

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

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ABSTRACT

Hexastylis viridistylis (Aristolochiaceae) is described as a novel species distinguished from other species in the genus by a unique combination of morphological characters including style and ovary color and dimensions, stamen morphology, calyx tube dimensions, and fruiting characteristics. The range, habitat, phenology, and potential affinities to other species in the group are discussed in detail. We propose treating a number of taxa at species rank, elevating them from infraspecific ranks, to appropriately recognize their degree of isolation and distinctiveness compared to their relatives: **Chrysopsis dressii** (Semple) Weakley & S.G. Ward, **Echinacea neglecta** (McGregor) Weakley & A.P. Campos, **Echinacea strigosa** (McGregor) Weakley & A.P. Campos, **Phacelia lundelliana** (Constance) E.L. Keith & Weakley, and **Houstonia glabra** (Terrell) Weakley & D.B. Poind. In *Dioscorea*, we reassess a long-ongoing controversy regarding whether to recognize two or three native species, and clarify the distinctions between and distributions of **Dioscorea villosa** and **D. quaternata**, recognizing them at species rank, in addition to the uncontroversial *D. floridana*. In *Sideroxylon* sect. *Frigoricola*, we propose that the taxon named by J.K. Small as **Bumelia lacuum** does warrant taxonomic recognition as an entity separate from *Sideroxylon tenax*, but that the evidence suggests incomplete evolutionary separation of the two, and we therefore provide a name at varietal rank, **Sideroxylon tenax** var. **lacuum** (Small) S.G. Ward & Weakley and discuss its differentiation from var. *tenax*. Important distributional records (including additions, subtractions, clarifications, and other notable records) are made for the State of South Carolina and the Commonwealth of Virginia.

RESUMEN

Hexastylis viridistylis (Aristolochiaceae) se describe como una especie nueva diferenciada de otras especies del género por una combinación única de caracteres morfológicos, incluyendo el color y las dimensiones del estilo y el ovario, la morfología del estambre, las dimensiones del tubo del cáliz y las características del fruto. Se discuten en detalle su distribución, hábitat, fenología y las posibles afinidades con otras especies del grupo. Proponemos tratar varios taxones con el rango de especie, elevándolos desde rangos inferiores, para reconocer adecuadamente su grado de aislamiento y distintividad en comparación con sus parientes: **Chrysopsis dressii** (Semple) Weakley & S.G. Ward, **Echinacea neglecta** (McGregor) Weakley & A.P. Campos, **Echinacea strigosa** (McGregor) Weakley & A.P. Campos, **Phacelia lundelliana** (Constance) E.L. Keith & Weakley, y **Houstonia glabra** (Terrell) Weakley & D.B. Poind. En *Dioscorea*, reevaluamos una polémica que ha estado vigente por mucho tiempo sobre si se deben reconocer dos o tres especies nativas, y aclaramos las diferencias y distribuciones de **Dioscorea villosa** y **D. quaternata**, reconociéndolas a nivel de especie, además de la incontestable *D. floridana*. En *Sideroxylon* sect. *Frigoricola*, proponemos que el taxón nombrado por J.K. Small como **Bumelia lacuum** sí merece reconocimiento taxonómico como un ente separado de *Sideroxylon tenax*, pero que la evidencia sugiere una separación evolutiva incompleta entre ambos, por lo que proporcionamos un nombre a nivel de variedad, **Sideroxylon tenax** var. **lacuum** (Small) S.G. Ward & Weakley, y discutimos su diferenciación de la var. *tenax*. Se registran datos importantes de distribución (incluyendo adiciones, sustracciones, aclaraciones y otros registros notables) para el estado de Carolina del Sur y el estado de Virginia.

INTRODUCTION

We here present an eleventh volume of taxonomic descriptions, reassessments of taxonomy, generic transfers, rank changes, typifications, reassessments of nativity and establishment status in the regional flora, significant range records for native and non-native taxa, all related to the southeastern United States, as defined by the Southeastern Flora Project (Weakley & Southeastern Flora Team 2025). This 11th volume is contributed by 17 authors and follows similar conventions and philosophical approaches as the earlier volumes in the series, published from 2011 to 2023; citations for these can be found in Weakley et al. (2023, 2024). Primary authorship is cited for each section of this paper, as follows: *Hexastylis* (PDM, ZAH, ABI, HJ), *Chrysopsis* (ASW,

SGW), *Echinacea* (APC, ASW, ABu, NA, JT, TW), *Dioscorea* (BAS), *Phacelia* (ELK & ASW), *Houstonia* (ASW & DBP), *Sideroxylon* (SGW & ASW), South Carolina records (EU, KB), and a significant Virginia record (JS). These sections are citable based on the primary author(s) of the section.

ASARACEAE (OR ARISTOLOCHIACEAE S.L.)

Hexastylis viridistylis (Aristolochiaceae), a novel species from the Piedmont, Alabama Valley, and Cumberland Plateau of Alabama, and Piedmont and Blue Ridge of Georgia

Primary authors: Patrick D. McMillan, Zachary A. Hill, Adam Black, and Hayes Jackson

A study was initiated by the first author in 1994 during a course on plant biogeography as a student at the University of North Carolina at Chapel Hill with the goal of observing and collecting detailed morphological and ecological data on the *Hexastylis virginica* group. The initial results of this study were never published in the scientific literature but the results have been cited by others studying this taxonomically confusing group (Padgett 2004). The collection of data has continued for over 30 years and has resulted in a large dataset of morphological and ecological information as well as ground-truthing of over 1000 locations to better understand the geographic range of all morphological expressions within and among species. All taxonomic literature on this group prioritizes the shape and dimensions of the calyx in distinguishing taxa and this trait is difficult to preserve in dried specimens. This fact inspired the 30+ years of observation of live material in the field.

Well-curated living collections can be incredibly important for the observation of subtle variations, environmental requirements, and life-history information of individual species. Large collections representing populations of plants from throughout their geographic ranges can provide even more insight into taxa with difficult or imprecise definition. Such is the case with heartleaves (*Hexastylis*). The keen observation of Zac Hill, both in the field and in his role as taxonomist at Juniper Level Botanic Garden resulted in bringing the unusual plants that have been assigned to *Hexastylis heterophylla* from Alabama to the senior author's attention several years prior to the preparation of this manuscript. The senior author first encountered this distinctive species during a trip through north Georgia in 1995, but without the living material it might never have been distinguished.

Most species currently assigned to the *Hexastylis virginica* group are separated based on subtle differences in the calyx (Blomquist 1957; Gaddy 1987; Sinn 2015; Weakley & Southeastern Flora Team 2025). It was a surprise to find that plants from Alabama and Georgia representing this newly recognized taxon have a suite of distinctive and easy to observe morphological characteristics that clearly differentiate it from all other similar species. The distinctive color and morphology of the elongate style extensions and ovary are often evident even in dried specimens.

MATERIALS AND METHODS

Herbarium specimens were examined using SERNEC—Southeast Regional Network of Expertise and Collections (SERNEC Data Portal 2025). These specimens were utilized to identify populations for verification in the field. Georgia populations were visited and verified by the senior author in the spring of 1995 and 2025. Populations in Alabama were visited and verified by Adam Black and Hayes Jackson in the spring of 2025. Living specimens from Cleburne County, Alabama housed at the Juniper Level Botanic Garden were also utilized for morphological study. Fresh flowers from locations throughout the range of the species were examined, flowers and plants were photographed and morphological data was collected. In total, 77 fresh flowers from nine locations were used in the preparation of the morphological descriptions of the flowers. Vegetative data was collected from living specimens as well as herbarium specimens. This morphological data was compared to all other species in the *Hexastylis virginica* group using published descriptions and our morphologic data set (n=761).

This study is unique in the large number of flowers used for the description of the species. This has been done to encompass as much of the morphological variation as possible. Most descriptions and studies have

utilized very small data sets when describing novel species in the *Hexastylis virginica* species group with the largest set published being based on the examination of 42 individual flowers (Sinn 2015). Gaddy (1987) suggested that field biologists try to collect “average” flowers to correctly determine the species. *Hexastylis* produces flowers with different proportions and coloration depending on the degree of “protection” of the developing flowers; those produced under thick leaf litter or other cover are often larger in all respects, with thinner calyx walls, and light coloration. This study was designed to incorporate as much variation as possible so that any flowers seen by a researcher could be identified to the correct species.

The geographic range reported here is based on field verified specimens as well as those which represent this species based on evident characters of the styles observed in dried specimens. Observations reported on iNaturalist (2025) were also consulted. This was done by searching for *Hexastylis heterophylla* as well as *Hexastylis* in general.

Data on associated species and edaphic conditions were collected in the field by Patrick McMillan, Adam Black, and Hayes Jackson.

RESULTS

***Hexastylis viridistylis* P.D. McMillan, sp. nov. (Fig. 1).** TYPE: U.S.A. ALABAMA. Cleburne Co.: sandy loam of pine-hardwood ravine, just e of Coleman Lake and se Pine Glen, Talladega Nat. Forest, 24 Apr 1978, R. Kral 61636 (HOLOTYPE: BRIT:VDB).

Diagnosis.—*Hexastylis viridistylis* is superficially similar to *Hexastylis heterophylla*, *H. shuttleworthii*, and *H. harperi*. The calyx dimensions are similar in size to *H. heterophylla*. *Hexastylis viridistylis* can be distinguished from *H. heterophylla* by the conspicuous, and longer green, yellow or white styles and ovary, and the smaller stigma. It is additionally distinguished by the nearly sessile or very short filaments that are adnate to the ovary over ½ or more of their length and attached well above the base of the ovary. It also consistently lacks a conspicuous flare on the calyx tube. It is easily distinguished from *H. shuttleworthii* and *H. harperi* by calyx shape and size, being smaller in all dimensions of the calyx tube and with tubes cylindrical to broadly cylindrical in outline not broadly urceolate-campanulate as in *H. shuttleworthii* and *H. harperi*. Additionally, in flowering material examined before the ovary expansion following pollination, the ovary is not nearly as raised or narrow as that of *H. harperi* or *H. shuttleworthii*.

Description.—Evergreen perennial herb, clump-forming with short rhizomes. Petioles smooth, 5–20 cm long; Leaf blades with minutely revolute, entire margins, glabrous, 4.4–9.0 cm long, cordate, triangular-cordate to narrowly triangular-cordate, rarely nearly hastate, blades dark lustrous green adaxially, typically strongly mottled with lighter coloration, the variegation pattern following the venation, or less commonly lacking variegation, pale green abaxially, the margins entire. Leaf base cordate. Leaf apex obtuse to rounded, frequently emarginate. Venation of leaves with primary and secondary veins slightly impressed on the adaxial surface, raised on the abaxial surface. Calyx tubes not particularly brittle, rather thin in texture, cylindric to broadly cylindric, lacking a significant flare or with a slight flare located above the middle of the calyx tube; tubes lacking a constriction near the calyx lobes or with a slight constriction near the calyx lobes, this constriction gradual and less than 3.2 mm narrower than the maximum width of the calyx tube; the fused portion of calyx 9.8–20.4 mm long and 11.2–20 mm wide, 0.78–1.26 × longer than wide; outer surface of calyx tube glabrous, the coloration a dingy brownish-purple, often suffused with green in flowers developing above the leaf cover or otherwise exposed, light tan or even cream with pinkish freckles in flowers protected by deep leaf cover; inner surface of calyx tube with short puberulent reddish trichomes in the distal half, reticulate in the proximal portion of the tube with prominent vertical ridges and weakly defined, lower, and irregular horizontal ridges, these horizontal ridges more developed and taller in flowers exposed to the elements and weak or even virtually absent in flowers protected by deep litter; the ridges anastomosing to produce broad pits, particularly in exposed flowers; opening width of calyx tube at lobes (6.4) 7.9–14.2 mm wide; calyx lobes triangular, with small auricles where the lobes are reflexed away from the calyx tube, the actual attachment extending down the tube a short (<1 mm) distance from the point of reflection; 5.4–14.5 mm long and 7.1–17.4 mm wide, generally wider than long; the lobes generally reflexed nearly 90 degrees from the plane of the calyx tube and often



FIG. 1. *Hexastylis viridistylis* (left) type specimen, (right) detail of dried flowers from the type showing the preservation of yellowish-green coloration of styles.

with the tips recurved towards the base of the calyx tube; calyx lobes smooth on outer surface, puberulent with reddish trichomes on inner surface; inner surface rugulose to ridged reticulate with a shorter continuation of the dense ridged reticulation of the inner calyx tube; inner surface of calyx lobes varying in base color from purple-brown with lighter spotting to cream with pinkish or purplish spotting or reticulate patterns. *Stamens* with a very short (<0.2 mm) filament below thecae, the filaments adnate to the developing ovary for $\frac{1}{2}$ of their length or more, attached to the elevated base of the ovary; filament and connective flattened in cross section and extending a very short distance beyond the thecae; thecae 2.0–3.7 mm long, dehiscence extrorse. Ovary 6-locular, superior, white, yellowish or greenish in coloration; styles 3.4–5.9 mm long, green, greenish white, yellowish-green or white, often becoming more vibrant green towards the style extension. **Fruit** a 6-carpellate green or whitish fleshy capsule that matures and dehisces while the calyx is still in vibrant condition; the developing fruit does not generally distort the shape of the calyx tube as it expands; fruit dehiscence occurs through

initial splitting longitudinally followed by disintegration of the fruit, which becomes mealy and shatters, releasing the endocarp which splits longitudinally to release seeds. **Seeds** 3.0–3.2 mm long and 2.0–2.2 mm wide, smooth, broadly crescent-shaped and pale tan to glossy caramel brown with a narrow, brilliant orangish-yellow to caramel colored aril running the length of the seed.

Phenology.—Flowering (December) February–May, *fruiting* late April–June.

Distribution.—In central Alabama in The Central Uplands of the Northern Piedmont extending into the Valley and Ridge and the Warrior Basin of the Cumberland Plateau. In west-central, central and north-central Georgia in the Piedmont and lower elevations of the Blue Ridge and Ridge and Valley. Elevation: 250–725 m.

Habitat.—Found growing in mildly acid to strongly acid soils of mixed deciduous forests on bluffs, slopes, and stream banks, particularly those with a north or northeast-facing aspect and also in level ground around small intermittent or small order streams without significant sediment deposition during flooding. In Alabama many populations are found in shallow layers of loamy soil deposits over Paleozoic age Heflin Phyllite within the Talladega Metamorphic Belt. In Georgia found growing in areas of mica schist, gneiss, and amphibolite geology. Closely associated species found at most or all locations include *Liriodendron tulipifera* L., *Quercus alba* L., *Acer rubrum* L., *Pinus strobus* L., *Tsuga canadensis* (L.) Carrière, *Kalmia latifolia* L., *Rhododendron maximum* L. (GA), *Hydrangea arborescens* L. (GA), *Hydrangea quercifolia* Bartram (AL), *Polystichum acrostichoides* (Michx.) Schott, *Galax urceolata* (Poirot) Brummitt, *Trillium catesbaei* Elliott, and *Viola hastata* Michx. A more thorough list of associates is presented in Table 2.

