTRAND, S. & P. KORALL. 2016b. A subgeneric classification of *Selaginella* (Selaginellaceae). Amer. J. Bot. 103:2160–2169.

WESTSTRAND, S. & P. KORALL. 2016a. Phylogeny of Selaginellaceae: There is value in morphology after all! Amer. J. Bot. 103:2136–2159.

WIEGAND, K.M. 1900. Juncus tenuis Willd. and some of its North American allies, Bull. Torrey Bot. Club 27:523–524.

WILBUR, R.L. & M.K. WHITSON. 2005. The identity of Riddell's seven validly published but over-looked pteridophytic binomials. Amer. Fern J. 95:160–169.

WUNDERLIN, R.P. & B.F. HANSEN. 2001. Seven new combinations in the Florida flora. Novon 11:366–369.

- WUNDERLIN, R.P. & B.F. HANSEN. 2011. Guide to the vascular plants of Florida, third edition. University Press of Florida, Gainesville, Florida, U.S.A.
- YAN, H.-F., C.-Y. ZHANG, A.A. ANDERBERG, G. HAO, X.-J. GE, & J.J. WIENS. 2018. What explains high plant richness in east Asia? Time and diversification in the tribe Lysimachieae (Primulaceae). New Phytologist 219:436–448.
- ZHOU, X.-M. & L.-B. ZHANG. 2015. A classification of *Selaginella* (Selaginellaceae) based on molecular (chloroplast and nuclear), macro-morphological, and spore features. Taxon 64:1117–1140.
- ZHOU, X.-M., C.J. ROTHFELS, L. ZHANG, Z.-R. HE, T. LE PECHON, H. HE, N.T. LU, R. KNAPP, D. LORENCE, X.-J. HE, X.-F. GAO, & L.-B. ZHANG. 2016. A large-scale phylogeny of the lycophyte genus *Selaginella* (Selaginellaceae: Lycopodiopsida) based on plastid and nuclear loci. Cladistics 32:360–389.