Conservation.—This distinctive species appears to have substantial populations over a very limited range and should likely be assigned a global ranking of G3 and a corresponding rank of S2/S3 in Alabama and S2/S3 in Georgia. The populations are mostly contained on property that has been preserved as National Forest or otherwise maintained as green space through wildlife management areas or other state or local designations. It is unlikely to be lost to development or other pressures. Outlying populations should be sought in adjacent regions and any populations discovered would be targets for conserving the species and unique genetic lineages. Thorough surveying of suitable habitat in areas adjacent to known populations and range limits will likely lead to the discovery of other populations. Georgia populations are growing near Tennessee and North Carolina, where it should be sought.

Etymology.—Named for the most distinctive and easy to observe characteristic of this species, the long, green or greenish style appendages that often protrude from the flowers as the ovary expands, *viridistylis*.

Representative specimens examined: U.S.A. **ALABAMA. Calhoun Co.:** 23 Apr 1990, R. Kral 77388 (BRIT:VDB). **Cleburne Co.:** 24 Apr 1978, R. Kral 61628 (APSC, BRIT:VDB, UWAL); 24 Apr 1978, R. Kral 61639 (APSC, BRIT:VDB, UWAL); 27 Apr 1979, R. Kral 63398 (BRIT:VDB); 24 May 1987, Robert F.C. Naczi 1627 (BRIT:VDB); 23 May 1996, Robert F.C. Naczi 5475 (BOON, BRIT:VDB, KNK). **Cullman Co.:** 9 May 1985, Harold Ray s.n. (BRIT:VDB). **Etowah Co.:** 15 Apr 1991, S.P. Liverett 178 (AU). **Walker Co.:** 5 May 1956, Bruce Roberts s.n. (JSU). **Winston Co.:** 15 Apr 1973, John A. Churchill 73-41525 (MARY); 16 Apr 1978, R. Kral 61522 (BRIT:VDB, UWAL); 16 Apr 1978, R. Kral 61530 (APSC, BRIT:VDB, UWAL, VSC); 6 May 1978, R. Kral 61660 (BRIT:VDB); 21 May 1996, Robert F.C. Naczi 5432 (BOON, KNK); 21 May 1996, Charles T. Bryson 15292 (MISS). **GEORGIA. Cherokee Co.:** 28 Dec 2019, Richard Hull 733 (GA). **Dawson Co.:** 9 May 2001, Lisa Kruse 01-108 (GA, VSC); 4 Jun 2002, Lisa Kruse 02-209 (GA). **Gilmer Co.:** 12 May 1982, M. Medley 4450-82 (APSC); 17 May 1995, Patrick D. McMillan 1007 (NCU). **Murray Co.:** 26 Apr 1953, Wilbur B. Duncan 15781 (GA); 25 May 1979, N.V. Mody s.n. (GA). **Pickens Co.:** 27 May 1978, R. Kral 61598 (BRIT:VDB, FSU, TROY, UAM). **Union Co.:** 10 Jun 1942, Wilbur H. Duncan 3340 (GA).

Discussion.—Plants identified here as *Hexastylis viridistylis* have consistently been identified as *Hexastylis heterophylla* by past researchers (Blomquist 1957; Gaddy 1987; Padgett 2004). This is primarily due to the size and dimensions of the calyx tube which overlap that of *H. heterophylla* (Table 1). The most obvious features of *Hexastylis viridistylis* are the green, greenish, yellowish or white ovary and styles. No plants have been located with the dark reddish or purplish styles and style extensions that are typical of the various forms of *Hexastylis heterophylla*. *Hexastylis heterophylla* has been a “catch-all” designation for any plant with divergent to reflexed calyx lobes and a wide opening to the small calyx tube. The consequence has been the overlooking of various geographically coherent “forms” that likely represent valid taxa. A visual comparison of the flowering features of *H. viridistylis* with each of the three predominant geographical “forms” of *H. heterophylla* we have encountered is presented in Fig. 2.

TABLE 1. Calyx tube, thecae, filament, and style comparisons of *H. heterophylla* and *H. viridistylis*.

	Calyx tube length	Calyx tube width	Calyx tube length/ calyx tube width	Thecae	Filament	Styles
<i>Hexastylis heterophylla</i> from NC, SC, GA, TN (n=48)	9.2–19.9 mm	9.02–17.08 mm	0.68–1.4 x as long as wide	2.3–3.9 mm	adnate for short distance in rim-like base of ovary, not rising significantly during ovary maturation	2.9–4.7 mm, dark purple or purplish brown
<i>Hexastylis viridistylis</i> (n=77)	9.8–20.4 mm	11.2–20.0 mm	0.78–1.26 x as long as wide	2.0–3.7 mm	adnate for more than 1/2 of length, attached well-above the base of ovary, rising significantly during ovary maturation	3.4–5.9 mm, greenish to white rarely with rosy tinge towards tip of style extension

TABLE 2. Associated species noted growing in close association with *Hexastylis viridistylis*. Taxonomy and nomenclature follow Weakley & Southeastern Flora Team (2025).

<i>Acer rubrum</i>	<i>Dioscorea villosa</i>	<i>Luzula acuminata</i>	<i>Sanicula canadensis</i>
<i>Amauropelta noveboracensis</i>	<i>Endodeca serpentaria</i>	<i>Magnolia macrophylla</i>	<i>Sanicula smallii</i>
<i>Amelanchier arborea</i>	<i>Epigaea repens</i>	<i>Magnolia tripetala</i>	<i>Sitobolium punctilobulum</i>
<i>Aralia spinosa</i>	<i>Erythronium umbilicatum</i>	<i>Maianthemum racemosum</i>	<i>Smilax glauca</i>
<i>Arundinaria appalachica</i>	<i>Euonymus americanus</i>	<i>Mitchella repens</i>	<i>Smilax rotundifolia</i>
<i>Asimina triloba</i>	<i>Fagus grandifolia</i>	<i>Oxydendrum arboreum</i>	<i>Solidago tarda</i>
<i>Athyrium asplenoides</i>	<i>Galax urceolata</i>	<i>Parthenocissus quinquefolia</i>	<i>Solidago vaseyi</i>
<i>Betula lenta</i>	<i>Halesia tetraptera</i>	<i>Pinus strobus</i>	<i>Tiarella wherryi</i>
<i>Bignonia capreolata</i>	<i>Hamamelis virginiana</i>	<i>Pinus taeda</i>	<i>Tipularia discolor</i>
<i>Calycanthus floridus</i>	<i>Hexastylis ruthii</i>	<i>Polygonatum biflorum</i>	<i>Toxicodendron radicans</i>
<i>Carya tomentosa</i>	<i>Houstonia caerulea</i>	<i>Polystichum acrostichoides</i>	<i>Trillium catesbaei</i>
<i>Chamaelirium luteum</i>	<i>Hydrangea arborescens</i>	<i>Pyrularia pubera</i>	<i>Tsuga canadensis</i>
<i>Chasmanthium laxum</i>	<i>Hydrangea quercifolia</i>	<i>Quercus alba</i>	<i>Uvularia perfoliata</i>
<i>Chrysogonum repens</i>	<i>Ilex montana</i>	<i>Quercus coccinea</i>	<i>Vaccinium pallidum</i>
<i>Coreopsis pubescens</i>	<i>Ilex opaca</i>	<i>Quercus velutina</i>	<i>Viola blanda</i>
<i>Cornus florida</i>	<i>Kalmia latifolia</i>	<i>Rhododendron maximum</i>	<i>Viola hastata</i>
<i>Dichantherium dichotomum</i>	<i>Liriodendron tulipifera</i>	<i>Rubus sp.</i>	<i>Vitis rotundifolia</i>

Hexastylis viridistylis is immediately separated from the wide-ranging *H. heterophylla* based on characteristics of the ovary and style which are green, greenish-white, white or very rarely tinged with a small amount of rose towards the tip of the style extension. The green coloration of the ovary and style is best developed in flowers that are exposed to the elements and not covered by a deep layer of leaf litter (Fig. 3). When protected by litter the ovary and styles are typically pale and often more whitish than green (Fig. 4). The styles are proportionally longer compared to *H. heterophylla* and the stigmatic surface is comparatively smaller and falls apart soon after becoming viable to leave a tiny remnant mark on the style. The ovary itself has a greatly elevated base compared to *H. heterophylla* and the filaments of the stamens are adnate for approximately 1/2 or more of their length, thus often appearing sessile to the naked eye—with only the connective and thecae appearing free. This characteristic is apparent with ovary expansion following pollination. The stamens in *H. viridistylis* arise from above the base of the ovary and the position of the stamens continues to rise in position as the fruit develops. In *H. heterophylla* the stamens arise from near the base of the ovary and do not significantly change position when the ovary swells as fruits mature.

The calyx tube lacks a significant flare and has at most a very slight flare above the middle of the tube. This characteristic overlaps with some populations of *H. heterophylla* from northeastern Tennessee but otherwise *H. heterophylla* has a much better developed flare than *H. viridistylis*. The calyx tube and lobes in



FIG. 2. *Hexastylis heterophylla* (top left, Sullivan Co., TN; top right, Bath Co., VA; bottom left, Wise Co., VA) and *Hexastylis viridistylis* (bottom right). Note all forms of *Hexastylis heterophylla* display well-developed filaments below thecae and *H. viridistylis* appears nearly sessile.

H. viridistylis are considerably thinner in texture and not rigid and thick as is typical for *H. heterophylla*. Additionally, the base color of the tube is not pinkish or purplish as in *H. heterophylla* but is cream, tan, or a dingy greenish-brown with purplish or pinkish freckles or reticulations as is typical of the calyx tubes of *H. shuttleworthii* and *harperi*.

The overall resemblance of *H. viridistylis* appears closer in many ways to *H. shuttleworthii* and *H. harperi* to which we suggest it is more closely allied. The coloration of the calyx tubes is similar and the position of the stamens which arise above the base of the elevated ovary are traits shared with *H. shuttleworthii* and *H. harperi*. The styles are however much more divergent than either *H. shuttleworthii* or *H. harperi*. The stamens are not nearly as elevated and the ovary is much shorter and wider than is found in either *H. shuttleworthii* or *H. harperi*. The size of the calyx falls outside the range of even the smallest forms of *H. shuttleworthii* and only the largest flowers of *H. viridistylis* are close to *H. harperi*. The shape of the calyx tube is decidedly cylindrical or broadly cylindrical in *H. viridistylis* versus the urceolate-campanulate tube of both *H. shuttleworthii* and *H. harperi*. Flowering also begins earlier, during late winter or early spring in *H. viridistylis* compared to nearby or sympatric populations of *H. shuttleworthii* and *H. harperi*. The foliage of *H. viridistylis* has the gestalt of *H. shuttleworthii* and is often tinged with purple in the winter. A visual comparison with *H. harperi* is shown in Fig. 5.

The range of *H. viridistylis* overlaps with both *H. shuttleworthii* and *H. harperi* in Georgia but it is the only member of the *Hexastylis virginica* species group within its range in Alabama. The habitat where *H. viridistylis* grows is typical for the species group, being found on steep slopes and bluffs in moderately acid to hyperacid soils where it is most often found in association with *Kalmia latifolia* and other acidophiles though it has also been found on more level ground at the bases of coves along intermittent or small streams where flooding is rare. It has been found and confirmed growing sympatric with *H. shuttleworthii* at a location in Pickens County, Georgia and it is likely to be found growing with this species at other locations in northern Georgia. It has also been found growing near *H. harperi* in Georgia, though *H. harperi* consistently occupies more level and “boggy” ground. A list of species frequently associated with *H. viridistylis* is presented in Table 2.

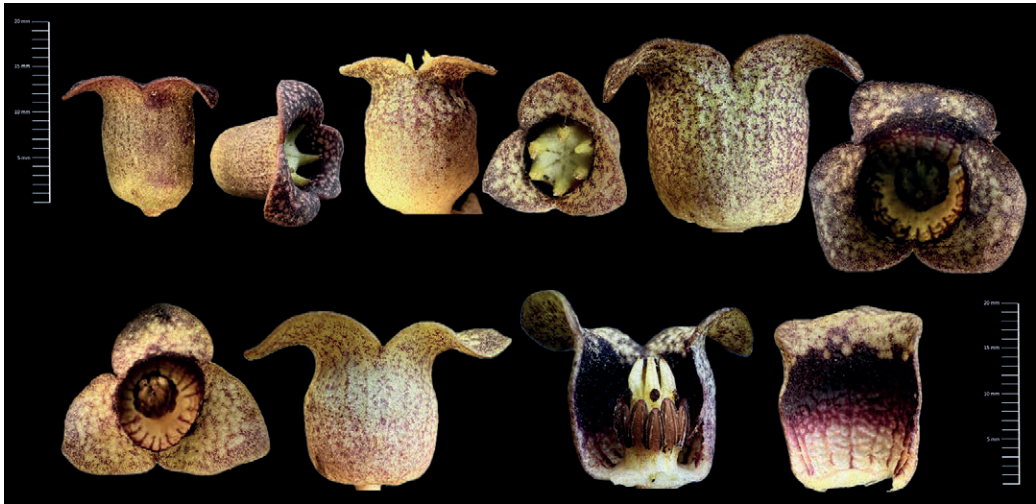


Fig. 3. Variation in calyx of flowers exposed above leaf litter in *Hexastylis viridistylis*.



Fig. 4. Variation in calyx of flowers protected by leaf litter in *Hexastylis viridistylis*.

The fruit of *H. viridistylis*, a fleshy capsule, ripens while the calyx is still in prime condition. The authors have noted this to be the case in a few individuals of *Hexastylis heterophylla* and some individuals of *Hexastylis shuttleworthii*. The fruit splits longitudinally along the carpel on the upper surface and disintegrates as it turns to a mealy texture, as is common in most *Hexastylis*. A very high percentage of flowers in a given population appear to set fruit. During field investigations in the spring of 2025 we found that there were very large numbers of newly germinated seedlings very near or among the parent plants. This may indicate that the plant is either very successful at pollination or perhaps using an alternative method for setting seed.

The remarkable conformity in morphological characteristics that distinguish this species is unique in the *Hexastylis virginica* group. Many of the taxa display wide overlap in distinguishing traits. The clear



FIG. 5. *Hexastylis viridistylis* (left) compared with *Hexastylis harperi* (right).

delineation of this taxa, now segregated from a much too inclusive *Hexastylis heterophylla*, is indicative of a group in need of more morphological and genetic research.

ASTERACEAE

Chrysopsis: *Chrysopsis dressii* at species rank

Primary authors: A.S. Weakley and S.G. Ward

Semple (1978) cleared up a long-standing taxonomic confusion in Florida *Chrysopsis* by separating *Chrysopsis linearifolia* Semple from confusion with *C. hyssopifolia* Nutt., and additionally separated disjunct and morphologically distinct populations of his new species into two subspecies, by naming *C. linearifolia* Semple subsp. *dressii* Semple. This taxonomy has been generally followed since, by Semple (1981, 2006, 2025) and others. But the two entities are separable by multiple morphological characters, seem as distinct from one another as many “taxon pairs” in the genus *Chrysopsis* which are recognized at species rank, and the two entities are disjunct from one another, well separated from one another geographically, with subsp. *linearifolia* in the western Florida panhandle and subsp. *dressii* in the Florida peninsula. The distribution of each is similar to a suite of other taxa recognized at species rank, correlated with well-known endemism patterns in the North American Coastal Plain: Pattern 8 and Pattern 12 of Sorrie & Weakley (2001). Semple (1981) stated that “the occurrence of a few individuals of the Florida peninsula morphotype, subsp. *dressii*, within the panhandle Florida distribution of the type subspecies made it unsound to recognize each morphotype at the species level, though someone else might wish to do so.” Semple (1981) also mentioned similarity of each subspecies to and possible confusion with other taxa (*Chrysopsis cruiseana* Dress and *C. hyssopifolia* Nutt.). We find that species in *Chrysopsis* are characteristically imperfectly separated from one another morphologically, and are not troubled by difficult individuals when populations are distinctive. Put another way, more modern species concepts are more based on lineage and relationship than on precise morphotype. We are uncertain that *C. linearifolia* subsp. *dressii* and subsp. *linearifolia* are more closely related to one another than they are to other taxa. By modern species concepts utilizing all data currently available, we consider that they are best and most simply recognized as independent evolutionary entities—as species.

Chrysopsis dressii (Semple) Weakley & S.G. Ward, **comb. nov.** BASIONYM: *Chrysopsis linearifolia* Semple subsp. *dressii* Semple, Brittonia 30:494. 1978. TYPE: U.S.A. FLORIDA. Brevard Co.: Merritt Is., Dummit Core, Rte 3, 2 Oct 1976, Semple, Wunderlin, Poppleton, & Norman 2530 (HOLOTYPE: MO; ISOTYPES: US, USF, WAT).

Echinacea: A reassessment of some of the western taxa

Primary authors: Alan S. Weakley, Aidan Campos, Amy Buthod, Nathan Aaron, Justin Thomas, and Theo Witsell

Echinacea is a small genus (with 4–11 species and 6–11 total taxa) in Asteraceae, tribe Heliantheae, subtribe Zinniinae, natively distributed in southeastern and central North America (McGregor 1968; Foster 1991; McKeown 1999; Binns et al. 2002; Urbatsch et al. 2006; Zhang et al. 2017; Skibicki 2025). It has been of considerable taxonomic interest because a) many of its species are narrowly endemic and of conservation concern, b) it has traditional and modern medicinal uses, c) it has significant horticultural interest and use, and d) it has economic value derived from a), b), and c). Despite extensive study using diverse methods, there remains a discordance between published taxonomic treatments and what many observers see as the taxonomic and biological realities of taxa in this genus, as they occur and interact in natural landscapes.

Westwards, the “*atrорubens* complex” (three entities) and the “*angustifolia* complex” (two entities) have been particularly problematic. McGregor (1967, 1968) treated *Echinacea atrорubens* (Nutt.) Nutt. as a pink-rayed species of eastern Kansas, eastern Oklahoma, and eastern Texas, and *E. paradoxa* (J.B.S.Norton) Britt. as a separate species with two allopatric varieties, one (var. *paradoxa*) with yellow rays and endemic to the Ozarks of Missouri and n. Arkansas, and one (var. *neglecta* McGregor) with purple, pink, or white rays endemic to the Arbuckle Mountains region of southcentral Oklahoma. Later authors have sometimes treated the three components of the “*atrорubens* complex” as three varieties of *E. atrорubens* (Binns et al. 2002). In morphologically based studies, Binns et al. (2002) suggested that “when geographical data are unavailable, ray floret color is the only reliable way to distinguish between *E. atrорubens* var. *neglecta* and *E. atrорubens* var. *paradoxa*. Other characteristics distinguish var. *atrорubens*.” McGregor (1967, 1968) recognized *E. angustifolia* DC. with two varieties, a more western var. *angustifolia* and more eastern var. *strigosa* McGregor, and discussed var. *strigosa* as having a hybrid origin from hybridization or introgression from *E. angustifolia* and *E. atrорubens* var. *atrорubens*.

Molecular phylogenetic analyses have shown relationships among these entities that contradict these taxonomic treatments. In a diversity of analyses of phylogenetic relationships in subtribe Zinniinae, Skibicki (2025) consistently showed *E. paradoxa* as clading closely with *E. purpurea* and well away from *E. atrорubens*, which suggests that it should not be treated as associated with *E. atrорubens* as a variety.

We reviewed the various findings in the literature, reviewed herbarium specimens, and also relied on our field experiences with these taxa. We conclude that a different taxonomy will serve botanists better. To implement this new taxonomy, we make the following new combinations, and explain the rationales below.

Echinacea neglecta (McGregor) Weakley & A.P. Campos, **comb. nov.** BASIONYM: *Echinacea paradoxa* (Norton) Britt. var. *neglecta* McGregor, Trans. Kansas Acad. Sci. 70:370. 1967. TYPE: U.S.A. OKLAHOMA. Murray Co.: Platt National Park, 7 Jun 1959, McGregor 14324 (HOLOTYPE: KANU).

Compared to *Echinacea paradoxa*, *E. neglecta* can be readily distinguished in the color of its ray florets (pink to pale pink or white in *E. neglecta* vs. yellow and occasionally crimson-tinged basally in *E. paradoxa*). *Echinacea neglecta* differs from *E. atrорubens* in its longer ray florets (30–70 mm long in *E. neglecta* vs. 19–36 mm long in *E. atrорubens*), its ray cypselae which are distally pubescent at least on their margins (these distally glabrous in *E. atrорubens*), and in the lacunae (air canals) of its petioles, which are present only in the proximal section of the petiole in *E. neglecta* (vs. bearing three large lacunae which are continuous throughout the length of the petiole as in *E. atrорubens*) (McGregor 1968; Keller 2014). *E. neglecta* differs from *E. strigosa* in its longer ray florets (30–70 mm long in *E. neglecta* vs. 23–31 mm long in *E. strigosa*). Additionally, *E. neglecta* is unique within the genus in being the only species known to possess brachysclereids (stone cells) in its aerial tissues, found in the petioles (McGregor 1968; Keller 2014). We concur with Binns et al. (2002) that “many populations [of *atrорubens* and *neglecta*] are in proximity, and hybrid swarms exist,” which to us does not undermine their status as separate species.

In ecogeographic occupancy, *E. neglecta* is widely separated from *E. paradoxa*, with *E. neglecta* being endemic to the Arbuckle Mountains and adjacent areas of southern Oklahoma and possibly extreme north-central Texas (McGregor 1967) and *E. paradoxa* endemic to the Ozark Highlands of Missouri and Arkansas. While the geographic range of *Echinacea neglecta* lies within that of *E. atrorubens*, *E. neglecta* is restricted to the area surrounding the Arbuckle Mountains of southern Oklahoma, where it mostly replaces *E. atrorubens*. The range of *E. atrorubens* is comparatively extensive, from eastern and central Texas to Oklahoma and eastern Kansas. Similarly, while *E. neglecta* and *E. strigosa* come within close geographic proximity of each other in southern Oklahoma, they are largely ecogeographically separated, as *E. strigosa* occupies primarily sandy-clay or gypsiferous soils to the west of the calcareous clays preferred by *E. neglecta*. Reports of *E. neglecta* from southeastern Texas (Kartesz 2015) remain unconfirmed and are likely to represent variation within *E. atrorubens*.

We therefore propose to treat the “*neglecta*,” “*paradoxa*,” and “*atrорubens*” entities as separate at species rank.

Echinacea strigosa (McGregor) Weakley & A.P. Campos, **comb. nov.** BASIONYM: *Echinacea angustifolia* DC. var. *strigosa* McGregor, Trans. Kansas Acad. Sci. 70:368. 1967. TYPE: U.S.A. OKLAHOMA. Stephens Co. 3 mi w Velma, open wooded sandy hillside, 7 Jun 1959, McGregor 14329 (HOLOTYPE: KANU).

Echinacea strigosa differs from *E. atrorubens* primarily in its shorter average height (2–6.5 dm tall vs. 5–10 dm tall in *E. atrorubens*), frequently branched habit (vs. typically unbranched in *E. atrorubens*), and in its lack of longitudinally extensive lacunae within the petioles (these limited to the proximal part of the petiole in *E. strigosa* vs. throughout the length of the petiole, as in *E. atrorubens*). In contrast to the hirsute to tuberculate-hirsute or tuberculate-hispid stems of *Echinacea angustifolia*, the stem pubescence of *E. strigosa* is strigose to strigose-hirsute. *E. strigosa* also branches more frequently than *E. angustifolia* and often has flexuous stems.

Echinacea strigosa occupies a geographic region largely between that of its two putative ancestors, *E. angustifolia* and *E. atrorubens*, though it is usually not in contact with either species except for on its western flank where it apparently hybridizes with *E. angustifolia* (McGregor 1968). It has been often suggested that the “*strigosa* entity” is of hybrid origin involving *E. angustifolia* (sensu stricto) and *E. atrorubens* (sensu stricto). We agree that some sort of past hybridization or introgression is likely involved in its origin, though that appears to be conjectural, and the existence of characters different than either parent, or not intermediate between them, suggests that the situation may not be one of (at least simple) hybridization or introgression. We draw attention to McGregor’s (1968) statement: “*Echinacea angustifolia* var. *strigosa* appears to be a rather stable population except for the merging with var. *angustifolia* on the west. The future status of var. *strigosa* is uncertain, but the tetraploid colonies forming the southern segment of the population indicate genetic isolation is taking place.” If the “*strigosa* entity” is indeed of hybrid origin, two questions or considerations emerge as to its most appropriate taxonomic treatment. A hybrid population should not be treated as a variety of one of its parents. If it is largely a “stable population” separated from one of its parents (*E. atrorubens*) by geography, habitat, and an absence of intermediates, and separated from its other parent (*E. angustifolia*) less solidly by geography and habitat, we consider it better to regard the “*strigosa* entity” as a species of hybrid origin, but now with a separate evolutionary trajectory, and because of its full fertility, different morphology, and largely separate ecology and distribution from each of its putative parents, as a species not marked with the hybrid or nothotaxon marker “x.” Because of the very extensive “messiness” of reticulate evolution in plants, we agree with the increasingly common practice of reserving the hybrid or nothotaxon marker “x” for F1 or other evolutionarily more trivial hybrids—“one offs.” Use of the hybrid “x” also has conservation implications often not appreciated in the taxonomic community—it implies to conservation practitioners that the entity is not worthy of conservation attention, an evolutionarily trivial “dead end.” This implication is moreover formally written into some conservation legislation, such as the U.S. Endangered Species Act of 1973. The “*strigosa* entity” seems to us an evolutionary actor worth recognition, monitoring, study, and conservation separate from its parents and not merely as a hybrid. On the western edge of its distribution, there appear to be some hybrids between it and *E. angustifolia* sensu stricto—these we regard as appropriately treated as hybrids, but

decline to create a new hybrid binomial for them, considering that they can be referred to as needed with the hybrid formula *Echinacea angustifolia* × *strigosa*.

With these proposed changes, we consider the genus *Echinacea* to include 11 species: *E. angustifolia* DC., *E. atrorubens* (Nutt.) Nutt., *E. laevigata* (C.L.Boynt. & Beadle) Blake, *E. neglecta* (McGregor) Weakley & A.P. Campos, *E. pallida* (Nutt.) Nutt., *E. paradoxa* (J.B.S.Norton) Britt., *E. purpurea* (L.) Moench, *E. sanguinea* Nutt., *E. simulata* McGregor, *E. strigosa* (McGregor) Weakley & A.P.Campos, and *E. tennesseensis* (Beadle) Small.

Solidago: *Solidago ptarmicoides* at a new isolated and relictual spot in the Southeast

Primary author: Jennifer Stanley

Solidago ptarmicoides (= *Oligoneuron album*) is reported as new to Virginia based on a collection made in 2025 (Dinwiddie County) by Jennifer Stanley (Fig. 6). A total of 360 plants were counted along a 130 m stretch of roadside. The plants were growing in an open right-of-way along an infrequently traveled gravel road through pine plantation underlain by diorite and gabbro (Rader & Evans 1993). The roadside supported a high diversity of native herbs with very few exotics.

This large-flowered goldenrod is usually now classified in the genus *Solidago*, subgenus *Pleiactila*, section *Ptarmicoidei* (Semple & Beck 2021, 2023; Semple et al. 2023), though that section has sometimes also been treated as a separate genus, *Oligoneuron*. It is the only species of *Solidago* that has both white ray flowers and a corymbiform inflorescence. The species has a primary distribution in the northern Midwest of the United States (especially Michigan, northern Illinois, northern Iowa, Minnesota, South Dakota, and North Dakota) and southern Canada (southern Ontario and southern Manitoba), with isolated relictual populations scattered in the Ozark Plateau of southern Missouri and northern Arkansas, New England and New York, and a scattering of populations in eastern Tennessee, northeastern Alabama, northern Georgia, central South Carolina, central North Carolina, and now southcentral Virginia (Kartesz 2015; Weakley & Southeastern Flora Team 2025). Southeastern populations seem to exclusively be found on soils with high base status such as those derived from mafic or calcareous rock.

Solidago ptarmicoides is considered Globally Secure (G5) by NatureServe (2025), though Subnational Ranks for southeastern states range from S1-S3 (Critically Imperiled to Vulnerable) (NatureServe 2025). While small pockets of suitable habitat exist in Virginia, the likelihood of finding additional occurrences is low.

Specimen: **U.S.A. VIRGINIA. Dinwiddie Co.:** open right-of-way along east side of Shippings Road. Remnant Piedmont prairie on diorite/gabbro adjacent to loblolly pine plantation. Associated taxa: *Agalinis* sp., *Aletris farinosa*, *Angelica venenosa*, *Asclepias viridiflora*, *Coleataenia* cf. *anceps*, *Helianthus divaricatus*, *Hexasepalum teres*, *Lespedeza virginica*, *Liatris pilosa*, *Parthenium integrifolium* var. *integrifolium*, *Pityopsis aspera*, *Pycnanthemum tenuifolium*, *Schizachyrium scoparium*, *Scleria* sp., *Silphium asteriscus*, *S. compositum* var. *compositum*, *Solidago nemoralis*, *Stylosanthes biflora*, *Symphyotrichum dumosum*; adjacent pine plantation with young *Benthamidia florida*, *Cercis canadensis* var. *canadensis*, *Liquidambar styraciflua*, *Quercus marilandica* var. *marilandica*, *Q. rubra*, *Q. velutina*, *Q. stellata*, *Ulmus alata*. 3 Sep 2025, J. Stanley 1664 (GMUF & WILLI).

DIOSCOREACEAE

Dioscorea: Taxonomy and distribution of native taxa of eastern North America

Primary author: Bruce A. Sorrie

The most recent taxonomic treatment of this group of plants was Flora of North America (Raz 2002). She recognized as full species two North American native entities: *Dioscorea floridana* Bartlett and *D. villosa* Linnaeus. The latter included as synonyms several taxa that in the past have had a checkered career re taxonomic acceptance: *D. quaternata* Walter, *D. glauca* Muhl. ex L.C. Beck, *D. paniculata* Michx., and *D. hirticaulis* Bartlett.

In defense of her position to treat *D. villosa* in an inclusive sense, Raz (2002) stated: “*Dioscorea villosa* is a highly polymorphic species, exhibiting complex patterns of variation across its geographic range. Characters that have been used previously to delineate taxonomic boundaries within this complex—pubescence, glaucousness, rhizome thickness and shape, length of internodes within the inflorescence, arrangement of



FIG. 6. *Solidago ptarmicoides* new to Virginia, in Dinwiddie County. Photo by Zach Bradford.

proximal leaves, geometry of the stem, and fruit and seed size/shape—fail when individuals from all parts of the range and specimens representing both apical and basal portions of single stems can be examined. At its morphological extremes, *D. villosa* comprises 1) small vines with tightly congested inflorescences, winged stems, and variously pubescent leaves, occurring in bogs and branch swamps; and 2) robust plants, rigid at the base, the proximal leaves verticillate with large glaucous blades, from the axils of which arise lax spikes or panicles, inhabiting rocky, upland woods and steep talus slopes. As well as the morphological extremes, every intermediate condition can be found. That there is a significant degree of genetic variability within the complex is evident from the chromosome counts thus far reported [$2n = 20, 36, 54, 60$]. At present I can find no natural gaps in the variation between the plants that have been called *D. villosa* and those called *D. quaternata*.”

In contrast, Al-Shehbaz and Schubert (1989) recognized both *D. quaternata* and *D. villosa* at species level. They stated that “*Dioscorea quaternata* is the most variable and widely distributed of the North American species. It is distributed primarily east of the 95th meridian and between 27 and 45 north latitude. It does not grow in New England and is very rare in New Jersey, New York, Wisconsin, Minnesota, Iowa, Kansas, Oklahoma, and Texas. It is sporadic in southern Ontario, Canada. *Dioscorea quaternata* grows in moist, rich or rocky woods and thickets, on limestone or talus slopes, in creek bottoms, and along roadsides, railroad tracks, and borders of swamps, ponds, and marshes.” The authors cited chromosome numbers of $2n = 36, 54$, and 60 for *D. quaternata*.

Al-Shehbaz and Schubert go on to state that “*Dioscorea villosa* is distributed from southwestern (sic, southeastern) Massachusetts, Rhode Island, and western Connecticut south along the coastal plain of all states to northern Florida. Furthermore, the species is disjunct and probably introduced to Kentucky.[Beckett 651 (GH), Clark County]. The species is common in Virginia and the Carolinas, where it grows in bogs, peaty depressions and swamps. *Dioscorea villosa* is easily recognized by its narrowly winged, polygonal (8–14 angled) stems [see their Figure 1m], alternate lower leaves, and densely grouped glomerules on short (2–4 cm) staminate inflorescences. The closely related *D. quaternata* has terete, wingless stems, whorled lower leaves (3–9 per node), and lax, longer inflorescences. Field notes on the phyllotaxy of lower nodes are useful for separating the two species.” The authors stated that there were no known chromosome counts for *D. villosa*.

Al-Shehbaz and Schubert (1989) further stated that “The identities of *Dioscorea hirticaulis*, *D. quaternata*, and *D. villosa* have been confused. A few authors (e.g., Ahles 1968; Gleason 1952; MacRoberts 1984; E.B. Smith 1978) suggested that first and/or second be reduced to synonymy of the last. As shown above, however, *D. quaternata* and *D. villosa* are very distinct and therefore should be maintained at specific rank. Both *Dioscorea villosa* and *D. quaternata* are highly variable in stem pubescence. Forms with densely pubescent to completely glabrous leaves that are either glaucous or non-glaucous occur in populations of both species. Bartlett’s (1910) recognition of four species in this complex was based primarily on the branching of rhizomes, and pubescence, color (green vs. glaucous) and number of leaves per node. These alleged distinctions are far from being realistic. In fact, characters of rhizome branching, thickness, and surface configuration can be modified by soil texture, habitat, and environment. Furthermore, leaf pubescence and glaucescence, and fruit length show continuous variations of no taxonomic value.” I agree with their assessment of leaf pubescence and glaucescence as being ineffective; thus I also lump *D. hirticaulis* into *D. villosa*.

The discrepancies between the treatments above of *D. quaternata* and *D. villosa* were striking and warranted further investigation. Raz (2002) treated all native North American *Dioscorea*, except *D. floridana*, as a single very widespread and very variable species *D. villosa*, whereas Al-Shehbaz and Schubert (1989) treated *D. villosa* and *D. quaternata* as separate species. They treated *D. villosa* as occurring mostly in the Atlantic Coastal Plain, extending northeastward to southern New England; while *D. quaternata* occurs in the Piedmont and Appalachian Mountains of Atlantic states, barely reaching New York (Chemung County, cited by Werier [2017], and Erie County, probable ID, two specimens at FLAS). Al-Shehbaz and Schubert treated all plants from west of the Appalachians and south to the Gulf Coastal Plain as *D. quaternata*. Both sets of authors

lumped *D. hirticaulis* within *D. villosa* sensu stricto, and both treated *D. floridana* as a separate and distinct species (more on this last species elsewhere in this paper).

Several Midwestern manuals, such as Illinois (Mohlenbrock and Ladd 1978), Indiana (Deam 1940), Missouri (Steyermark 1963; Yatskievych 1999), and Ohio (Braun 1967), have treated *D. quaternata* and *D. villosa* as separate species. Their maps showed the former as occurring only in the southern tiers of counties; the latter throughout. In contrast, other Midwestern authors treated all their specimens as *D. villosa*: e.g., Arkansas (Gentry et al. 2013), Michigan (Voss 1972; Voss & Reznicek 2012), Tennessee (Chester et al. 1993; Tennessee Flora Committee 2015).

DISTINGUISHING CHARACTERS

In order to make sense of the differences of taxonomic opinion, it was imperative to find characters that reliably separated *D. quaternata* and *D. villosa*. In my home region of south-central North Carolina, these two species can easily and reliably be separated by the presence of a whorl of 3–7 (reportedly more) leaves at the first stem node above the rhizome in *D. quaternata* (there may be one or more additional whorls above the first node); *D. villosa* lacks whorls entirely, according to Al-Shehbaz and Schubert (1989) and Gleason (1952). The latter statement contradicts the keys in floras and manuals which recognized both species (e.g. Deam 1940; Fernald 1950; Braun 1967), in which *D. villosa* was alleged to have alternate leaves and/or a whorl of three, whereas *D. quaternata* possessed whorls of 4 or more leaves. Those keys were used by botanists for decades, and led to many misidentifications. Examination of hundreds of specimens online (SERNEC 2025) and in hand at NCU has convinced me that Al-Shehbaz and Schubert and Gleason were correct: *D. villosa* lacks proximal stem leaf whorls. Note, for example, the key and drawing in Braun (1967), which clearly shows a whorl of three leaves for *D. villosa* and five for *D. quaternata*. As further corroboration of Al-Shehbaz and Schubert (1989) and Gleason (1952), in North Carolina *D. villosa* (no whorls) occurs strictly in poor, acid soils within the Coastal Plain and lower Piedmont, whereas *D. quaternata* (whorls present) occurs in the Mountains and Piedmont, sparingly on the Coastal Plain along nutrient-rich brownwater rivers such as the Cape Fear, Neuse, and Roanoke.

Here I assess a few other distinguishing characters used by authors:

- 1) Basal or stem leaves glabrous beneath in *D. quaternata* vs. pubescent in *D. villosa*. Specimens examined at NCU showed that abaxial surfaces of *D. quaternata* possessed very short, appressed, spicule-like trichomes along most veins. Abaxial surfaces of *D. villosa* varied from that condition to densely velutinous. This character may be useful with in-hand specimens, but online imagery lacks the necessary clarity for sure identification.
- 2) Stem terete, without wings or angles in *D. quaternata* vs. narrowly winged, polygonal (8–14 angled) stems (Al-Shehbaz and Schubert 1989, their Figure 1m). Under a dissecting scope, these characters did not hold. There was a tendency in *D. villosa* to possess polygonal stems with low ridges, but none I examined at NCU matched the drawing in Al-Shehbaz and Schubert (1989). Stems of *D. quaternata* were not strictly terete, but possessed less distinct, low, rounded ridges, these sometimes faint (and would be difficult to see in the field under 10x). Mid-to upper stems tended to show more definition of angles, but lacked consistency among specimens. Again, this character may be useful with in-hand specimens, but online imagery lacks the necessary clarity for sure identification.
- 3) Capsule length, larger in *D. quaternata* than in *D. villosa*. Braun's (1967) key stated that fruits of *D. villosa* were 2.0 cm long vs. 2.5 cm for *D. quaternata*. Fernald's (1950) text stated that fruits of *D. villosa* were 1.5–2.0 cm long vs. 2.5–3.0 cm for *D. quaternata*. Measurements of capsules in-hand at NCU and online at various herbaria indicated that capsule length was 1.4–1.9 (–2.0) cm (mean 1.7) in *D. villosa*; (2.1–) 2.2–2.7 cm (mean 2.4) in *D. quaternata*. This character appeared to be strong and, when combined with presence/absence of lower stem leaf whorls, clearly distinguished *D. quaternata* from *D. villosa*.

KEY TO NATIVE *DIOSCOREA* OF SOUTHEASTERN UNITED STATES

1. Staminate inflorescences 2–3 in axils of upper leaves, staminate tepals yellow or orange-yellow, filaments strongly and inwardly curved; lower stem leaves not whorled; Coastal Plain of SC-GA-FL _____ ***D. floridana***
1. Staminate inflorescences single in axils of upper leaves, staminate tepals dull greenish or whitish green, filaments not inwardly nor strongly curved; lower stem leaves whorled or not; plants collectively widespread
 2. Basalmost leaves in whorls of 3–7 (reported to 9); leaves glabrous or glabrate beneath (may have some appressed, spicule-like hairs on veins); capsules (2.1–) 2.2–2.7 cm long (mean 2.4); plants mostly inland and often in higher pH and more nutrient-rich soils _____ ***D. quaternata***
 2. Basalmost leaves not whorled; leaf pubescence highly variable (glabrate to densely appressed pubescent beneath); capsules 1.4–1.9 (–2.0) cm long (mean 1.7); plants mostly on Coastal Plain and adjacent lower piedmont; in lower pH and poorer soils _____ ***D. villosa***

SPECIMEN SEARCH

Armed with the morphological characters of whorls vs. no whorls, and capsule size, I examined online all specimens at the SERNEC website (SERNEC Data Portal 2025) of *D. villosa* and *D. quaternata* (treated by SERNEC as one species, *D. villosa*). I noted whether the specimen had whorl(s), number of leaves per whorl, whether it had a rhizome, and length of longest capsule. Presence of a rhizome was critical if the specimen lacked whorl(s), for by knowing definitely that the lowest nodes lacked whorls I could be certain that the specimen was *D. villosa*. Unfortunately, the majority of herbarium specimens lacked a rhizome—stems were broken off somewhere above the rhizome, thus rendering impossible a positive identification of *D. villosa*, unless capsules were present. Specimens with or without a rhizome, but with whorl(s) of 3 or more leaves on lower stem nodes, were assigned to *D. quaternata*; capsule size also allowed identification of many specimens.

RESULTS—DISTRIBUTION OF SPECIES

Dioscorea villosa

As stated by Al-Shehbaz and Schubert (1989), *Dioscorea villosa* ranges from southeastern Massachusetts (Bristol County) southward on the Coastal Plain and adjacent lower Piedmont to northeastern Florida (Duval County) (Fig. 7). Inland records were obtained as far as Ulster County, New York (specimen at GA), Adams County, Pennsylvania (at PH), Anson County, North Carolina (at NCSC), Saluda County, South Carolina (at USCH), McDuffie County, Georgia (at DUKE), and Baker County, Georgia (at ICHAUWAY). All of these specimens possessed a rhizome but no stem whorls basally.

I found three possible *D. villosa* specimens in Ohio, one in Indiana, one in Michigan, and two in Illinois. In Ohio, a specimen from Clinton County (Terrell 2151 OS) had a rhizome; the first stem node had one leaf, the second node had two leaves, the rest had a single leaf. A specimen from Lorain County (Day s.n. OS) had a rhizome; the first node had two leaves, the rest a single leaf. A specimen from Noble County (Cowles s.n. OS) had a rhizome; all nodes had a single leaf. In Indiana, a specimen from DeKalb County (Deam 50326 IND) had a rhizome but the lower and midstem nodes were obscured by leaves. In Michigan, a specimen from Berrien County (Hickman s.n. MOR) had a rhizome, along with the lowermost portion of the stem; but the stem section that would have included the lower few nodes was missing. In Illinois, a specimen for Peoria County (Chase 8948 LSU) had a rhizome; lower stem nodes had a single leaf. However, a second specimen with same location, collector and number (at SIU) also had a rhizome but the first node had a whorl of three leaves plus another leaf close by. A specimen from Knox County (Chase 10759 IND), had a rhizome; all nodes had a single leaf. I was unable to find online the specimen of *D. villosa* reported by Al-Shehbaz and Schubert from Clark County, Kentucky.

The paucity of the above putative specimens of *D. villosa* contrasted strikingly from data mapped from those states. For example, in Indiana (Deam 1940) and Ohio (Braun 1967), the authors mapped *D. villosa* throughout each state, while in Illinois (Mohlenbrock and Ladd 1978) the authors stated that it occurred “in every county.” My research showed that, based on presence of whorls of three or more leaves, it is *D. quaternata* that occurs throughout those states. The relatively small number of specimens that I attributed to *D.*

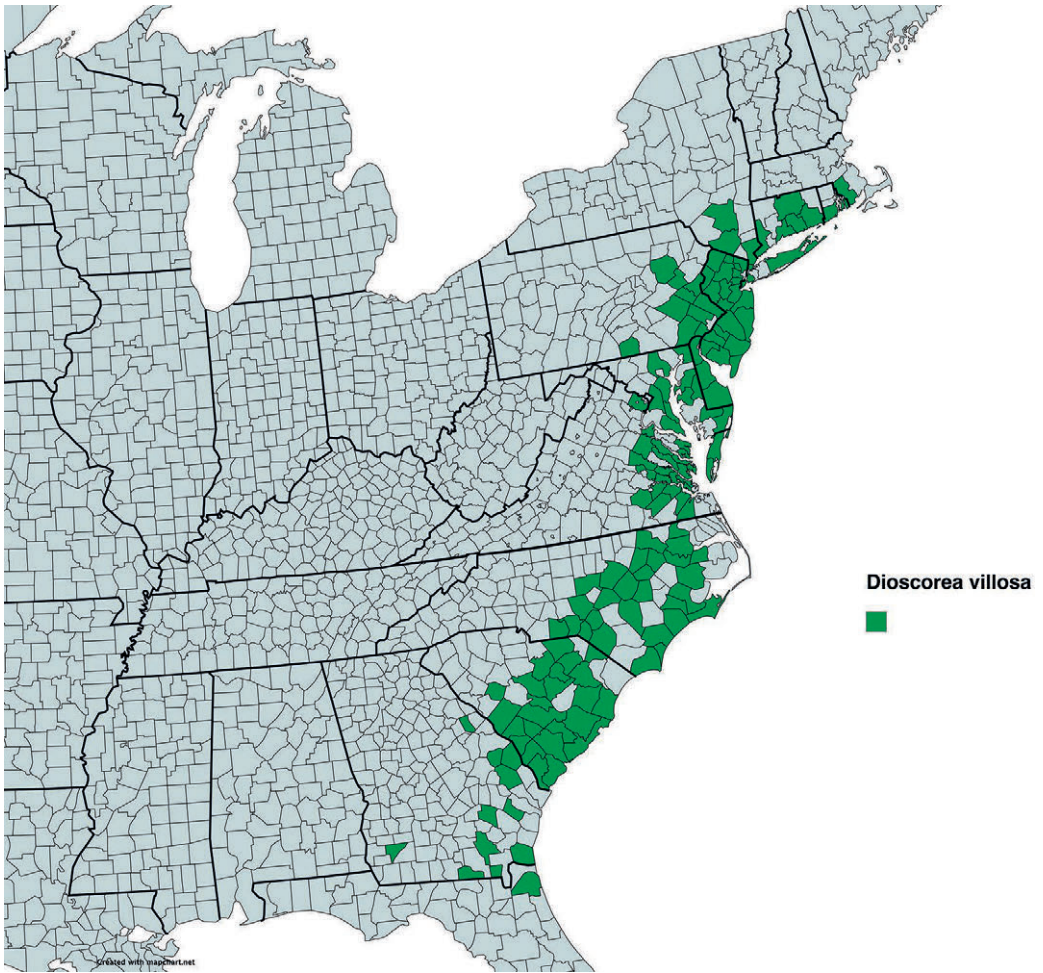


FIG. 7. Distribution of *Dioscorea villosa*.

quaternata in Indiana and Illinois was due to the lack of rhizomes and lower stem nodes on most of the collections seen from those two states.

Dioscorea quaternata

The distribution of this species is primarily west of the Appalachians, spilling over those mountains to the Piedmont of New York (Chemung County) and Pennsylvania south to Georgia and Alabama (Fig. 8). A small number of collections were from the Coastal Plain of tidewater Delaware, Maryland, and Virginia. Other collections were taken from the Coastal Plain of a few river systems in North Carolina and the Apalachicola River in southern Georgia, Alabama, and Florida. It occurs on the Gulf Coastal Plain from Florida and Georgia to eastern Texas, thence northward to the Great Lakes states and southern Ontario. A specimen of uncertain identity was taken from Erie County, New York (at FLAS).

Dioscorea floridana

The pale creamy or yellowish rhizome, lack of lower stem leaf whorl(s), male inflorescences 2–3 panicles per node, and yellow or yellow-orange tepals (vs. greenish in *D. villosa* and *D. quaternata*) render this species very

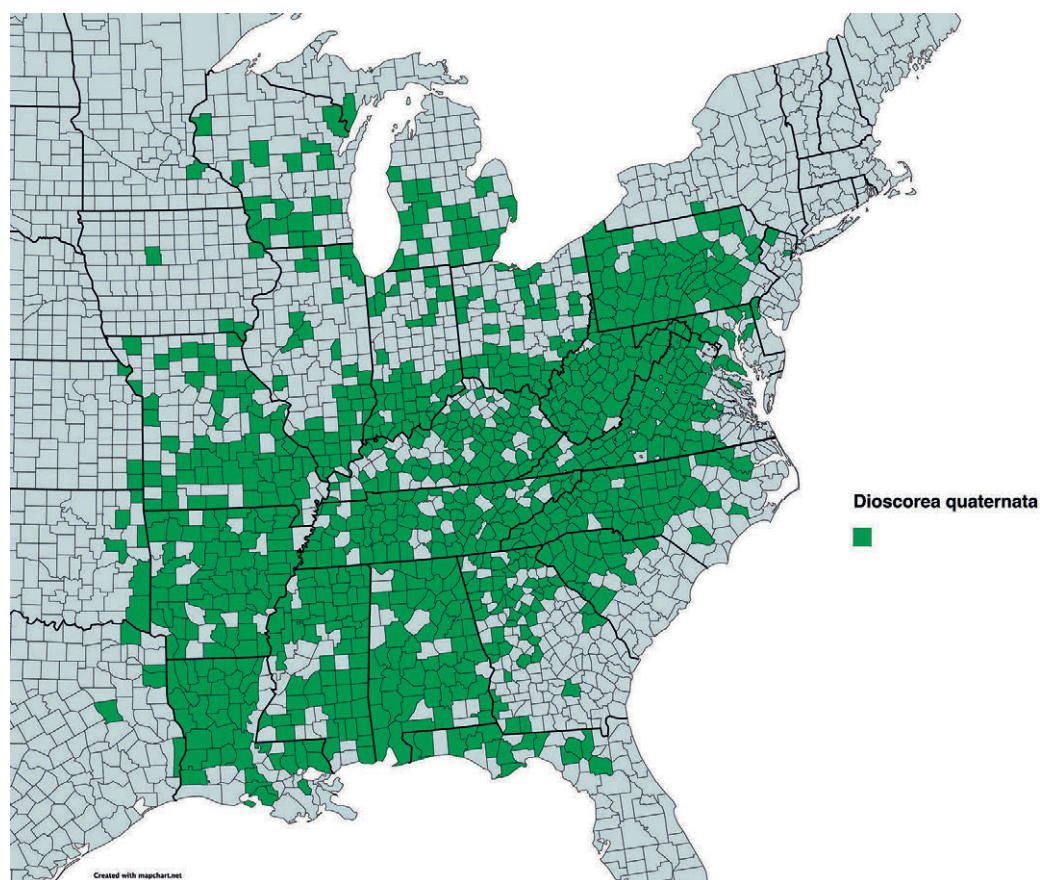


FIG. 8. Distribution of *Dioscorea quaternata*.

distinct. The distribution of *D. floridana* is on the Atlantic and Gulf Coastal Plains from Williamsburg County, South Carolina, to Houston County in central Georgia, south to Polk County in central Florida, and west to Washington County in the Florida Panhandle (Fig. 9). A 1924 specimen from Clark County in the Piedmont of Georgia was from “campus” (Miller E2400 GA) and is treated here as planted or accidentally introduced. There are no verified records from Alabama. A disjunct specimen from Marengo County in the Black Belt of western Alabama (England 2069 TROY) lacks a rhizome and the lower portion of stem, and has flowers only, no capsules. I cannot identify it positively, but suspect it to be *D. quaternata*.

HYDROPHYLLACEAE (OR BORAGINACEAE S.L.)

Phacelia: A new combination in *Phacelia* of Texas and Oklahoma

Primary authors: Eric L. Keith and Alan S. Weakley

Constance (1949) described three varieties of *Phacelia strictiflora* (Engelm. & A. Gray) A. Gray following field studies undertaken in Spring of 1948 in eastern Texas. Constance assumed that *P. strictiflora* var. *lundelliana* represented the “pure” or “original” form of *P. strictiflora* and was “relatively unaffected by genes from other species.” He further explained that it occupied a wide geographic area (northcentral Texas and western Oklahoma) with little overlap in range with the other varieties and is “extremely uniform.” It can be distinguished by its combination of slightly succulent green and shallowly lobed leaves and striking enlargement of

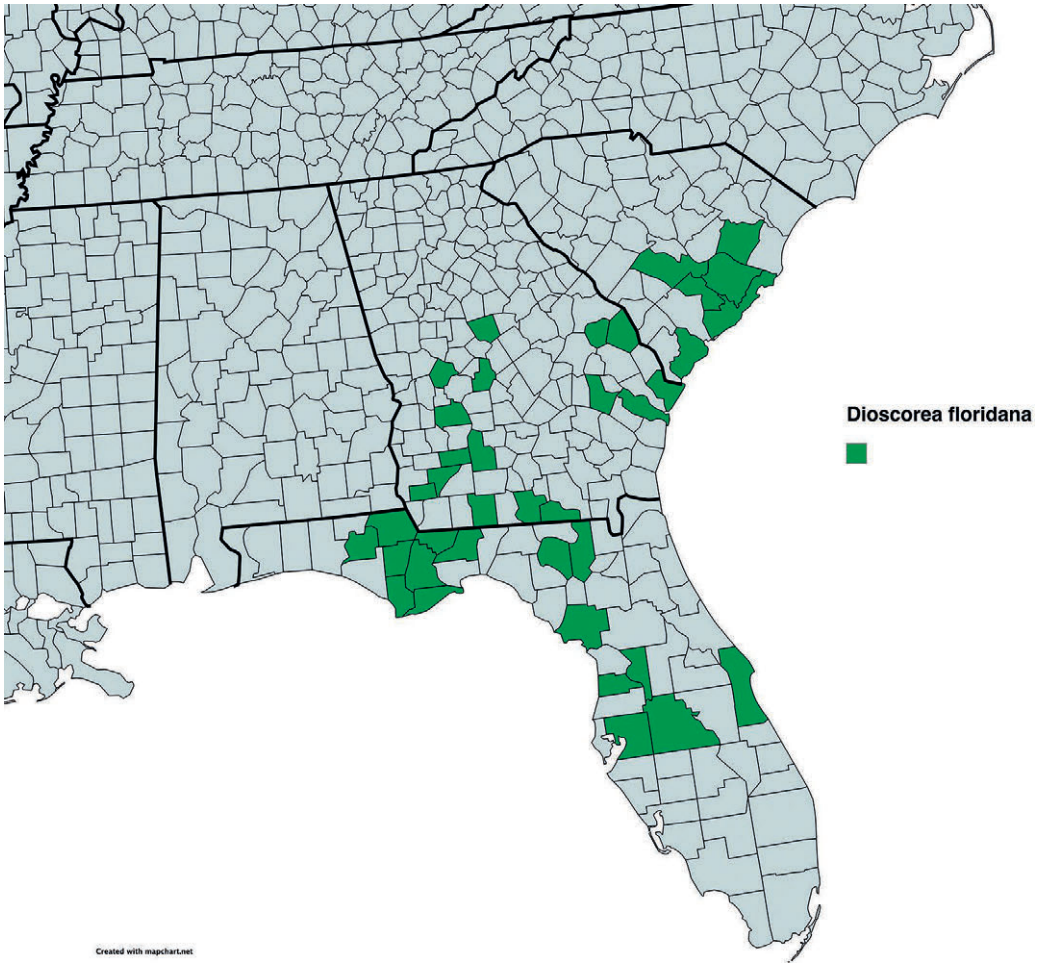


Fig. 9. Distribution of *Dioscorea floridana*.

the lower sepal lobes. Examination of live plants, herbarium specimens, and online photos confirm that this taxon forms a discrete population with a consistent and distinctive morphology and is deserving of specific rank. There is no evidence that it interacts biologically in any way with *Phacelia strictiflora* and its varieties. We therefore make the necessary combination.

Phacelia lundelliana (Constance) E.L. Keith & Weakley, **comb. et stat. nov.** BASIONYM: *Phacelia strictiflora* (Engelm. & A. Gray) A. Gray var. *lundelliana* Constance, Contr. Gray Herb. 168:20–21. 1949. TYPE: U.S.A. TEXAS: Taylor Co.: sandy soil of fallow field, 3 mi NNW of the center of Abilene, 12 Apr 1948, Constance & Cory 3249 (HOLOTYPE: US; ISOTYPES: LSU-NO, NY, OKL, SMU, UTC, internet images!).

RUBIACEAE

Houstonia: Species rank for the Granite Dome Bluet, formerly known as *H. longifolia* var. *glabra* or simply included in *H. tenuifolia* s.l.

Primary authors: Alan S. Weakley & Derick B. Poindexter

Terrell (1959) studied *Houstonia purpurea* Linnaeus and related species of eastern North America, and recognized three taxa at variety rank within *H. longifolia*: var. *longifolia* (the “Northern Group,” mainly from New

England and New York across through the Great Lakes to Alberta), var. *compacta* Terrell (the “Appalachian Group,” centered in the Central Appalachians), and var. *glabra* Terrell (the “Glabra Group,” tightly endemic in the southern end of the Southern Blue Ridge, south and west of the Asheville Basin). Terrell (1988) neotypified *H. longifolia*, with a type from var. *compacta*; Haines (2025) pointed out that this changed the application of the autonym *H. longifolia* var. *longifolia* to apply to var. *compacta* sensu Terrell (1959), and established that the correct name for the “Northern Group” is var. *musci* Boivin. When Terrell (1996) revisited the group, he declined to recognize varieties of *H. longifolia* and additionally included *H. tenuifolia* in a broadly defined and widely distributed *H. longifolia* sensu lato. We disagree, and consider that he was closer to an accurate taxonomy in Terrell (1959). We here recognize *H. longifolia* var. *longifolia*, *H. longifolia* var. *musci*, *H. tenuifolia*, *H. ouachitana* (E.B. Sm.) Terrell (see Smith 1976 and Terrell 1988), and give *H. tenuifolia* var. *glabra* a new combination at species rank.

Houstonia glabra (Terrell) Weakley & D.B. Poind., **comb. nov.** BASIONYM: *Houstonia longifolia* Gaertn. var. *glabra* Terrell, Rhodora 61:204, 1959. TYPE: U.S.A. NORTH CAROLINA. Jackson Co.: crevices of rocks in exposed places and in moist loam in woods, summit of Whitesides Mountain, alt 4900 ft, ca. 5 mi NE of Highlands, 1 Jul 1956, E.E. Terrell 3095 (HOLOTYPE: GH! by image).

Houstonia glabra is tightly endemic to granitic gneiss domes and other outcrops at moderate to high elevations in the “southern Southern Blue Ridge Mountains” of southwestern North Carolina, and adjacent northwestern South Carolina and northeastern Georgia. It grows in crevices and shallow soil mats that receive semi-permanent to seasonal seepage from upslope. It frequently co-occurs in these habitats with other Southern Blue Ridge endemics, though their distributions differ somewhat in some cases: *Carex biltmoreana* Mack., *Packera millefolium* (Torr. & A. Gray) W.A. Weber & Á. Löve, *Solidago simulans* Fernald, *Hypericum buckleyi* M.A. Curtis, *Krigia montana* (Michx.) Nutt., *Rhododendron vaseyi* A. Gray, *Bryodesma tortipilum* (A. Braun) Soják [= *Selaginella tortipila* A. Braun], and *Gentiana latidens* (House) J.S. Pringle & Weakley.

Houstonia glabra has a narrow distribution in which it is locally common in its specialized habitat. It has an allopatric distribution relative to its closest relatives, and occurs at higher elevations and moister sites compared to the nearest populations of its relatives. Though morphologic characters are relatively subtle, they are consistent, and the clumped growth form with many (to a hundred or more) stems from the base is not matched by its relatives (Figs 10, 11, 12). Glennon & Church (2015) ran structure analyses on microsatellite data of the *Houstonia purpurea* group; in their “diploids only” analysis and their “diploids plus tetraploids” analysis, samples of *H. glabra* were diploid and grouped together, while other populations of *H. longifolia* sensu lato formed groups separate from *H. glabra* and were either diploid or tetraploid, supporting Terrell’s (1959) recognition of *H. glabra* as a taxon (which he treated at varietal rank).

SAPOTACEAE

Sideroxylon: A new combination in *Sideroxylon* for *Bumelia lacuum*

Primary authors: Scott G. Ward and Alan S. Weakley

In his 1933 flora, John K. Small published the name *Bumelia lacuum*, representing an inland scrub segregate of the more widespread *Bumelia* (*Sideroxylon*) *tenax* (Small 1933). Described from Kuhlman (just east of modern-day Lake Josephine, south of Sebring), Small’s description was minimal but emphasized two main characters in his key: shorter, more slender pedicels and ovate calyx lobes (vs. suborbicular). A few decades following Small’s description, Olga Lakela began to similarly focus her effort on inland scrub plants of *B. tenax*, providing further taxonomic support using a combination of leaf pubescence, leaf size, growth form, and pedicel length (Lakela 1963). A half century later Paul Corogin’s (2015) intensive morphological research on *Sideroxylon* section *Frigoricola* revealed inland scrub specimens with enough intergradation that he chose to instead include Small’s *Bumelia lacuum* within a broader concept of *Sideroxylon tenax*, explaining “differences [in leaf size and pedicel length] are not sharply demarcated to warrant separate taxonomic status for the interior scrub variant of *S. tenax*.”

He added, “... the trend on the inland ridges [for plants of *Sideroxylon tenax*] is toward darker-colored



FIG. 10. *Houstonia glabra*. Sunset Rock, Macon County, NC, August 5, 2017. Photo by Alan Weakley.

and less lustrous abaxial leaf pubescence, smaller leaves, shorter pedicels, and perhaps a greater tendency to form stoloniferous clones. The variants intergrade over a wide area, therefore the inland variant cannot be recognized as a separate taxon.” Potentially contrarily, however, Corogin then states, “but this regional difference suggests that the inland populations have been isolated in the geological past from the coastal populations, when sea level rose high enough to inundate all but the central ridges of the Florida peninsula.” Corogin seems to potentially hint towards a taxon of more incomplete separation, unlike his more clearly differentiated concept of *Sideroxylon alachuense*. It is clear in reviewing specimens that some intermediacy exists within plants growing in more open or “scrubbier” coastal habitats and more closed or “hammock-like” sites inland that sit adjacent to sandhill or scrub habitats (in landscape “fire shadows”). Further sampling is needed in these minority cases to better parse out potential intergrades.

Conversely, one needs to compare only a few specimens of coastal *Sideroxylon tenax*, especially from areas north of Florida, with those from central Florida scrub to discern conspicuous differences between growth form, leaf size and pubescence, and pedicel length, among other characters (Fig. 13, 14, 15). Furthermore, seedlings grown from coastal plants have also been shown to maintain their distinctiveness, apparently growing more vigorously and appearing larger at the seedling stage than seedlings from inland ridge sites (Nancy Bissett, pers. comm., 2025). Endemism has long been an important factor of central Florida ridge ecology (Huck 2001; DeLaney et al. 2003), particularly as botanists unravel the remaining taxonomic complexities of the North American Coastal Plain (McClelland, Weakley, & Poindexter 2023; Bridges and Orzell 2024), and support species recognition within previously lumped complexes (e.g., *Chrysopsis scabrella* and *Eryngium integrifolium* complexes; see Semple and Steenhof 2025 and Kees et al. 2024, respectively). We



FIG. 11. *Houstonia glabra*, showing habit. Black Balsam, NC, July 25, 2023. Photo by Alan Weakley.

feel that in an area continually recognized for its vascular plant endemism and unique geologic past that there is ample evidence to afford plants of the central Florida ridges varietal status so that significant and regionally correlated variation is not lost to view. We present a new combination and revised dichotomous key for the *Sideroxylon tenax* complex below.

Sideroxylon tenax* L. var. *lacuum* (Small) S.G. Ward and Weakley, **comb. nov.* BASIONYM: *Bumelia lacuum* Small, Man. S.E. Fl. 1034. 1933. TYPE: U.S.A. FLORIDA. Highlands Co.: Ancient sand dunes n of Kuhlman, 25 Apr 1921, J.K. Small & J.B. DeWinkeler 9965 (LECTOTYPE: NY!; ISOLECTOTYPES: FLAS!, GH!, TENN!).

Key adapted from Weakley and Southeastern Flora Team (2025), available from the FSUS website. Type description adapted from Corogin (2015), who designated the lectotype.

8. Young twigs glabrous or with a few scattered, quickly deciduous pale trichomes; twig surface green to cream-white, becoming light grey; leaf pubescence silvery-white to very slightly golden _____ ***Sideroxylon alachuense***
8. Young twigs densely pubescent; twig surface pinkish or reddish-brown to dark brown; leaf pubescence silvery-white to golden or rusty brown _____ **9**
9. Mean pedicel length (2–) 4.8 (–11) mm long, shorter or about as long as the corolla lobes (or fruit, if present); largest leaves on short shoots almost all <4.5 cm long; leaf undersurface typically tawny to very dark brown, and appearing dull and finely woolly (rarely silky-sericeous, if so the hairs slightly coarse); plants usually clonal shrubs, growing low (0.5–3 m tall); [sandhills and scrub habitat of the c. FL ridges] _____ ***Sideroxylon tenax* var. *lacuum***
9. Mean pedicel length (4–) mean 9.3 (–15) mm long, notably longer than the corolla lobes (or fruit, if present); largest leaves on short shoots to 8 cm long (usually some at least on a plant >5 cm long); leaf undersurface typically tawny to sericeous and silky-lustrous, the hairs silvery-white, light-gold or if sometimes golden-brown to chestnut-brown then the abaxial leaf hairs primarily silky-sericeous (not slightly coarse) and most leaves on a plant not distinctly dark-rusted); plants many-stemmed, clumped shrubs to single-trunked trees (to 9 m tall); [e. NC south to s. FL, primarily in maritime or hammock situations] _____ ***Sideroxylon tenax* var. *tenax***



FIG. 12. *Houstonia glabra*, detail. Black Balsam, NC, July 25, 2023. Photo by Alan Weakley.

Additions, subtractions, clarifications, and other notable records of vascular flora of South Carolina

Primary authors: Eric Ungberg and Keith Bradley

Ongoing field work, botanical exploration, and herbarium study has resulted in collections of a number of new vascular plant species for South Carolina, as well as clarifications of the ranges of certain species, and removal from the state flora of several species that we found to be lacking corroborating specimens or credible iNaturalist (2025) observations. Several collections that we consider notable with regards to particularly rare species or unusual range extensions are also reported.

ASTERACEAE

Marshallia trinervia (Walter) Trel.: Clarification of its historic range, which includes **Berkeley Co.**, South Carolina

There is conflicting information about whether or not *Marshallia trinervia* occurs in South Carolina. The *Flora of the Southeastern United States* calls it “biogeographically improbable” and consider reports erroneous, while the *Flora of North America* and other sources accept its presence in South Carolina to varying degrees (Weakley & Southeastern Flora Team 2025; Watson 2006). NatureServe (2025) designates it “Exotic” in South Carolina. A search for specimens on SERNEC yielded just one result, a misidentified instance of *Marshallia graminifolia* (Walter) Small from Berkeley Co. (Priester #210).

Seemingly overlooked, the Walter Typification Project (Ward 2007) designated an 1841 collection by Cranmore Wallace as the neotype for *M. trinervia*. The specimen, examined in person by Heritage Trust staff at the Charleston Museum in 2025, is indeed *M. trinervia*. The label information states “St. Johns, Berkely [sic],



FIG. 13. **A.** *Sideroxylon tenax* var. *tenax* common growth form; ©Eric M. Powell. **B.** Abaxial leaf vestiture of *S. tenax* var. *tenax* (three on left) and *S. tenax* var. *lacuum* (furthest right), ©Scott Ward. **C.** Pedicels of *S. tenax* var. *tenax*, ©Scott Ward. **D.** Stem and abaxial leaf vestiture of *S. tenax* var. *tenax*, ©Eric M. Powell. **E.** Stem and abaxial leaf vestiture of *S. tenax* var. *lacuum*, ©Scott Ward. **F.** Pedicels of *S. tenax* var. *lacuum*, ©Scott Ward. **G.** *S. tenax* var. *lacuum* common growth form, ©Joshua Doby.



FIG. 14. Lectotype of *Bumelia lacuum* Small (Small and DeWinkeler 9965), described from "Ancient sand dunes north of Kuhlman [Sebring, FL]."



FIG. 15. Holotype of *Sideroxylon tenax* (Corogin 2015; LINN 261.5). The label (not shown) provides a short botanical description of the species and the locality which is applied broadly to "siccioribus Carolinae" (drier Carolinas).

So. Ca.” in handwriting that appears to be of the time, or at least not obviously added later. Cranmore Wallace was also known to have lived in the area at the time (Strong & McClintock 1880).

While its apparent occurrence in South Carolina is somewhat biogeographically improbable, we think that suitable habitat exists or may have once existed for the species in the area. *Marshallia trinervia* inhabits moist rocky streambanks and calcareous clays (Weakley & Southeastern Flora Team 2025). The area around St. Johns in Berkeley County is known to harbor calciphilic plants, including the state’s largest populations of *Carya myristiciformis* (F. Michx.) Elliott, and the only South Carolina record of *Zanthoxylum americanum* Mill. *Coreopsis integrifolia* Poir., another rare species associated with limestone and calcareous clays, has been collected numerous times in the area. Prior to the damming of the Cooper River and subsequent flooding of the area with the creation of Lake Moultrie, Ravenel collected many unusual calciphiles from sites along the Old Santee Canal (e.g. *Eriocaulon ravenelii* Chapman), which terminates near St. John’s. We therefore find it plausible that *M. trinervia* was a native component of the South Carolina flora, and apply a NatureServe subnational conservation ranking of SX, or extirpated.

Specimen: U.S.A., **SOUTH CAROLINA. Berkeley Co.** St Johns, Berkeley, So. Ca. *Cranmore Wallace s.n.* (CHARL).

Solidago aestivalis E.P. Bicknell: Not present in South Carolina

This species was previously considered an earlier flowering variety of wrinkle-leaf goldenrod (*Solidago rugosa* P. Miller var. *sphagnophila* C. Graves). It is thought to occur in bogs and coastal wetlands from New England to as far south as South Carolina, where there was a single 1957 specimen from Horry County (J.A. Duke #0022). The taxon’s confusing nomenclatural history was clarified by Uttal and Porter (1988), who also outlined floral and vegetative characters distinguishing *S. aestivalis* and the similar *S. latissimifolia*. We agree with Uttal and Porter (1988) that there is an obvious difference in capitula size and phyllary width but have had less success applying the specific vegetative characters they mention as distinguishing the two taxa (though there are differences in overall gestalt that we consider sufficient for identification). Further exploration of the validity and usefulness of potential vegetative characters is probably warranted, but we consider the gestalt of J.A. Duke #0022 to easily fall within *S. latissimifolia*, a determination which is corroborated by the large heads and width of the phyllaries. See also Sorrie (2018) for discussion of these taxa.

Specimen: U.S.A., **SOUTH CAROLINA. Horry Co.** Edge of swale on US 70, 70 St. North Myrtle Beach. 19 Oct 1957. J.A. Duke 0022 (NCU).

Solidago ulmifolia Muhl. ex Willd.: Not present in South Carolina

Elm-leaved Goldenrod is one of the most frequently misidentified species of *Solidago* on the East Coast. It inhabits dry, rocky, and calcareous woodlands, which are generally rare in both North and South Carolina. An investigation of *S. ulmifolia* herbarium records by the first author in North Carolina found all but one of about 45 specimens to be erroneous. Specimens identified as *S. ulmifolia* showed a wide range of morphology and were, in fact, a mix of at least 7 different taxa, including a heavily duplicated collection of *S. latissimifolia* Mill. from the sandhills region (Bozeman #11610). The situation is similar in South Carolina. An investigation into the 25 or so specimens resulted in zero actual collections of *S. ulmifolia*, and instead several other species, including: *S. brachyphylla* Chapm. ex Torrey & A. Gray, various varieties of *S. rugosa* Mill., plants belonging to the *S. arguta* Aiton complex, and others. Given the lack of correctly identified collections or iNaturalist (2025) observations, we regard it as not ever having occurred in South Carolina.

Symphyotrichum grandiflorum (L.) Nesom: Not present in South Carolina

Surprisingly, an examination of the few specimens of *Symphyotrichum grandiflorum* from South Carolina found none that were correctly identified and were instead a number of other taxa, including *S. cordifolium* (L.) Nesom, *S. georgianum* (Alexander) Nesom, *S. patens* (Aiton) Nesom, and a *Eurybia* sp. (in need of in-person examination). A survey of iNaturalist (2025) observations also yielded only a single planted instance at a user’s home garden that has since been deleted, and a wild observation just miles from the South Carolina border in Anson County, North Carolina. Given how common this species is in North Carolina, often in areas

close to its southern border, we hope additional survey work in north-central South Carolina may yet yield a first record of this species for the state.

CYPERACEAE

Carex lutea LeBlond: New record for Horry Co., South Carolina

Carex lutea LeBlond is a globally imperiled (G2) and federally endangered species that was, until recently, considered narrowly endemic to calcareous pine savannas and adjacent swamp forests in Pender and Onslow Counties in North Carolina (NatureServe 2025). In 2021, it was discovered in Liberty County, Florida by Lilly Anderson-Messec and Nicole Zampieri, and shortly after in Charleston County, South Carolina by Bob Dellinger (Poindexter et al. 2024).

In April of 2025, while conducting botanical inventory in Horry County on a tract of the Waccamaw River Heritage Preserve, yet another new population of *C. lutea* was found along the shoulders and ditches of an access road/easement into the tract (Fig. 16). The population appeared to extend into the adjacent swamp forests to some degree, though these areas were on private lands and therefore were not surveyed. This new population occurs about halfway between the previously known Pender and Onslow County populations in North Carolina and the newly discovered Charleston County, South Carolina population.

In the absence of more extensive surveys of the surrounding area, we consider it at least somewhat plausible that this population was introduced, perhaps via crushed paving limestone sourced from quarries in Pender and Onslow Counties of North Carolina. However, old ridge and swale systems in the floodplain of the Waccamaw River, which this road crosses, are home to a number of rare species, some of which are disjunct from portions of their ranges, and include *Muhlenbergia torreyana* (Schult.) Hitchc., *Coreopsis rosea* Nutt., and *Lophiola aurea* Ker Gawl. The *C. lutea* population observed here was also occurring with one of the species commonly associated with it in North Carolina: *Scirpus lineatus* Michx., which is a tracked rare species in that state but becomes more common in South Carolina.

No voucher collection was made due to its status as federally endangered and because it was occurring on privately held lands for which we lacked collection permits. The distinctiveness of this species negates the necessity of a physical specimen for identification. The presence of a second population in South Carolina does not appreciably affect the NatureServe subnational conservation rank of S1.

DROSERACEAE

Drosera filiformis Raf. var. **filiformis**: Clarification of historic range, which includes Orangeburg Co., South Carolina

Threadleaf Sundew is here recognized as having historically occurred in South Carolina, clarifying previous conflicting reports. Sorrie (1998) studied the distribution of both *D. filiformis* and *D. tracyi* (Diels) Macfarl. and found no credible reports for South Carolina. In recent years, efforts of herbaria to digitize collections have greatly improved the availability of specimens, and a 1907 NYBG specimen from Orangeburg County has been made available online. The specimen is filed under *D. tracyi*, and the original determination of *D. filiformis* has been crossed out in pencil. It is unknown who annotated it to *D. tracyi*. Regardless, Bruce Sorrie examined this specimen online and determined it to be *D. filiformis* var. *filiformis* on the basis of the color of the glandular hairs (personal communication, Bruce Sorrie 2025). We have determined a NatureServe subnational conservation rank of SX (extirpated).

Specimen: U.S.A., SOUTH CAROLINA. Orangeburg Co.: Swamp, Orangeburg, 8 May 1907, H.D. House 3336 (NY).

FABACEAE

Lupinus texensis Hook.: New state record, naturalizing in Georgetown Co., South Carolina

Lupinus texensis is an annual species native to Texas and adjacent states that is widely available in the horticultural trade. It is becoming established in disturbed or urban areas at several locations around Georgetown, South Carolina, and has been reliably observed in the spring for the past three years.

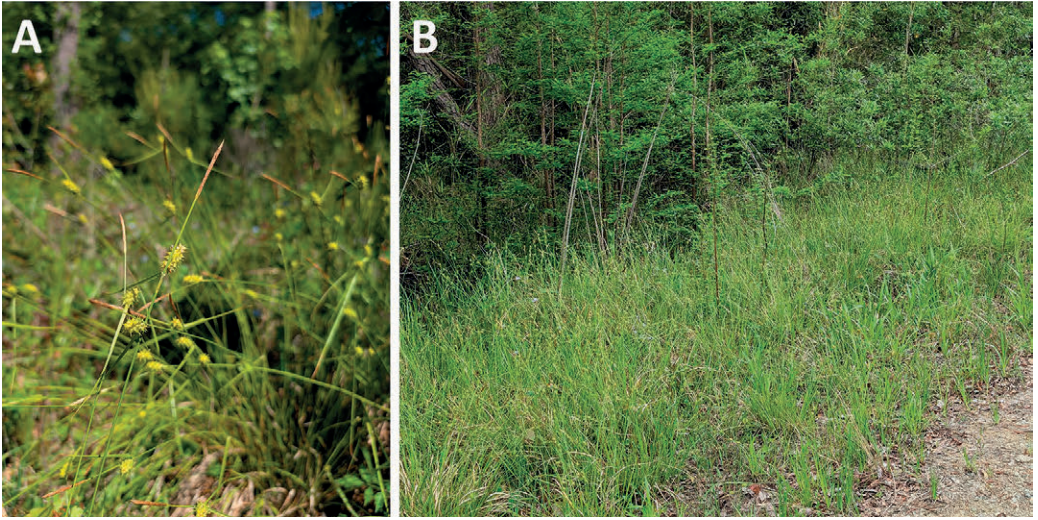


FIG. 16. *Carex lutea* occurrence in Horry Co., South Carolina. A. Detail and growth habit. B. Roadside habitat, extending into adjacent swamp forest.

Specimen: U.S.A., South Carolina, Georgetown Co.: growing out of sidewalk cracks and into adjacent disturbed sandy soils, along W side North Fraser Street in Georgetown, South Carolina, just n of its intersection with County Road S-22-174; escaped from nearby plantings in residential neighborhood and has become established, 33.40127, -79.28921; elev 20', 8 Apr 2024, Eric Ungberg 1139 (USCH).

ONAGRACEAE

Ludwigia ravenii C.I. Peng: New record for Hampton Co., South Carolina

Raven's Seedbox is globally critically imperiled (G1G2) and a candidate for federal listing under the Endangered Species Act (NatureServe 2025). It is known from Virginia, North Carolina, South Carolina, and Florida, and has a subnational conservation rank of S1 in all but the latter, where it is SH. During botanical inventory at Coosawhatchie Wildlife Management Area and Heritage Preserve, several new sub-populations were discovered in seepage slopes and low areas under a large powerline right-of-way. This is the first record from Hampton County and as far as we are aware, the southern-most extant population.

Specimen: U.S.A., SOUTH CAROLINA. Hampton Co.: occurring in and on margins of nice herbaceous seepage slope, under NE-SW oriented powerline right-of-way; also observed at several less well-developed seepages and low spots to the northeast, 32.66633, -80.93200; elev 70', 24 Aug 2023, Eric Ungberg 1214 (USCH).

PLANTAGINACEAE

Leucospora multifida (Michx.) Nutt.: New state record, from Berkeley Co., South Carolina

A population of *Leucospora multifida* was found growing in gravel on the edge of a road through Bonneau Ferry Wildlife Management Area (Berkeley County). While undoubtedly introduced, presumably via paving materials or grading equipment, it is apparently the first record of this species occurring in South Carolina (Freeman 2019; Radford, Ahles, & Bell 1968).

Specimen: U.S.A. SOUTH CAROLINA. Berkeley Co.: growing out of crushed rock at edge of Bonneau Ferry Drive, just s of the main entrance gate, 33.11625, -79.87423; elev 40', 4 Aug 2023, Eric Ungberg 1135 (USCH).

POACEAE

Dichanthelium inflatum (Scribn. & J.G. Sm.) J.R. Thomas: Newly documented in South Carolina, from Berkeley, Colleton, and Hampton Cos

Thomas recently gave this taxon a new combination, at the species level, in the genus *Dichanthelium*, previously having been recognized at the infraspecific level as both a variety and subspecies (depending on the author) of *Panicum sphaerocarpon* Elliott. It differs from that species (now *Dichanthelium sphaerocarpon*) in having narrower leaves with fewer marginal cilia, smaller spikelets, and a distinctly ciliate ligule up to 1.0 mm long. Unlike the widely ranging *D. sphaerocarpon*, *D. inflatum* has thus far only been found in the coastal plain of the Southeastern United States from Maryland to Arkansas (Thomas 2017). During botanical inventory in the spring and early summer of 2024 *D. inflatum* was collected at two sites: first in Colleton County, at Crosby Oxypolis Heritage Preserve on 23 May and again in Hampton County, at Coosawhatchie Wildlife Management Area and Heritage Preserve on 20 June. In the course of examining specimens for this report, a third specimen, from Berkeley County, was found (Nelson 44769). Given the rather disturbed habitats it was collected from, we doubt that this species is particularly rare and tentatively apply a subnational conservation rank of S3.

Specimens: **U.S.A. SOUTH CAROLINA. Berkeley Co.:** patches on damp ground with *Rhexia alifanus* on flatwoods/savanna remnant on n side of Dinah House Road on W side of Upper Reserve Pond, 0.6 mi NW of Bossis Road, 2.6 mi airmi SE of Cordesville Post Office, 33.10261, -79.85989, 16 Jun 2023. **Nelson #44769. Colleton Co.:** in peaty soil on margin of ditch at edge of extensive depression wetland intersected by State Route 63, S side of road, 32.88836, -80.80776; elev. 80', 23 May 2024, *Eric Ungberg #1190*. **Hampton Co.:** in low wet spot with remnant savanna vegetation at intersection of unnamed access road/firebreak and large NE/SW oriented powerline right-of-way, right before it bends to E-NE, 32.67060, -80.92733; elev. 70', 20 Jun 2024, *Eric Ungberg 1234* (USCH).

Sporobolus teretifolius R.M. Harper: New record for Lexington Co., South Carolina

Wireleaf dropseed is a globally imperiled (G2) rare species and candidate for federal listing under the Endangered Species Act (NatureServe 2025). We report here the first occurrence of this species in the Sandhills ecoregion, in Lexington County, South Carolina, well outside of its previously known range (Weakley & Peterson 1998). In the course of botanical inventory carried out at Congaree Creek Heritage Preserve in July 2025, the first author encountered a large clump of what he thought at the time was wiregrass, in the so-called “wiregrass gap” in South Carolina that separates the ranges of *Aristida stricta* Michx. to the north and *A. beyrichiana* Trin. & Rupr. to the south. However, examination of a small portion of the collected clump revealed it to be *S. teretifolius*. All leaf blades were entirely 3-dimensional in cross-section and lacked any portions that were merely flattened. The leaf margins were glabrous and showed the distinctive tuft of hairs at the apex of the sheath that distinguishes this species from similar perennial clumping grasses. Compared with other specimens of *S. teretifolius* housed at NCU, it was indistinguishable, and we are confident in the identification despite the lack of reproductive parts.

The plants were found about half-way down a gentle seepage slope under a powerline right-of-way, with a small blackwater stream at the base, where several species rare in South Carolina also occur. This instance of *Sporobolus teretifolius* was growing immediately adjacent to a large clump of *S. pinetorum* Weakley & P.M. Peterson, which showed the typical morphology of that species (Weakley & Peterson 1998). The two species are known to co-occur, especially at certain pine savannas in southeastern North Carolina; this is the first time they have been recorded together outside of that context.

Specimen: **U.S.A. SOUTH CAROLINA. Lexington Co.:** on middle slope of open herbaceous seepage slope under EW oriented powerline right-of-way just S of Shady Lane, with several other rare species, including *S. pinetorum*; first record of this species occurring in the sandhills region. 33.95000, -81.06311; elev 150', 16 Jul 2025, *Eric Ungberg 1233* (USCH).

POLYGONACEAE

Rumex paraguayensis D. Parodi: New state record from Georgetown Co., South Carolina

This species was found along the edge of a waterfowl impoundment at Yawkey Wildlife Center and Heritage Preserve in Georgetown County, South Carolina. Discernment of *R. paraguayensis* D. Parodi from the very similar *R. obovatus* Danser is challenging. The specimen exhibited tepals that were universally <4.0 mm and tepal tubercles that were minutely honeycombed, which we think better fits a description of “punctate” than “verrucose.” As far as we can discern, this seems to be the first record for South Carolina and northern-most record for the United States (Mosyakin 2005; Radford, Ahles, & Bell 1968; Weakley & Southeastern Flora Team 2025).

Specimen: **U.S.A. SOUTH CAROLINA. Georgetown Co.:** on disturbed edges of berm on N edge of a large waterfowl impoundment near the SE corner of Tom Yawkey Wildlife Center, 33.20385, -79.25784; elev 2', 1 May 2025, *Eric Ungberg 1235 with Keith Bradley* (USCH).

TOFIELDIACEAE

Triantha racemosa (Walter) Small: First occurrence in the mountains of the Carolinas

The “ice pond” relict flora community below Table Rock Mountain in Pickens County, South Carolina, is a unique site comprised of a narrow terrace of more or less level terrain (elevation: 2600') with two shallow ponds and sandy soils situated at the base of a tall north facing cliff. The site is home to a number of rare and disjunct species, as outlined by Hill (1999), including *Carex barrattii* Schwein. & Torr., *C. buxbaumii* Wahlenb., *Sanguisorba canadensis* L., and *Trichophorum cespitosum* (L.) Hartm. Unfortunately, Hill was only afforded two sampling days, once in June of 1992 and another in May of 1993, and therefore was likely unable to observe species with later phenology. One such species, observed by Heritage Trust staff in December of 2023, was *Triantha racemosa* (Walter) Small. This species typically occurs in the coastal plain, but does have disjunct inland occurrences in Alabama, Georgia, Tennessee, and Virginia (Weakley & Southeastern Flora Team 2025). This is the first time *T. racemosa* has been documented in the mountains of the Carolinas and is over 100 miles from the nearest extant location. The small fruits relative to the tepal size and seed characteristics easily differentiated this species from the more biogeographically plausible *T. glutinosa* (Michx.) Baker.

Specimen: **U.S.A. SOUTH CAROLINA. Pickens Co.:** on margins of “ice ponds” at base of N-facing cliff below summit of Table Rock Mountain, first record of this species from the mountains of the Carolinas, 35.05382, -82.70095; elev 2600', 13 Dec 2023, *Eric Ungberg 1224 with Samantha Tessel and Gemma Milly* (USCH).

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REFERENCES

- AHLES, H.E. 1968. Dioscoreaceae. In: A.E. Radford, H.E. Ahles, & C.R. Bell. Manual of the vascular flora of the Carolinas. UNC Press, Chapel Hill, U.S.A. Pp. 317–318.
- AL-SHEHBAZ, I.A. & B.G. SCHUBERT. 1989. The Dioscoreaceae in the southeastern United States. *J. Arnold Arbor.* 70:57–95.
- BINNS, S.E., B.R. BAUM, & J.T. ARNASON. 2002. A taxonomic revision of *Echinacea* (Asteraceae: Heliantheae). *Syst. Bot.* 27:610–632.
- BLOMQUIST, H.L. 1957. A revision of *Hexastylis* of North America. *Brittonia* 8:255–281.
- BRAUN, E.L. 1967. The Monocotyledoneae. Cat-tails to orchids. Ohio State Univ. Press, Columbus, U.S.A.
- BRIDGES, E.L. & S.L. ORZELL. 2024. Systematics of the unifoliolate Floridian *Lupinus* clade (Leguminosae: Papilionoideae). *Phytoneuron* 2024-4:1–61.

- CHESTER, E.W., B.E. WOFFORD, R. KRAL, H.R. DE SELM, & A.M. EVANS. 1993. Atlas of Tennessee Vascular Plants. Vol. 1, Pteridophytes, Gymnosperms, Monocots. Center for Field Biology, Austin Peay State Univ., Clarksville, U.S.A.
- CONSTANCE, L. 1949. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). Contr. Gray Herb. 168:1–48.
- COROGIN, P.T. 2015. *Sideroxylon* Section *Frigoricola* (Sapotaceae): a clade endemic to temperate North America. Ph.D. dissertation, Univ. of Florida, Gainesville, U.S.A.
- DEAM, C.C. 1940. Flora of Indiana. Burford Printing Co., Indianapolis, U.S.A.
- DELANEY, K.R., R.P. WUNDERLIN, & J.C. SEMPLE. 2003. *Chrysopsis delaneyi* (Asteraceae, Astereae), another new species from peninsular Florida. Bot. Explorer 3:1–40.
- FERNALD, M.L. 1950. Gray's manual of botany. Eighth Edition. American Book Co., Boston, U.S.A.
- FLORA OF NORTH AMERICA EDITORIAL COMMITTEE, eds. 1993+. Flora of North America North of Mexico [Online]. 25+ vols. New York and Oxford. <http://beta.floranorthamerica.org>. Accessed 01 September 2025.
- FOSTER, S. 1991. *Echinacea*: nature's immune enhancer. Healing Arts Press, Rochester, U.S.A. 150 pp.
- FREEMAN, C.C. 2019. *Leucospora*. In: Flora of North America Editorial Committee. 2019. Flora of North America north of Mexico. Volume 17, Magnoliophyta: Tetrachondraceae to Orobanchaceae. Oxford Univ. Press, New York, U.S.A. 737 pp.
- GADDY, L.L. 1987. A review of the taxonomy and biogeography of *Hexastylis* (Aristolochiaceae). Castanea 52:186–196.
- GENTRY, J.L., G.P. JOHNSON, B.T. BAKER, C.T. WITSELL, & J.D. OGLE. 2013. Atlas of the vascular plants of Arkansas. Univ. Arkansas, Fayetteville, U.S.A.
- GLEASON, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden, New York, U.S.A.
- GLENNON, K.L. & S.A. CHURCH. 2015. Gene flow contributes to genetic diversity of tetraploid populations of the North American plant genus *Houstonia* (Rubiaceae). Rhodora 117:41–66.
- HAINES, A.A. 2025. The variety of northern *Houstonia longifolia* (Rubiaceae). Bot. Notes 19:3–5.
- HILL, S.R. 1999. The relict flora of ice ponds in South Carolina. Castanea 64:14–22.
- HUCK, R.B. 2001. Two new infraspecific taxa in Florida *Dicerandra* (Labiateae). Novon 11:417–420.
- iNATURALIST. 2025. Available from <https://www.inaturalist.org>. Accessed 01 September 2025.
- KARTESZ, J.T. 2015. The Biota of North America Program (BONAP). Biota of North America, Chapel Hill, U.S.A. www.bonap.net.
- KEES, J.C., A.S. WEAKLEY, & D.B. POINDEXTER. 2024. Towards a revision of the *Eryngium integrifolium* complex (Apiaceae). Phytoneuron 2024-70:1–25.
- KELLER, H.W. 2014. The genus *Echinacea* (Asteraceae): floral, stem, and petiole morphology. J. Bot. Res. Inst. Texas 8:87–126.
- LAKELA, O. 1963. The identity of *Bumelia lacuum* Small. Rhodora 65:280–282.
- MACROBERTS, D.T. 1984. The vascular plants of Louisiana. Bull. Mus. Life Sci. Louisiana State Univ., Shreveport 6:1–165.
- MCCLELLAND, R.K.S., A.S. WEAKLEY, & D.B. POINDEXTER. 2023. Seven new species of *Trichostema* (Lamiaceae: Ajugoideae) from the North American Coastal Plain biodiversity hotspot. Phytotaxa 603:95–149. doi:10.11646/phytotaxa.603.2.1
- MCGREGOR, R.L. 1967. A new species and two new varieties of *Echinacea* (Compositae). Trans. Kansas Acad. Sci. 70:366–370.
- MCGREGOR, R.L. 1968. The taxonomy of the genus *Echinacea* (Compositae). Univ. Kansas Sci. Bull. 48:113–142.
- MCKEOWN, K. 1999. A review of the taxonomy of the genus *Echinacea*. In: J. Janick (ed.). Perspectives on new crops and new uses. ASHS Press, Alexandria, VA. <https://api.semanticscholar.org/CorpusID:2095281>. Accessed 21 March 2026.
- MOHLENBROCK, R.H. & D.M. LADD. 1978. Distribution of Illinois Vascular Plants. Southern Illinois Univ. Press, Carbondale, U.S.A.
- MOSYAKIN, S.L. 2005. *Rumex*. In: Flora of North America Editorial Committee. 2005. Flora of North America north of Mexico. Volume 5, Magnoliophyta: Caryophyllidae, part 2. Oxford Univ. Press, New York, U.S.A. 656 pp.
- NATURESERVE. 2025. NatureServe Network Biodiversity Location Data accessed through NatureServe Explorer. NatureServe, Arlington, Virginia. Available <https://explorer.natureserve.org/>. Accessed 12 September 2025.
- PADGETT, J.E. 2004. Biogeographical, ecological, morphological, and micromorphological analyses of the species in the *Hexastylis heterophylla* complex. Master's Thesis, Appalachian State Univ., Boone, North Carolina, U.S.A. 125 pp.
- POINDEXTER, D.B., L. ANDERSON-MESSEK, J.B. FULLER, B. DELLINGER, E.A. UNGBERG, & A.S. WEAKLEY. 2024. Discovery of disjunct populations of the federally threatened Golden Sedge (*Carex lutea*, Sect. *Ceratocystis*) and first reported chromosome counts of the species, aided by social media and iNaturalist. In: Weakley et al. 2024. Studies in the vascular flora of the southeastern United States. X. J. Bot. Res. Inst. Texas 18:17–77.

- RADER, E.K. & N.H. EVANS. 1993. Geologic map of Virginia; expanded explanation: Virginia Division of Mineral Resources, U.S.A. 80 pp.
- RADFORD, A.E., H.E. AHLES, & C.R. BELL. 1968. Manual of the vascular flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, U.S.A.
- RAZ, L. 2002. Dioscoreaceae. In Flora of North America, vol. 26, Magnoliophyta: Liliidae: Liliales and Orchidales. Oxford Univ. Press, New York, U.S.A.
- SEMPLE, J.C. 1978. Application of the name *Chrysopsis hyssopifolia* Nutt. (Compositae) and a new name for an "old" species. *Brittonia* 30:492–495.
- SEMPLE, J.C. 1981. A revision of the goldenaster genus *Chrysopsis* (Nutt.) Ell. nom. cons. (Compositae–Asteraceae). *Rhodora* 83:323–384.
- SEMPLE, J.C. 2006. *Chrysopsis*. In: Flora of North America Editorial Committee. 2006b. Flora of North America north of Mexico. Volume 20, Magnoliophyta: Asteridae, part 6: Asteraceae, part 2. Oxford Univ. Press, New York, U.S.A. 666 pp.
- SEMPLE, J.C. 2025. *Chrysopsis*. Asteraceae lab website. <https://uwaterloo.ca/asteraceae-lab/goldenasters/chrysopsis>. Accessed 07 September 2025.
- SEMPLE, J.C. & J.B. BECK. 2021. Revised infrageneric classification of *Solidago* (Asteraceae: Asteraceae). *Phytoneuron* 2021-10:1–6. Published 26 Feb 2021.
- SEMPLE, J.C. & J.B. BECK. 2023. A revised intuitive phylogeny of *Solidago* (Asteraceae: Asteraceae) based on a polygenomic phylogeny of diploids. *Phytoneuron* 2023-41:1–5. Published 31 October 2023.
- SEMPLE, J.C., H. McMINN-SAUDER, M. STOVER, A.R. LEMMON, E. MORIARTY LEMMON, & J.B. BECK. 2023. Goldenrod herbariomics: Hybrid-sequence capture reveals the phylogeny of *Solidago*. *Amer. J. Bot.* doi: 10.1002/ajb2.16164
- SEMPLE, J.C. & N. STEENHOF. 2025. A multivariate morphometric study of the *Chrysopsis scabrella* complex (Asteraceae: Asteraceae). *Phytoneuron* 2025-05:1–13. Published 30 April 2025.
- SERNEC DATA PORTAL. 2025. <http://sernecportal.org/index.php>. Accessed on 01 September 2025.
- SINN, B.T. 2015. *Asarum chueyi* (Aristolochiaceae), a new species from the foothills of the Blue Ridge Mountains of Tennessee and Virginia, U.S.A. *Phytotaxa* 224:85–95.
- SKIBICKI, S.V. 2025. Phylogenomics and biogeography of Zinniinae (Asteraceae: Heliantheae) using plastome and nuclear datasets. Ph.D. dissertation, West Virginia Univ., Morgantown, U.S.A. Graduate Theses, Dissertations, and Problem Reports. <https://researchrepository.wvu.edu/etd/12835>
- SMALL, J.K. 1933. Manual of the southeastern flora. Univ. of North Carolina Press, Chapel Hill, U.S.A.
- SMITH, E.B. 1976. *Hedyotis ouachitana* (Rubiaceae): a new species from the Ouachita Mountains of Arkansas and Oklahoma. *Brittonia* 28:453–459.
- SMITH, E.B. 1978. An atlas and annotated list of the vascular plants of Arkansas. Univ. of Arkansas Herbarium, Fayetteville, U.S.A.
- SORRIE, B.A. 1998. Distribution of *Drosera filiformis* and *D. tracyi* (Droseraceae): Phytogeographic implications. *Rhodora* 100:239–260.
- SORRIE, B.A. 2018. *Solidago aestivalis* in the Carolinas. In: 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.
- SORRIE, B.A. & A.S. WEAKLEY. 2001. Coastal plain vascular plant endemics: phytogeographic patterns. *Castanea* 66:50–82.
- STEYERMARK, J.A. 1963. Flora of Missouri. Iowa State Univ. Press, Ames, U.S.A.
- STRONG, J. & J. MCCLINTOCK. 1880. The cyclopedia of biblical, theological, and ecclesiastical literature. Harper and Brothers, New York, U.S.A.
- TENNESSEE FLORA COMMITTEE. 2015. Guide to the vascular plants of Tennessee. E.W. Chester, B.E. Wofford, J. Shaw, D. Estes, and D.H. Webb, eds. Univ. Tennessee Press, Knoxville, Tennessee, U.S.A.
- TERRELL, E.E. 1959. A revision of the *Houstonia purpurea* group (Rubiaceae). *Rhodora* 61:157–181, 188–207.
- TERRELL, E.E. 1988. Nomenclatural notes on *Houstonia* (Rubiaceae). *Phytologia* 65:119–121.
- TERRELL, E.E. 1996. Revision of *Houstonia* (Rubiaceae–Hedyotidae). *Syst. Bot. Monogr.* 48:1–118.
- THOMAS, J.R. 2017. New additions, vouchers of old additions, and a new combination (*Dichanthelium inflatum*) for the Missouri flora. *Missouriensis* 34:4–19.
- URBATSCH, L.E., K.M. NEUBIG, & P.B. COX. 2006. *Echinacea*. In: Flora of North America Editorial Committee. 2006. Flora of North America north of Mexico. Volume 21, Magnoliophyta: Asteridae, part 6: Asteraceae, part 3. Oxford Univ. Press, New York, U.S.A. 616 pp.

- UTTAL, L.J. & D.M. PORTER. 1988. The correct name for Elliott's goldenrod. *Rhodora* 90:157–168.
- VOSS, E.G. 1972. Michigan flora. Part 1, Gymnosperms and Monocots. Cranbrook Inst. of Sci. and Univ. Michigan Herbarium, Bloomfield Hills, U.S.A.
- VOSS, E.G. & A.A. REZNICEK. 2012. Field manual of Michigan flora. Univ. of Michigan Press, Ann Arbor, U.S.A.
- WARD, D.B. 2007. Thomas Walter Typification Project, II: The known Walter types. *J. Bot. Res. Inst. Texas* 1:407–423.
- WATSON, L.E. 2006. *Marshallia*. In: Flora of North America Editorial Committee. 2006. Flora of North America north of Mexico. Volume 21, Magnoliophyta: Asteridae, part 6: Asteraceae, part 3. Oxford Univ. Press, New York, U.S.A. 616 pp.
- WEAKLEY, A.S. & P.M. PETERSON. 1998. Taxonomy of the *Sporobolus floridanus* complex (Poaceae: Sporobolinae). *Sida* 18:247–270.
- WEAKLEY, A.S., J.C. KEES, B.A. SORRIE, S.G. WARD, D.B. POINDEXTER, M. BROCK, L.D. ESTES, E.L. BRIDGES, S.L. ORZELL, G.A. LEVIN, R.K.S. MCCLELLAND, R.J. SCHMIDT, & S.A. NAMESTNIK. 2023. Studies in the vascular flora of the southeastern United States. IX. *J. Bot. Res. Inst. Texas* 17:191–257.
- WEAKLEY, A.S., R.J. LeBLOND, P.D. McMILLAN, B.A. SORRIE, D.B. POINDEXTER, J.B. FULLER, E.L. BRIDGES, B.J. BUDACH, S.C. CARR, A.A. CROWL, P. MANOS, P.W. FRITSCH, S.L. ORZELL, J.K. WIPFF, L. ANDERSON MESSEC, B. DELLINGER, E.A. UNGBERG, N.D. YAWN, A.M. CRESSLER, T.W. BARGER, J. R. CARTER, A.J. FLODEN, W.M. KNAPP, I. COPEN, A.M. JENKINS, E.L. HUGHES, J. ANNIS, W. BAKER, & R.L. MEARS. 2024. Studies in the vascular flora of the southeastern United States. X. *J. Bot. Res. Inst. Texas* 18:17–77.
- WEAKLEY, A.S. & SOUTHEASTERN FLORA TEAM. 2025. Flora of the southeastern United States Web App. Univ. of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, U.S.A. fsus.ncbg.unc.edu. Accessed 12 September 2025.
- WERIER, D. 2017. Catalogue of the vascular plants of New York state. *Mem. Torrey Bot. Soc.* 27.
- YATSKIEVYCH, G. 1999. Steyermark's flora of Missouri. Volume 1. Missouri Bot. Garden Press, St. Louis, U.S.A.
- ZHANG, N., D.L. ERICKSON, P. RAMACHANDRAN, A.R. OTTESEN, R.E. TIMME, V.A. FUNK, Y. LUO, & S.M. HANDY. 2017. An analysis of *Echinacea* chloroplast genomes: implications for future botanical identification. *Scientific Reports* 7:216.